THE IMPACT OF THE
INTERNATIONAL LIVESTOCK
RESEARCH INSTITUTE

EDITED BY JOHN MCINTIRE AND DELIA GRACE

ILRI
INTERNATIONAL
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INSTITUTE

CGIAR

CABI

The Impact of the International Livestock Research Institute

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Edited by:

John McIntire

and

Delia Grace

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Foreword

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It gives me pleasure to provide the foreword to this important scientific record of 45 years of livestock and livestock-related science conducted by the International Livestock Research Institute (ILRI, 1995–2019) and its two predecessors, the International Laboratory for Research on Animal Diseases, based in Kenya (ILRAD, 1973–1994), and the International Livestock Centre for Africa, based in Ethiopia (ILCA, 1974–1994), as well as selected key partners of these three institutions. ILRI—and ILRAD and ILCA before it—is a member of CGIAR, a global research-for-development partnership of 15 centres working with hundreds of partners around the world for a food-secure future.

Co-hosted by Kenya and Ethiopia and working through a network of offices and projects across Asia and Africa, ILRI's multidisciplinary staff and programs develop and deliver science-based solutions, provide evidence for decision-making, and develop capacities of livestock-sector stakeholders for more equitable, broad-based and sustainable livestock development.

ILRI's research for development agenda covers laboratory-based biosciences to field-based research to policy support. The main topics include animal productivity (health, genetics and feeds), food safety and zoonoses, livestock systems and the environment, gender and livelihoods, and policy and markets. The institute's core scientific competencies span the breadth of livestock science, from biosciences to social sciences, agricultural economics to human nutrition, disease epidemiology to environmental sciences. With such diverse disciplinary work conducted under one roof, ILRI works to integrate and share this knowledge and expertise in systems-level solutions that improve global food, nutritional, economic and environmental security. Gender, research methods, communications, knowledge management and business and capacity development are central to ILRI's mandate and cut across all of its research and development areas.

The rich diversity and complexity of livestock livelihoods in Africa and Asia are exceptional. A glance at the chapter titles and contents of this volume will attest to the diversity of research approaches employed over the years to better exploit and sustain that richness for the larger purpose of closing great disparities in global economic and nutritional well-being and human and environmental health. Some big ideas are presented here, along with some approaches that were tested and then let go; there are both success and failure stories, as is only proper in such a record. And there are breakthroughs and scientific and development impacts to laud, including developing-world solutions for developing-world problems.

This volume can serve as a reference and resource for all interested in the role of livestock in agricultural transformation and sustainable development. It should be useful for distilling, learning from, and building on past work and lessons. We hope it will inform and inspire students, researchers and research managers and their investors.

Professor Peter C. Doherty AC, FAA, FRS
Animal scientist
Nobel Prize Laureate for Physiology or Medicine - 1996

Preface

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A note from ILRI Director General Jimmy Smith

No endeavour can be more important than feeding our world without jeopardizing our future. Repeated, catastrophic hungers have punctuated human history and inadequate nutrition, which still afflicts two billion people, remains a too often invisible health catastrophe. Half a century ago, CGIAR's research into high-yielding, disease-resistant cereals launched the Green Revolution, saving more than a billion people from starvation. CGIAR, a global network of 15 research centres, was created to perpetuate more socially equitable, and economically and environmentally sustainable, agricultural revolutions. One of these centres, the International Livestock Research Institute (ILRI), is dedicated to research on livestock in developing countries. Here, as in the following pages, mention of ILRI typically encompasses the work of ILRI's two predecessors, the International Laboratory for Research on Animal Diseases [ILRAD] and the International Livestock Centre for Africa [ILCA].

As the spectre of global famine began to recede in the middle of the last century, new challenges, as well as new opportunities, emerged, many of which ILRI's livestock research was uniquely positioned to address. The challenges included increasing disease epidemics, including zoonotic pandemics such as coronavirus disease 2019 (COVID-19); rising demand for meat, milk and eggs, particularly in developing countries; a rise in 'hidden hunger' due to micronutrient deficiencies; climate change, poor animal welfare, and widespread ill health caused by unsafe foods.

This book describes the evolving and multi-faceted roles of ILRI in addressing these and other global challenges in nearly a half century of research. ILRI researchers and partners took leading roles, for example, in the following.

LIVESTOCK REVOLUTION: As more and more people in the global south are moving out of poverty and into cities, their demand for livestock products is rising dramatically (especially for the fast-reproducing, easy to intensify pig and poultry systems). Finding ways to meet this rising demand without threatening human, animal and environment health is critically important. Doing so requires a deep understanding of the socioeconomics of livestock economies, of the diverse livestock value chains that are the mainstay of smallholder agriculture and an ability to influence livestock policy and practice. Sustainable livestock intensification also requires better livestock breeding, feeding and management.

LIVESTOCK DISEASE: Tackling neglected livestock diseases of greatest importance to the world's poor was a major driver for the foundation of ILRI and remains a major constraint and in a globalized

world, where diseases can spread fast and severely damage economies. Pastoralist systems are especially vulnerable, due to high contact with animals and often poor access to services. Moreover, most new human diseases originate in animals, livestock as well as wildlife, so controlling these diseases in animal populations, before they spread to human populations, is essential.

HIDDEN HUNGER: The success of the Green Revolution helped to shift attention from a world shortage of calories to a shortage of essential micronutrients, which are abundant in milk, meat and eggs. This fact is putting these nourishing livestock-derived foods centre stage on the world's development agenda. At the same time, obesity and its attendant health issues are growing problems, even in countries were nutrition is insecure. These health problems have been associated with increased consumption of highly processed or unhealthily cooked livestock products.

CLIMATE CHANGE: With the threat of climate change looming and the role of livestock production as an emitter of greenhouses gases taking the limelight, transforming livestock systems into sustainable as well as inclusive systems has become a critical goal of the world's environmental agenda. At the same time, livestock systems must adapt to changing climates.

FOOD SAFETY AND ANIMAL WELFARE: And as more and more people in developing countries are consuming livestock-derived foods that are among the foods most likely to become contaminated and cause human illness, and as more and more people in developed countries are concerned by poor animal welfare, populations are becoming increasingly concerned about the safety and provenance of the food they eat.

Over the years, ILRI expanded its remit from better controlling a few deadly tropical animal diseases and better understanding livestock production systems in Africa to a broad portfolio of research for livestock development globally with a focus on Africa and Asia where poverty rates were highest. This broader agenda covered—in addition to livestock health, feed, genetics, trade, marketing and consumption—the gender aspects of livestock systems, the impacts of livestock on the natural resource base and planetary boundaries and the roles of livestock in societies.

This work produced many outputs. This book documents and quantifies some of these in terms of technologies and innovations discovered and disseminated, papers written and cited, students taught and graduated, policies influenced and written, and global endeavours—such as building sustainable livestock systems and empowering women in livestock agriculture—supported and advanced.

More difficult to document, but ultimately more important, are ILRI's direct contributions to improving lives and livelihoods of the one billion poor people that remain dependent on livestock and the more than six billion poor people (living on less than $10 a day) that use livestock or consume or sell livestock products. Research, of course, is only one part in the complex 'innovation systems' that lead to human betterment. This book documents many actual and potential development impacts and many more opportunities for impact as innovation moves from the library and laboratory to the farm and kitchen.

This unique book documents 45 years of impacts of livestock research in regions of the developing world, particularly in Africa and Asia. The voices of the authors of these chapters are culturally and scientifically diverse. That was purposeful. The authors of this book are acutely aware that their voices are only representative of the larger work in which they are engaged. Unavoidably, many livestock scientists and important pieces of livestock research are missing or presented only briefly in these pages. It is, of course, the larger canvas of livestock work that matters most in delivering on the global sustainable development agenda.

It is our hope that this record—with its many examples of the wealth of scientific and public goods emanating from long-term intellectual and financial livestock research investments and partnerships—helps others to build on this legacy to create more sustainable as well as equitable livestock systems in future years.

A note from ILRI Board of Trustees Chair Lindsay Falvey

As chair of the ILRI Board of Trustees, I am delighted to welcome this important publication, documenting the many benefits of the research-for-development work conducted by ILRI and its many partners. This volume captures much of the history of innovation in livestock research in and for low- and middle-income countries, especially in Africa, which could otherwise be lost. By analysing the challenges and failures as well as successes of this mission-oriented livestock research, this book provides an honest and objective guide to managing, planning and implementing agricultural research for development. While its focus is retrospective, this publication also sets out a path for ILRI's future work in these uncertain times. I am confident ILRI is well placed to help meet the world's 17 Sustainable Development Goals, based on historic successes and on-going efforts and I thank the editors, authors and editorial and research support staff who have devoted so much time to developing and finalizing this important publication.

Acknowledgements

Elaine Grings, Guido Gryseels, Peter Hazell, Tony Irvin, Martyn Jeggo, Steve Kemp, Romano Kiome, Jeffrey Mariner, Peter Matlon, Roger Morris, Ivan Morrison, Jan Naessens, Jerry Nelson, Vish Nene, Hung Nguyen, An Notenbaert, Clare Oxby, Ekta Patel, Bruce Pengelly, Michael Peters, Mark Powell, Ed Rege, Jonathan Rushton, Rainer Schultze-Kraft, Carlos Seré, Emmy Simmons, Werner Stur, Jim Sumberg, Gbassy Tarawali, Shirley Tarawali, Bill Thorpe, Laurian Unnevehr and Trevor Wilson.

Nomenclature

Trypanosomiasis, also known as trypanosomosis, is the name of several diseases in vertebrates caused by parasitic protozoan trypanosomes of the genus *Trypanosoma.* This disease in humans includes sleeping sickness (human African trypanosomiasis, or HAT). The disease in livestock is called *nagana* (African animal trypanosomiasis, or animal African trypanosomiasis, abbreviated to AAT). Because ILRAD used the terms 'trypanosomiasis' and 'African animal trypanosomiasis', and because 'trypanosomiasis' is the term preferred by the Centers for Disease Control and Prevention, the Food and Agriculture Organization of the United Nations and the World Health Organization, that is the term used in this volume. The research centres formerly known as Bioversity Intl. and Centro Internacional de Agricultura Tropical (CIAT) formed the 'Alliance of Bioversity Intl. and CIAT' on 1 January 2020. We have noted this in the affiliations of current staff of that Alliance in the 'List of Contributors' and at the appropriate places in Chapters 12 and 13. We have not otherwise changed the names of CIAT or of Bioversity Intl. where those names appear throughout the book.

Ethiopian names

We apologize to the many Ethiopian scientists who contributed to this book for the Western expression of their names. It proved impossible to correct this against the general trend of the scientific literature.

Maps
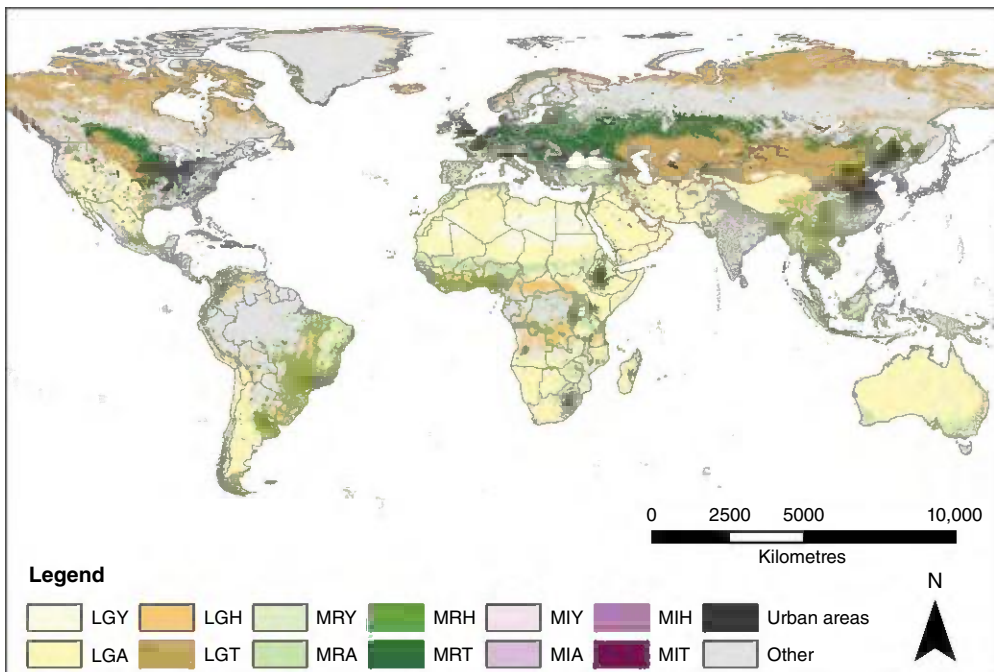
Map 1. Global livestock production systems. LGY, livestock/grazing/hyperarid; LGA, livestock/grazing/arid; LGH, livestock/grazing/humid; LGT, livestock/grazing/temperate and tropical; MRY, mixed/rainfed/hyperarid; MRA, mixed/rainfed/arid and semi-arid; MRH, mixed/rainfed/humid and subhumid; MRT, mixed/rainfed/temperate and tropical; MIY, mixed/irrigated/hyperarid; MIA, mixed/irrigated/arid and semi-arid; MIH, mixed/irrigated/humid and subhumid; MIT, mixed/irrigated/temperate and tropical.
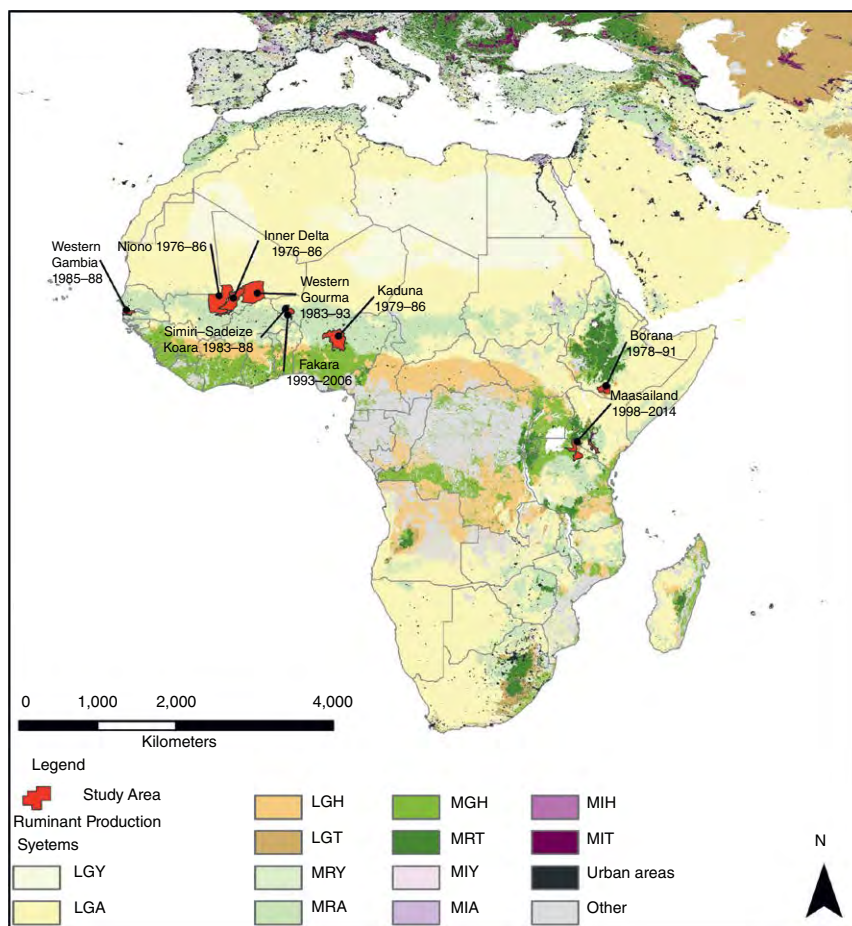
Map 2. African livestock production systems and principal study sites. LGY, livestock/grazing/hyperarid; LGA, livestock/grazing/arid; LGH, livestock/grazing/humid; LGT, livestock/grazing/temperate and tropical; MRY, mixed/rainfed/hyperarid; MRA, mixed/rainfed/arid and semi-arid; MRH, mixed/rainfed/humid and subhumid; MRT, mixed/rainfed/temperate and tropical; MIY, mixed/irrigated/hyperarid; MIA, mixed/irrigated/arid and semi-arid; MIH, mixed/irrigated/humid and subhumid; MIT, mixed/irrigated/temperate and tropical.
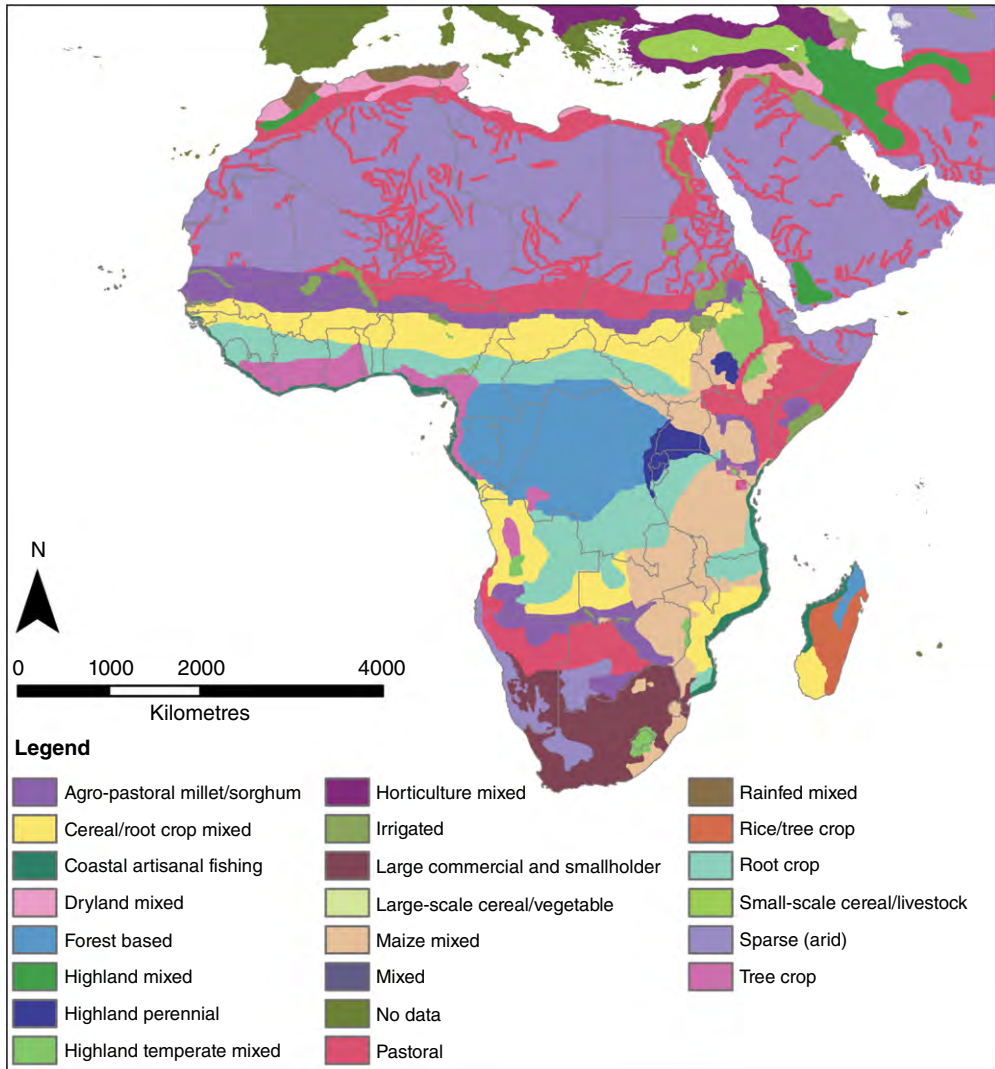
Map 3. African cropping systems, *c.*2010.
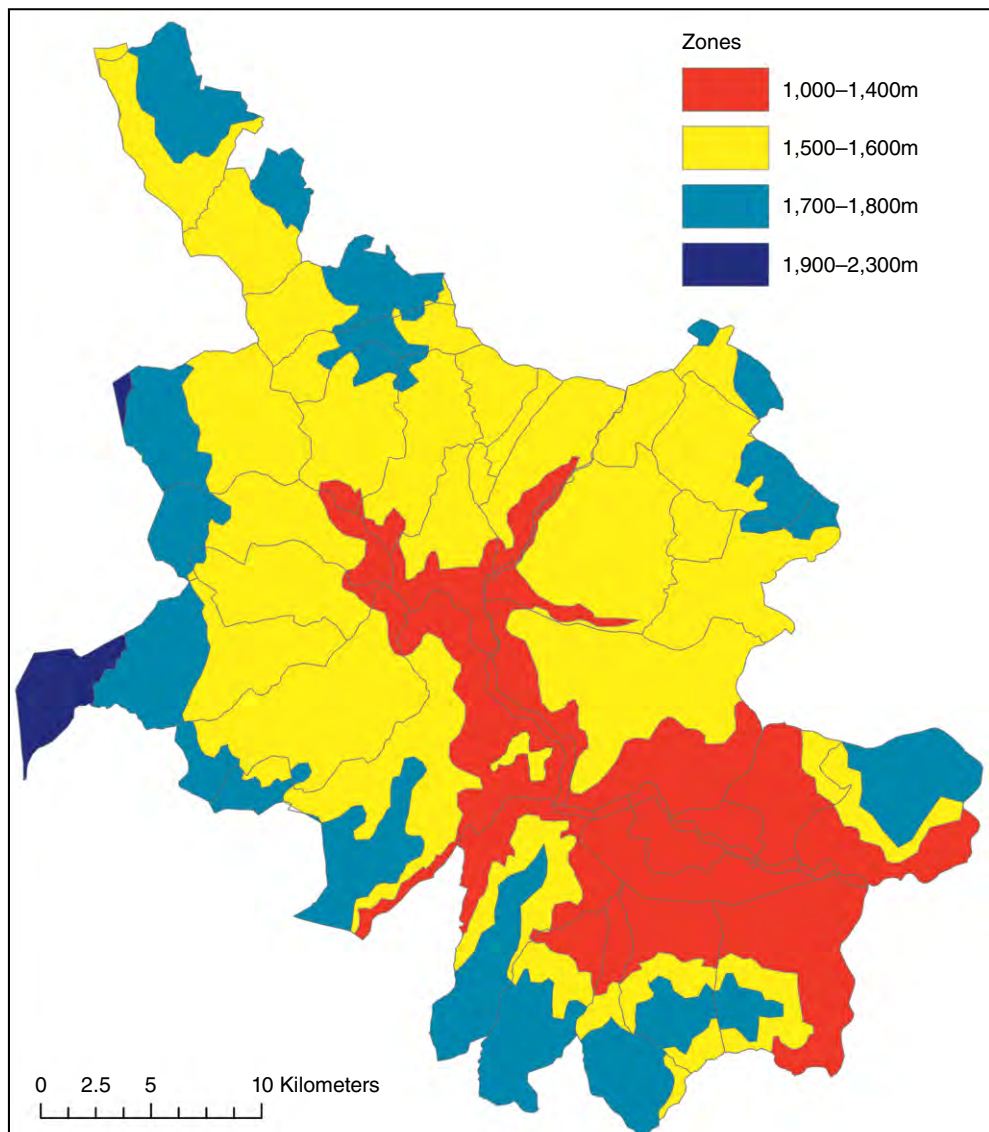
Map 4. The Ghibe study site, 1990–1993. (Data from Rowlands and Teale, 1994).

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A4NH   CGIAR Research Program on Agriculture for Nutrition and Health
AAT   African animal trypanosomiasis (also called animal African trypanosomiasis)
ACGG   African Chicken Genetic Gains project
ACIAR   Australian Centre for International Agricultural Research
ADF   acid detergent fibre
ADGG   African Dairy Genetic Gains project
ADL   acid detergent lignin
AEZ   agroecological zones
AFNETA   Alley Farming Network for Tropical Africa
AFRNET   African Feeds Research Network
Ag-ELISA   antigen enzyme-linked immunosorbent assay
AGTR   Animal Genetics Training Resource, of ILRI
AICRP   All-India Coordinated Research Project on Sorghum
AIDS   acquired immunodeficiency syndrome
ALPAN   African Livestock Policy Analysis Network, of ILCA
AMMA   African Monsoon Multidisciplinary Analysis
AnGR   animal genetic resources
APHISA   Animal and Plant Health Information System for Asia
AR4   Fourth Assessment Report of the Intergovernmental Panel on Climate Change
AR5   Fifth Assessment Report of the Intergovernmental Panel on Climate Change
ARC   Africa Risk Capacity
ASARECA   Association for Strengthening Agricultural Research in Eastern and Central Africa
ASEAN   Association of Southeast Asian Nations
ASF   African swine fever
ASF   animal-source food
ASFV   African swine fever virus
ATLN   African Trypanotolerant Livestock Network, of ILCA and ILRAD
AU-IBAR   African Union–Interafrican Bureau for Animal Resources
BBM   broad-bed maker
BBSRC   Biotechnology and Biological Sciences Research Council, of the UK
BecA   Biosciences eastern and central Africa-International Livestock Research Institute Hub
BiP   binding immunoglobulin protein
BMGF   Bill & Melinda Gates Foundation

BMZ	Bundesministerium für wirtschaftliche Zusammenarbeit und Entwicklung (Federal Ministry for Economic Cooperation and Development, of Germany)
BoLA	bovine lymphocyte antigen
BSE	bovine spongiform encephalopathy
BSL2	Biosafety Level 2
BTA	*Bos taurus* chromosome
BTV	bluetongue virus
CAAM	CIMMYT-Asia Association Panel
CAAS	Chinese Academy of Agricultural Sciences
CAFO	confined (or concentrated) animal feeding operation
CAPES	Brazilian Federal Agency for Support and Evaluation of Graduated Education
CBPP	contagious bovine pleuropneumonia
CCAFS	CGIAR Research Program on Climate Change, Agriculture and Food Security
CCPP	contagious caprine pleuropneumonia
CD	cluster-defined antigen (also called cluster of differentiation)
CDC	Centers for Disease Control and Prevention, USA
cDNA	complementary DNA
CFA franc	Communauté Financière d'Afrique (Financial Community of Africa)
CGE	computable general equilibrium model
CGIAR	Consultative Group on International Agricultural Research (former name of CGIAR, which is no longer spelled out)
CIAT	Centro Internacional de Agricultura Tropical (International Center for Tropical Agriculture), of CGIAR
CIDA	Canadian International Development Agency
CIMMYT	Centro Internacional de Mejoramiento de Maíz y Trigo (International Maize and Wheat Improvement Center), of CGIAR
CIRAD/EMVT	Centre de Cooperation International en Recherche Agronomique pour le Développement/Département d'Élevage et de Médecine Vétérinaire (French Agricultural Research Centre for International Development/Department of Livestock and Veterinary Medicine)
CIRDES	Centre International de Recherche-Développement sur l'Elevage en zone Subhumide (International Center for Research and Development on Livestock Production in the Subhumid Zone)
CISA	Centre for Animal Health Research
CK2	casein kinase 2
COCTU	Coordinating Office for Control of Trypanosomiasis in Uganda
CORPOICA	Corporacion Colombiana de Investigación Agropecuaria (Colombian Corporation for Agricultural Research)
CP	crude protein
CP	cysteine protease
CPH	cowpea haulm
CRD	cross-reacting determinant
CRISPR/Cas	clustered regularly interspaced short palindromic repeats/CRISPR-associated protein 9
CRP	CGIAR Research Programme
CSF	classical swine fever
CSIRO	Commonwealth Scientific and Industrial Research Organisation, of Australia
CSU	Colorado State University
CTL	cytotoxic T-lymphocyte
CTTDB	Centre for Ticks and Tick-Borne Diseases of Malawi
DAGRIS	Domestic Animal Genetic Resources Information Systems, of ILRI

DALY	disability-adjusted life year
DANIDA	Danish International Development Agency
DARI	Dryland Agricultural Research Institute, of Iran
DECUMA	Decisions under Conditions of Uncertainty by Modelled Agents
DEFRA	Department for Environment, Food and Rural Affairs
DFID	Department for International Development, of the UK
DGBC	dark-ground buffy coat
DGEA	Dairy Genetics East Africa project, of ILRI
DIVA	differentiation between infected and vaccinated animals
DM	dry matter
DPRA	Direction Provinciale des Ressources Animales (Provincial Directorate of Animal and Fisheries Resources), Burkina Faso
DSSAT	Decision-Support System for Agro-technology Transfer, of FAO
DTMA	Drought Tolerant Maize for Africa project, of CIMMYT
DTMR	densified total mixed ration
DVS	Department of Veterinary Services, Kenya
EADD	East Africa Dairy Development programme
EARO	Ethiopian Agricultural Research Organization
EATTRO	East African Tsetse and Trypanosomiasis Research and Reclamation Organisation
EAVRO	East African Veterinary Research Organization
ECAPAPA	Eastern and Central Africa Programme for Agricultural Policy Analysis
ECF	East Coast fever
EDRSAIA	Early Detection, Reporting and Surveillance for Avian Influenza in Africa project
EHDV	epizootic haemorrhagic disease virus
EHNRI	Ethiopian Health and Nutrition Research Institute
EIAR	Ethiopian Institute of Agricultural Research
ELISA	enzyme-linked immunosorbent assay
EMBRAPA	Empresa Brasileira de Pesquisa Agropecuária
EPMR	external programme and management review
epoR	erythropoietin receptor
ESAG	expression site associated gene
ESI	Essential Science Indicators database
ESRI	Environmental Systems Research Institute
ETB	Ethiopian birr
EU	European Union
FACS	fluorescence-activated cell sorter
FAO	Food and Agriculture Organization of the United Nations
FAOSTAT	Food and Agriculture Organization Corporate Statistical Database
FAVA	Federation of Asian Veterinary Associations
FBD	food-borne disease
FEAST	Feed Assessment Tool, of ILRI
FERG	Foodborne Disease Burden Epidemiology Reference Group, of WHO
FLI	Friedrich-Loeffler-Institut
FMD	foot-and-mouth disease
FPU	food production unit
FS	full-sibling
FTAI	fixed-time artificial insemination
FU-Berlin	Freie Universität Berlin (Free University of Berlin)
G×E	genotype–environment interaction
GALVmed	Global Alliance for Livestock Veterinary Medicines
GARP	Genetic Algorithm for Rule-set Prediction

GASFRA	Global African Swine Fever Research Alliance
GCM	general circulation model
GDP	gross domestic product
GENESYS	The global online genetic resources information system that replaced SINGER (Systemwide Information Network for Genetic Resources)
GFRA	Global Foot and Mouth Research Alliance
GFSP	Global Food Safety Partnership
GHG	greenhouse gas
GIS	geographic information system
GLOBIOM	Global Biosphere Management Model, of IIASA
GPI	glycosylphosphatidylinositol
GPRA	Global PPR Research Alliance
GREASE	Gestion des Risques Emergents en Asie du Sud-Est (Emerging Risk Management in South-east Asia)
GREP	Global Rinderpest Eradication Programme
GRID	Global Resource Information Database, of UNEP
GRU	Genetic Resources Unit, of CIAT
GS	genomic selection
GWAS	genome-wide association study
HAT	human African trypanosomiasis
HDL	high-density lipoprotein
HIV	human immunodeficiency virus
HLPE	High-Level Panel of Experts
HPAI	highly pathogenic avian influenza
HPS	haemophagocytic syndrome
Hsp	heat-shock protein
IAASTD	International Assessment of Agricultural Knowledge, Science and Technology for Development
IADG	Inter-Agency Donor Group
IAEA	International Atomic Energy Agency
IAMA	International Food and Agribusiness Management Association
IARC	international agricultural research centre
IBLI	Index-based Livestock Insurance project, of ILRI
ICAR	Indian Council for Agricultural Research
ICARDA	International Center for Agricultural Research in the Dry Areas, of CGIAR
ICIPE	International Centre of Insect Physiology and Ecology
ICRAF	International Centre for Research on Agroforestry, of CGIAR (now known as the World Agroforestry Centre)
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics, of CGIAR
ICT	information and communications technology
IDL	intermediate-density lipoprotein
IEMVT	L'Institut d'Elevage et de Médecine Vétérinaire des pays Tropicaux (Institute of Livestock and Tropical Veterinary Medicine)
IER	Institut d'Economie Rurale, Mali
IFAD	International Fund for Agricultural Development
IFDC	International Fertilizer Development Center
IFN	interferon
IFPRI	International Food Policy Research Institute, of CGIAR
IIASA	International Institute for Applied Systems Analysis
IIMR	Indian Institute of Millets Research
IITA	International Institute of Tropical Agriculture, of CGIAR

IL	interleukin
ILCA	International Livestock Centre for Africa, of CGIAR (predecessor of ILRI)
ILRAD	International Laboratory for Research on Animal Diseases, of CGIAR (predecessor of ILRI)
ILRI	International Livestock Research Institute, of CGIAR
IMPACT	International Model for Policy Analysis of Agricultural Commodities and Trade
INERA	Institut de l'Environnement et Recherches Agricoles, Burkina Faso
IPCC	Intergovernmental Panel on Climate Change
IPMS	Improving Productivity and Market Success
IRR	internal rate of return
IRRI	International Rice Research Institute, of CGIAR
ISVEE	International Symposium on Veterinary Epidemiology and Economics
ITC	International Trypanotolerance Centre
ITLN	International Trypanotolerance Improvement Network
ITM	infection-and-treatment method of immunization
ITPGRFA	International Treaty on Plant Genetic Resources for Food and Agriculture
IVEP	*in vitro* embryo production
IVOMD	*in vitro* organic matter digestibility
KALRO	Kenya Agricultural and Livestock Research Organization (formerly KARI)
KARI	Kenya Agricultural Research Institute (now KALRO)
KCC	Kenya Co-operative Creameries
KDB	Kenyan Dairy Board
KEMRI	Kenya Medical Research Institute
KETRI	Kenya Trypanosomiasis Research Institute
KEVEVAPI	Kenya Veterinary Vaccines Production Institute
KLIP	Kenya Livestock Insurance Project
LAMP	loop-mediated isothermal amplification
LCIRAH	Leverhulme Centre for Integrative Research on Agriculture and Health
LCV	Laboratoire Central Vétérinaire, Mali
LDL	low-density lipoprotein
LGA	livestock/grazing/arid
LGACC	Local Governance and Adaptation to Climate Change
LGH	livestock/grazing/humid
LGP	length of growing period
LGT	livestock/grazing/temperate and tropical
LOD	score logarithm of the odds (to the base 10)
LRA	livestock/rainfed/arid
LRH	livestock/rainfed/humid
LRT	livestock/rainfed/temperate and tropical
LSR	livestock systems research
LUCID	Land Use Change, Impacts and Dynamics
mAb	monoclonal antibody
MAPK	mitogen-activated protein kinase
MarkSim	rainfall simulation software
Mccp	*Mycoplasma capricolum* subsp. *capripneumoniae*
ME	metabolizable energy
MERS	Middle East respiratory syndrome
MERS-CoV	Middle East respiratory syndrome coronavirus
MHC	major histocompatibility complex
MIA	mixed/irrigated/arid and semi-arid
MIH	mixed/irrigated/humid and subhumid

MIT	mixed/irrigated/temperate and tropical
Mmc	*Mycoplasma mycoides* subsp. *capri*
Mmm	*Mycoplasma mycoides* subsp. *mycoides*
MRA	mixed/rainfed/arid and semi-arid
MRH	mixed/rainfed/humid and subhumid
mRNA	messenger RNA
MRT	mixed/rainfed/temperate and tropical
MT	metric tonne
NAICP	Nigerian Avian Influenza Control and Human Pandemic Preparedness and Response Project
NARES	national agricultural research and extension systems
NARS	national agricultural research systems
NASA	National Aeronautics and Space Administration, of the USA
ND	Newcastle disease
NDF	neutral detergent fibre
NDVI	normalized difference vegetation index
NIH	National Institutes of Health, USA
NIRS	near-infrared spectroscopy
NK	natural killer cells
NRCS	National Research Centre for Sorghum, of India
OAU	Organisation of African Unity
ODA	official development assistance
ODAP	oxalyldiaminopropionic acid
ODI	Overseas Development Institute
OECD	Organisation for Economic Co-operation and Development
OFAGE	orthogonal-field-alternation gel electrophoresis
OIE	Office International des Epizooties (World Organisation for Animal Health)
OPV	open-pollinated variety
PAAT	Programme Against African Trypanosomiasis
PANESA	Pasture Network for Eastern and Southern Africa
PANVAC	Pan African Veterinary Vaccine Centre
PARC	Pan African Rinderpest Campaign, of the African Union—Interafrican Bureau for Animal Resources
PBL	peripheral blood lymphocyte
PBMC	peripheral blood mononuclear cell
PCR	polymerase chain reaction
PCV	packed cell volume
PDSR	Participatory Disease Surveillance and Response programme, of FAO and Indonesia
PENAPH	Participatory Epidemiology Network for Animal and Public Health
PHEWS	Pastoral Household and Economic Welfare Simulator
PIM	CGIAR Research Program on Policies, Institutions and Markets
PLC	phospholipase C
PPPS	Projet Productivité Primaire au Sahel
PPR	peste des petits ruminants
QQR	quinquennial review, by CGIAR
QTL	quantitative trait locus
RABAOC	Réseau de Recherche en Alimentation du Bétail en Afrique Occidentale et Centrale
RESCAO	Réseau d'épidémiosurveillance de la résistance aux trypanocides et aux acaricides en Afrique de l'Ouest (Network of Epidemiomonitoring of Trypanocidal and Mitidicidal Chemoresistance in West Africa)
RHoMIS	Rural Household Multi-Indicator Survey

RIEPT	Red Internacional de Evaluación de Pastos Tropicales (International Tropical Pastures Evaluation Network), of CIAT
RVF	Rift Valley fever
RVFV	Rift Valley fever virus
SA/IA	System Analysis and Impact Assessment group
SADC	Southern Africa Development Community
SAM	social accounting matrix
SAMPLES	Standard Assessment of Agricultural Mitigation Potential and Livelihoods
SARS	severe acute respiratory syndrome
SEACFMD	South-East Asia and China Foot and Mouth Disease campaign
SEAFMD RCU	South East Asia Foot and Mouth Disease Regional Coordination Unit
SEAFRAD	South East Asian Forage and Feed Resources Network
SEARG	Southern and Eastern Rabies Group
SMTA	Standard Material Transfer Agreement
SNP	single nucleotide polymorphism
SPIA	Standing Panel on Impact Assessment, of ISPC
SPS	sanitary and phytosanitary
SRES	Special Report on Emissions Scenarios
SRR-SEA	Sub-Regional Representation for South-East Asia
STI	Swiss Tropical Institute
TAC	Technical Advisory Committee (superseded by ISPC of CGIAR)
TAD	transboundary animal disease
TB	tuberculosis
TbTfR	*Trypanosoma brucei* transferrin receptor
TCR	T-cell antigen-specific receptor
TD	T-cell-dependent
TFP	total factor productivity
TI-2	T-cell-independent type 2
Tir	trypanosome immune response
TL	Thymus–leukaemia antigen
TLU	tropical livestock unit
TNF	tumour necrosis factor
Tregs	regulatory T cells
TRIF	TIR-domain-containing adapter-inducing interferon/β
UNDP	United Nations Development Programme
UNEP	United Nations Environment Programme
UNFCCC	United Nations Framework Convention on Climate Change
USAID	US Agency for International Development
USDA	US Department of Agriculture
VMRD	Veterinary Medical Research and Development Centre, of the USA
VRL	Veterinary Research Laboratory
VSF-G	Vétérinaires sans Frontières-Germany (Veterinarians without Borders-Germany)
VSG	variable surface glycoprotein
WC1	Workshop Cluster 1
WELI	Women's Empowerment Livestock Index
WFP	World Food Programme
WHO	World Health Organization
WRL-FMD	World Reference Laboratory for Foot-and-Mouth Disease

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Introduction: The Evolution of IARC Livestock Research, 1975–2018

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Contents

Introduction

The international community invested more than US$1.8 billion in global livestock research from 1975 to 2018[1]. Most of this investment has been publicly financed in one institution – what is now the International Livestock Research Institute (ILRI) – and most of that investment has been in sub-Saharan Africa. The impact of ILRI research is therefore an important subject, given the size of the investments, the effects of livestock production and consumption on income, wealth, the environment and health, both human and animal, and the potential benefits of research for production costs, consumer welfare and the environment.

    This introduction traces the creation, evolution and achievements of ILRI and its predecessors as background to the thematic chapters that explore impacts in specific scientific fields. The chapter begins by introducing the scale of the livestock research problem in sub-Saharan Africa in the mid-1970s at the time of the creation of ILRI's predecessors, the International Livestock Centre for Africa (ILCA) and the International Laboratory for Research on Animal Diseases (ILRAD) and the subsequent changes in demography, land use and input use as they affected ruminant livestock production and productivity.

    The chapter then describes the history of the international livestock research institutions in sub-Saharan Africa, focusing on ILRI (1995–present), ILCA (1974–1994) and ILRAD (1973–1994), with some reference to the Centro Internacional de Agricultura Tropical (CIAT), International Center for Agriculture Research in the Dry Areas

(ICARDA) and other international institutions[2]. In describing that history, it discusses their research priorities, budgets, institutional evolution and achievements from 1975 to 2015. It then frames the thematic parts of the book, which evaluate ILRI's scientific and development impacts.

    The remaining parts of the book cover the major themes of ILRI's work:

Part I: Animal Genetics, Production and Health:

- Preface to Part I: Research Spending and Publications on Animal Genetics, Production and Health
- Chapter 1: Livestock genetics and breeding
- Chapter 2: Control of pathogenesis in African animal trypanosomiasis: a search for answers at ILRAD, ILCA and ILRI, 1975–2018
- Chapter 3: Tsetse and trypanosomiasis control in West Africa, Uganda and Ethiopia: ILRI's role in the field
- Chapter 4: Impact assessment of immunology and immunoparasitology research at ILRAD and ILRI
- Chapter 5: Veterinary epidemiology at ILRAD and ILRI, 1987–2018
- Chapter 6: The management and economics of East Coast fever
- Chapter 7: Transboundary animal diseases
- Chapter 8: Zoonoses
- Chapter 9: Food safety and nutrition
- Chapter 10: Ticks and their control

Part II: Primary Production:

- Preface to Part II: Research Spending and Publications on Primary Production

Part III: Tropical Livestock Systems:

Map 1 (p. XVII) shows the principal African research sites of ILCA, ILRAD and ILRI from 1975 to the present.

The Research Challenge of African Livestock Systems in the mid-1970s

This part of the introduction reviews the status of the main African ruminant livestock systems during the decade of the founding of ILRAD and ILCA – land use, human population, ruminant animal numbers, animal productivity, and the threats of trypanosomiasis and theileriosis. Jahnke's landmark book (Jahnke, 1982) summarized the basic characteristics of African ruminant livestock production at the founding of ILCA and ILRAD. From that work and other published material from that era, we can summarize the scale of the African livestock research challenge as it existed in the mid-1970s.

Land use and rural population

Figure I.1 shows, as of the mid-1970s, the basic relationships among land use, human population and population density, using Jahnke's system classification which was based on that of the Food and Agriculture Organization of the United Nations (FAO) (Higgins and Kassam, 1981), and which used data compiled from the mid-1970s.

There were some 22.4 million km^2 of land in sub-Saharan Africa in the mid-1970s, of which 37% was classed as 'arid', 18% as semi-arid, 22% as subhumid, 19% as humid and the balance of 4% as highland. The classification variable is the growing period for the zones, as indicated by aridity, except for the highlands. Arid zones have rainfall of less than 200 mm annually (with less than 90 days suitable for crop production); semi-arid, 200–600 mm (90–179 growing days); subhumid, 600–1200 mm (180–269 growing days); and humid, 1000–2000 mm (at least 270 growing days). The highlands are considered as being above 1500 m above sea level; their rainfall would be in the same broad range as that of the subhumid zone, but colder temperatures would reduce growing periods at some points during the year and Jahnke (p. 152) defines them as having 'a mean daily temperature of less than 20°C during the growing period'. The arid and highlands zones are alike in that their tsetse challenges are usually 'low' or 'very low' (see Fig. I.4b,c).

More detailed estimates of livestock systems scale were incomplete until the path-breaking work of Seré et al. (1996), which became the base of later classifications. Subsequent work included that of Delgado et al. (1999) and the land cover maps by Otte and Chilonda (2002) and Kruska et al. (2003), while Thornton (2010) and Robinson et al. (2011, pp. 8, 11, 38–39 and 145–152) refined the Seré and Steinfeld typology using remote sensing data, national surveys and an expert consultation (Map 1). While the Seré et al. (1996) classification included non-ruminants, we concentrate only on ruminants here.

The growth potential of livestock

Figure I.2 shows tropical livestock units (TLUs) and ruminant numbers by agroecological zone. The arid and semi-arid zones, dominant in Western and Eastern Africa, had the highest numbers of ruminants and TLU while having the lowest stocking rates, the smallest rural populations and the lowest rural population density. Their historical potential depended largely on growth of TLU numbers, an idea that has since been confirmed by the long-term experience with animal numbers and productivity per animal (see this volume, Chapter 15).

The growth potential of the highlands – found almost entirely in eastern Africa and having
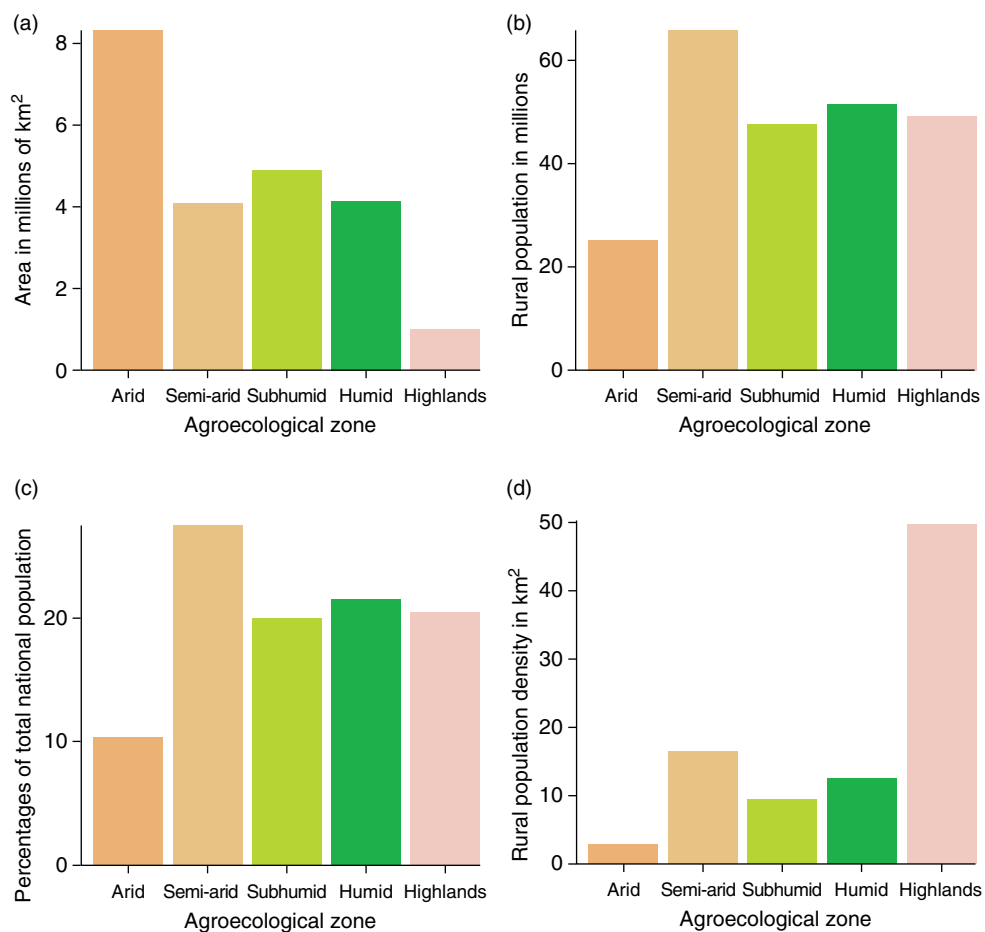
Fig. I.1. (a) Area of sub-Saharan Africa by agroecological zone, mid-1970s. (b) Rural population by agroecological zone, mid-1970s. (c) Zonal rural population shares, mid-1970s. (d) Zonal rural population densities, mid-1970s.
Arid zones have rainfall of less than 200 mm annually, with (< 90 days suitable for crop production); semi-arid, 200-600 mm (90-179 growing days); sub-humid, 600-1200 mm (180-269 growing days); and humid, 1000-2000 mm (>= 270 growing days). Jahnke (1982, p. 152) defines 'tropical highlands' as having 'a mean daily temperature of less than 20 C during the growing period'. (Data from Jahnke, 1982: Annex tables 1-11).

the highest TLU and human population densities – would depend almost entirely on a shift from meat animals to dairying and on rising productivity per animal in meat and in dairy given the existing land constraints at the time. Trypanosomiasis was a production risk on less than 5% of the highlands area and theileriosis was unknown in Ethiopia, which was the most populous highland nation.

Figure I.3 shows Jahnke's mid-1970s estimates of agricultural GDP in sub-Saharan Africa and of the share of livestock in agricultural GDP. Given the abundance of land in most of sub-Saharan Africa, it was thought in the mid-1970s that the livestock growth potential of the humid and subhumid zones would follow an extensive path given that those zones had lower population density and lower TLU density. Exploiting that growth potential therefore depended on the control or even elimination of trypanosomiasis, which affected one-third or more of the area of each. At the time of the founding of ILCA and of ILRAD, and of the
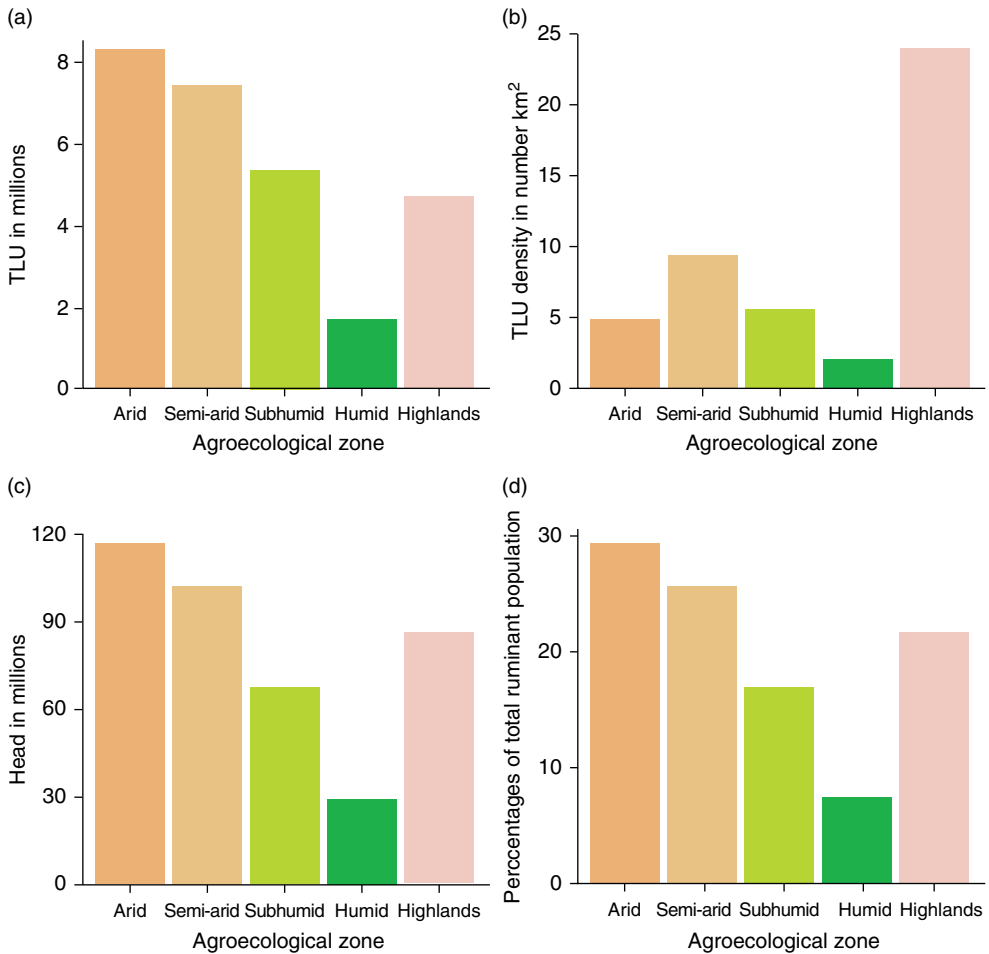
Fig. I.2. (a) Numbers of tropical livestock units by agroecological zone, mid-1970s. (b) Tropical livestock unit density by agroecological zone, mid-1970s. (c) Ruminant livestock numbers by agroecological zone, mid-1970s. (d) Zonal ruminant populations as percentages of total, mid-1970s. (Data from Jahnke, 1982: Annex tables 1-11.)

initial entry of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) into African research, the climate costs of land clearing for agriculture were not well understood.

Jahnke's summary (Jahnke, 1982, p. 35) of the (extremely limited) data on growth in livestock numbers in the 1960s and 1970s indicated that the principal ruminants, plus camels, were growing at about 1–2% annually. The weak growth in Africa was attributed entirely to an increase in TLUs, not to higher yield of meat or milk per animal (Jahnke, 1982, pp. 42–43). An early simulation of East African cattle herds argued that an annual growth rate of female cows of about 4%

was achievable under certain assumptions about management and its effects on calving rate, calf survival and adult mortality (Dahl and Hjort, 1976, and the discussion therein on pp. 66–75). Significant increases in herd growth, from existing breeds under African conditions, depended on levels of management, market access and sequences of good rainfall years that would have been uncommon at the time.

A summary of historical growth (Anteneh, 1984) after almost a decade of ILCA's work concluded that growth rates of the numbers of livestock units were about 1.2% annually in sub-Saharan Africa during the 1970s, a rate
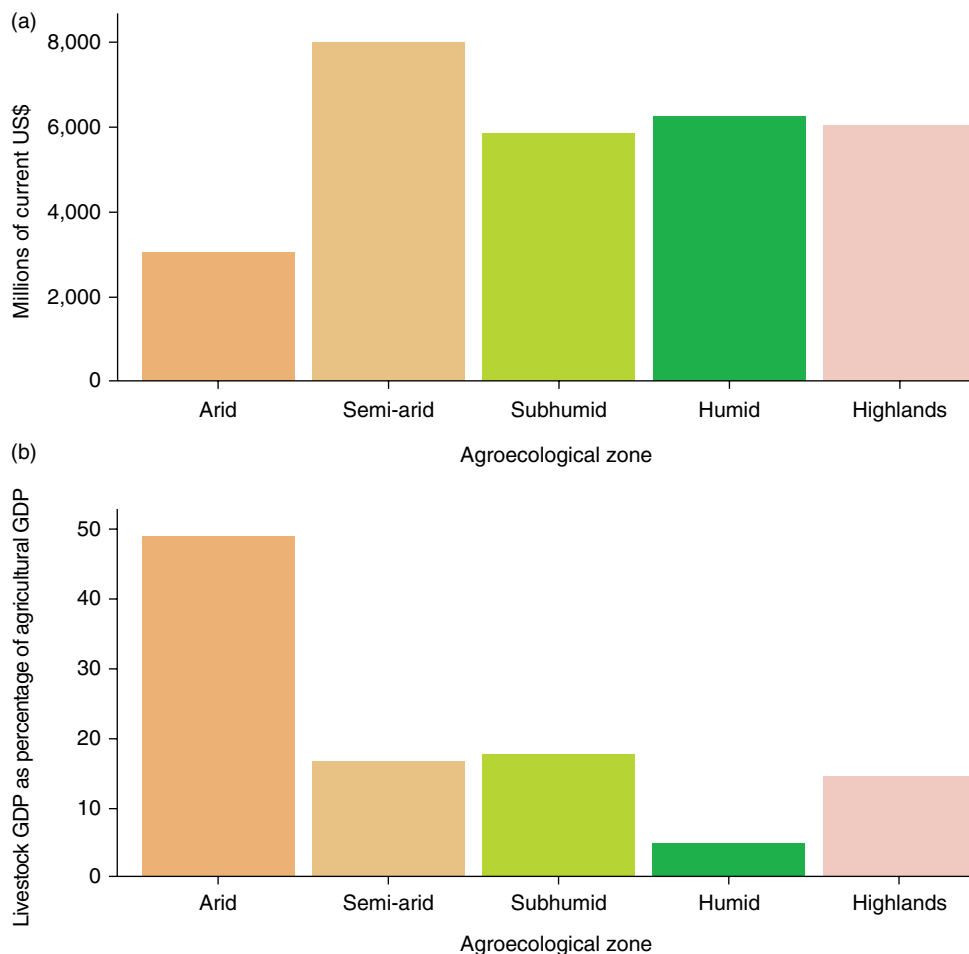
Fig. I.3. Agricultural gross domestic product (a) and livestock share of agricultural GDP (b) by agroecological zone, mid-1970s. (Data from Jahnke, 1982: Annex tables 1-11.)

lower than that of population growth rates; only in beef was there any sign of higher productivity per animal. Evidence over the period 1970–2016 (see Chapter 15, this volume) confirmed the finding that livestock production growth was a function of herd size and that productivity growth per animal was weak.

The problem of trypanosomiasis

The biology of trypanosomiasis and the tsetse vector had been well-studied (Mulligan and Potts, 1970) before the founding of ILRAD. Mulligan and Potts (1970), however, say practically nothing about economic aspects of trypanosomiasis control and admit (pp. 810–811) that '...the tsetse problem is too general or our knowledge of the ecology of the flies is still too limited, to enable an economic form of control or extermination to be devised which could be justified by the productive capacity of the reclaimed area'. The potential benefits to tsetse and trypanosomiasis control had been coarsely estimated by Jahnke (1982), using data from the mid-1970s (Fig. I.4). Beyond the evident facts that trypanosomiasis threatened a much smaller share of the arid, semi-arid and highlands zones compared with the wetter ones, there was a lack of information on losses to this disease and on potential benefits from various control methods.
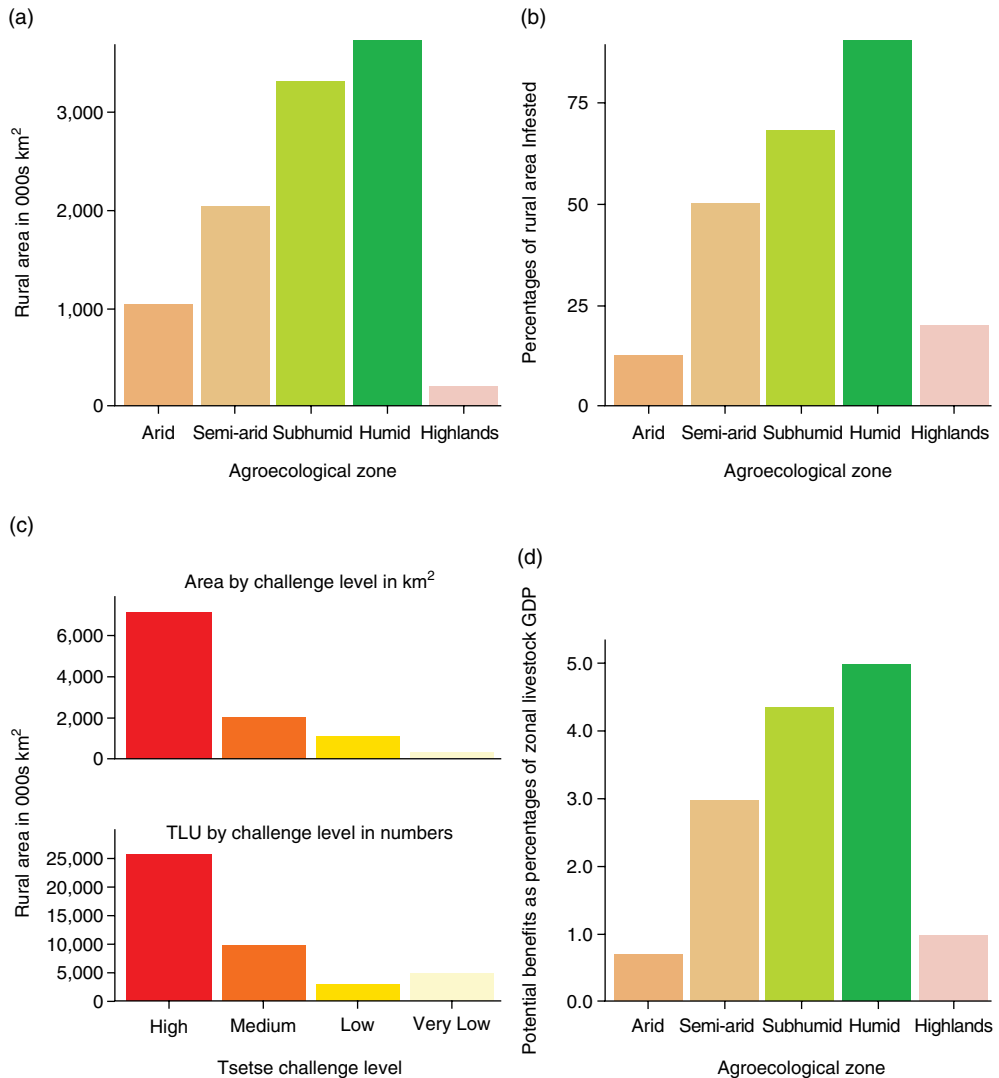
Fig. I.4. (a) Area of tsetse fly infestation by agroecological zone. (b) Zonal area shares infested by tsetse. (c) Ruminant TLU and area by tsetse challenge, mid-1970s. (d) Potential zonal gross benefits from tsetse clearance and trypanosomiasis control, mid-1970s. (Data from Jahnke, 1982: Annex tables 1-11.)

Much has been achieved in understanding the control of trypanosomiasis in sub-Saharan Africa since 1970. By the turn of the century it was understood, partly through the efforts of ILCA/ILRAD/ILRI, that the economic benefits of control would be large. Box I.1 highlights aspects of the economic burden of trypanosomiasis from the mid-1970s to the vaccine modelling done around the year 2000 to the most recent estimates of economic benefits from control.

Areas infested

The work of Ford and Katondo (1977) is the reference point for modern estimates of infested areas. Jahnke (1982) declared, based on the work of Ford and Katondo (1977), the affected areas to be roughly 10.3 million km² with data from the mid-1970s, of which 7.0 million km² were said to be in the more seriously infested humid and subhumid zones. An approximation

to 10 million km^2 became a standard figure in the past century. A study by Katondo (1984) gave revised data from ten countries but did not report a total infested area and concluded that 'a programme of intensive revision is needed before it can be claimed that tsetse situation in Africa is well understood'. An estimate included in the first published collection of the ILCA/ILRAD African Trypanotolerant Livestock Network (ATLN) gave the infested areas as 9.5 million km^2, based on updated information since the 1970s (Jahnke *et al.*, 1988).

Wint and Rogers (2000), using some of the original Ford and Katondo (1977) data, developed a prediction function and prepared detailed maps of infestation by species but did not state different total areas. Rogers and Robinson (2004) used satellite imagery to arrive at a continental estimate of 8.7 million km^2. Shaw (2004) summarized turn-of-the-century estimates as being in the range of '8–10 million km^2'.

Reid *et al.* (2000) used a sophisticated model of human population density, land use and tsetse species to project the impact of human population growth on the density and species composition of tsetse infestation to the year 2040. They estimated the land areas with 'high populations of savannah and forest flies' to be between 6 million and 7 million km^2 in 2000. Reid *et al.* (2000) forecast the area 'infested with riverine flies' to remain 'nearly 7 million' km^2 in 2040. They projected wide changes in species composition, with '[s]avanna and forest flies' to be in general decline, with no riverine types in southern Africa, and with the potential for human population growth to have eradicated the fly in some places. Reid *et al.* (2000, p. 232) predicted an infested area of the order of 5–5.5 million km^2 by the year 2020, but there is no current appraisal of the accuracy of that prediction.

Numbers of animals affected

Jahnke (1982) estimated numbers of ruminants affected by trypanosomiasis by mapping animal inventories to the level of tsetse challenge in the five agroecological zones of his study, as shown in Fig. I.4a–d. He reported approximately 148 million cattle of which perhaps 40 million were in the more severely infested subhumid and

humid zones. Kristjanson *et al.* (1999, p. 88), using data up to the mid-1990s, assumed tsetse-infested areas of 8.7 million km^2 and approximately 48 million cattle in those areas, or about 32% of the cattle in sub-Saharan Africa, in a model of the *ex ante* return to a (hypothetical) vaccine against trypanosomiasis. Reid *et al.* (2000, p. 231) did not predict animal numbers in their work, but they did argue that '5–17 million people' would still live 'in fly-infested areas' by the year 2040. Gradual cross-breeding is occurring between *Bos indicus* (Zebu) cattle types and *Bos taurus* (trypanotolerant cattle, such as the N'Dama) in West and Central Africa and this may reduce overall susceptibility to trypanosomiasis, although the productivity effects of such introgression are not well quantified (Traoré *et al.*, 2017).

Productivity effects

The productivity effects of trypanosomiasis were: (i) the inability to raise livestock in heavily infested areas; (ii) the substitution of less productive trypanotolerant animals for more productive trypanosusceptible stock in infested areas; (iii) the inability of trypanotolerant animals to reach their genetic potential under tsetse challenge; (iv) losses owing to increased mortality and morbidity in infected animals; and (v) the costs of sprays, drugs, traps and other resources needed to maintain livestock under challenge. Older estimates of these effects were even less reliable than estimates of infested areas because the data requirements of productivity studies were stricter; it remains impossible, even using modern survey tools, to calculate a reliable total effect and to partition it into the five components. A coarse estimate from Jahnke's mid-1970s data (Fig. I.4d) was made assuming that tsetse and trypanosomiasis control in the arid, semi-arid, subhumid and humid zones allowed TLU density gains per zone of 10%, 10%, 25% and 25%, respectively, with gains in productivity per animal of 5% in each zone. These modest gains in stocking rates and in yield per animal would, hypothetically, increase livestock GDP by zone in the range of 1% annually (semi-arid and highland zones) to 4-5 % in the subhumid and humid zones.

One appraisal at the outset of the ATLN was from Trail *et al.* (1979a, p. 91)[3], who reviewed 30 studies of the performance of trypanotolerant

stock at varying levels of management under village (n = 5) and ranch/experiment station (n = 25) conditions in West and Central Africa. Trail and colleagues found productivity effects per herd to range from –20% to –50% at 'low', 'medium' and 'high' trypanosomiasis risk compared with situations of 'zero' risk. They noted that the 'zero risk' levels were confounded with 'very high levels of feeding and management' and concluded that the direct trypanosomiasis effect on productivity per animal would have been overestimated.

The review by Swallow (2000, p. 7–12) of 13 studies of trypanotolerant and mixed (trypanotolerant and trypanosusceptible) cattle concluded that: 'The general implication is that the incidence of trypanosomiasis: (i) reduces calving rates by 1–12% in tolerant breeds of cattle and by 11–20% in susceptible breeds; and (ii) increases calf mortality by 0–10% in tolerant breeds of cattle and by 10–20% in susceptible breeds of cattle.'

Swallow further noted three herd studies (in southern Burkina Faso; Ghibe, Ethiopia; and northern Côte d'Ivoire) that have shown annual herd growth effects of control in a range of 1–3%. Kamuanga *et al.* (2001) reported a herd size gain of some 25% in a study of control with trypanotolerant stock, traps and pour-on treatments; the herd size effect was attributable to decreased mortality. Swallow's broad conclusion was that 'trypanosomiasis reduces cattle population by 30–50%' and productivity from affected cattle by 50%. The model of Kristjanson *et al.* (1999, p. 84) of a hypothetical vaccine against trypanosomiasis achieved productivity gains through steep declines in cattle mortality – and therefore, a commensurate rise in stocking rates and in commercial offtake – and with only modest gains in live weight, calving rates and lactation lengths.

Economic benefits of control

Jahnke's book contained little that was specific on the economics of control except to say that long-term control with drugs had been successful on some African ranches (Jahnke, 1982, p. 198). Tacher *et al.* (1988, pp. 331–335) reviewed the costs of traps, sprays and other methods in representative challenge situations and noted a few *ex post* calculations of benefit:cost ratios from spraying from Nigeria and Cameroon to be well above 1. Putt *et al.* (1980) reviewed the costs and benefits of tsetse control in Nigeria and found benefit:cost ratios ranging from 2.7 to 8.0 for selected ground and helicopter spraying operations. The dissertation of Itty (1992, p. 270) analysed the biological results from the ATLN in an economic model of herd productivity at seven humid and subhumid sites in sub-Saharan Africa. He found economic rates of return varying from 15% (Muhaka, Kenya) to 53% (Ghibe, Ethiopia) for treatments involving sprays, traps, trypanocides and trypanotolerant stock. Using data from a cross-section of ten humid African 'countries completely infested by tsetse', Swallow (2000, p. 35) constructed figures purporting to show that the impact of trypanosomiasis would be to lower agricultural GDP by 8–16%.

Shaw (2003) compared tsetse eradication with trypanocides in a hypothetical subhumid situation in West Africa at a range of human population densities. She found that a population density above 50 or so persons/km^2 reduced the incidence of the fly to a low, manageable level. Population densities below 10–20 persons/km^2 made tsetse control impractical. In the intermediate zone of 20–50 persons/km^2, a combination of trypanocides and tsetse elimination gave profitable benefit:cost ratios. Box 3.1 in Chapter 3 highlights successes and failures in community-based control of trypanosomiasis using several methods and notes the sustainability problems of both vector control and drug treatment.

Box I.1. Aspects of the economic burden of trypanosomiasis, 1975–2015

At the founding of ILRAD and ILCA, it was generally understood that trypanosomiasis was a stout barrier to expanding agricultural productivity in much of sub-Saharan Africa. However, beyond that general understanding, calculations of the costs of trypanosomiasis were sparse and unreliable. Variance in such calculations arose from unsolved problems in: (i) estimating the areas infested by the tsetse fly; (ii) calculating numbers of animals affected; (iii) productivity effects of trypanosomiasis; and (iv) benefits and costs of control. Nearly half a century has passed since the founding of ILRAD and ILCA and the same economic problems are now only partly resolved.

Shaw's compilation (2004) found benefit: cost ratios as follows: (i) Ethiopia in 1999, *ex post* evaluation of a pour-on trial, 4.3–8.0; (ii) Central African Republic in 1995, *ex post* evaluation of trapping, 3.1–5.9; (iii) Côte d'Ivoire in 1994, mixed *ex post* and *ex ante* evaluation of trapping, 2.3–4.0; (iv) Burkina Faso in 1988, various sterile insect techniques over 10 years, 0.49–1.56; (v) Nigeria in 1980, two districts, spraying with other local control practices, 2.7–8.0; and (vi) Kenya, prophylaxis with isometamidium chloride, 6.0–52.3.

Kristjanson *et al.* (1999) analysed the net potential benefits of a (hypothetical) vaccine against trypanosomiasis. That work integrated field data from experimental sites of the ATLN, GIS data on the continental distribution of tsetse challenge and affected animals, and an economic surplus model to calculate the aggregate welfare effects of a (hypothetical) vaccine. The study estimated the annual production and control costs of trypanosomiasis in sub-Saharan Africa to be of the order of US$1.3 billion (in 2000 prices). Eliminating those costs with a vaccine adopted over 12 years by a maximum of 30% of producers would give a benefit:cost ratio of 34:1. A fatal defect of this model is that it projected a vaccine adoption period of 12 years when experiments to develop a vaccine had already failed for more than 25 years and hence it is highly unrealistic to impute benefits, and the temporal pattern of benefits, to such a hypothetical vaccine.

Recent work by Shaw *et al.* (2014, 2015) presented benefit–cost models of trypanosomiasis control in eastern Africa – Uganda, Kenya, Ethiopia, Somalia, Sudan and South Sudan – differentiated by farming system, population density, and control strategy ('continuous control, and elimination'). Although there was no single control strategy applicable to all farming systems in the sample, high benefit:cost ratios were more likely in densely cultivated mixed farming areas in which oxen were used for power. Control was typically unprofitable in areas of low cattle density. Problems of programme management imply that elimination of tseste through large-scale campaigns would be infeasible.

A problem with some aggregate projections of trypanosomiasis control, by any method or combination of methods, is omission of general equilibrium effects. This is notable in the review of Swallow (2000), who postulates that a doubling of trypanosomiasis control inputs gives a proportionate change in agricultural GDP, and in the regional models of Shaw *et al.* (2015, p. 207 for 0.7 m km^2 in five countries of East Africa), which allows product and input prices to remain unaffected by large changes in livestock output over many years. The major microeconomic analysis of trypanotolerance (Itty, 1992) advocates a joint strategy of trypanotolerant cattle with chemotherapy without considering the land use effects of higher stocking density in areas of moderate trypanosome prevalence or without adequately discussing the evolution of resistance in the vector.

Except for Shaw's work on East Africa, there is little in the literature of the decade after 2010 on the economic problems of controlling tsetse and animal trypanosomiasis in Africa. The costs of gathering and analysing time-series data on the animal populations, disease incidence and the effects of control methods have stopped nearly all new research in this area.

Box I.1 describes some problems in estimating the economic burden of trypanosomiasis. Jahnke (1982) approximated the potential gross benefits to research from reducing trypanosomiasis in cattle by: (i) projecting additional numbers where tsetse challenge had been reduced modestly in each zone except the highlands, where challenge was already low; and (ii) projecting productivity gains per animal at low levels of management where tsetse challenge had been reduced. As shown in Figure I.4(d), the largest gains relative to zonal GDP from livestock would be achieved in the subhumid and humid zones even in the absence of a vaccine. This early calculation did not consider the costs of control from drugs, traps, sprays or other methods. The cost of maintaining vector control operations over time in less densely populated areas to prevent recolonization by the fly has meant, in practice, that the attractive benefit:cost ratios of vector control have not been sustainable over long periods and this fact has long been used by advocates of vaccine development, despite the failure to develop an effective vaccine.

Origins of the International Livestock Research Institutions

The creation of the international livestock research centres was due in part to the Green

Revolution in crops. It was believed that new animal research could produce gains like those achieved in rice and wheat, and that combating diseases in African ruminant livestock offered the greatest immediate potential for such gains. The mandate of the new livestock institutions did not include swine or poultry, which were then of less importance in most African systems or whose research needs could be met by technology transfer[4].

The influence of the Green Revolution

The roots of the Green Revolution were in technical assistance programmes introduced into Latin America in the 1940s. In 1960, the International Rice Research Institute (IRRI) was opened in the Philippines with a global mandate to increase rice production to 'solve this problem of rice' (Anderson *et al.*, 1991). The opening of IRRI together with that of the Mexico-based CIMMYT (Centro Internacional de Mejoramiento de Maíz y Trigo) produced the improved cultivars and management innovations of the Green Revolution (Ruttan, 1977).

The initial successes of rice and wheat led to the creation of a network of international agricultural research centres (IARCs), under the umbrella of CGIAR.[5] This network became the dominant model of publicly funded and conducted agricultural research in the tropical climates.

The rationale of CGIAR was that increased and stable funding of research with specific commodity agendas could supplement the limited capacity of developing-country national agricultural research systems and produce public goods that might otherwise never have been produced. The IARCs were conceived as engines to drive agricultural modernization and rural development, using science:

> ... two types of activity ... make sense: first, activities which explicitly face up to the complex and interrelated problems of ignorance and tradition, and to seek to attack those problems; and second, isolable technical problems which are so important that their solution would find acceptance and application even under present circumstances.
> Harrar *et al.* (1952, pp. 25–26).

Harrar's[6] perspective was influential both in defining agricultural problems in poor countries – 'ignorance and tradition' – and in proposing scientific solutions to those problems. Green Revolution packages of improved seeds, fertilizer and irrigation had a dramatic impact on agriculture. Between 1961 and 1985, cereal production in the Asian developing countries grew rapidly, with the increase attributed to seeds, fertilizer and irrigation, each factor having a research component.

The Asian successes in crops had bypassed sub-Saharan Africa up to about 1990 because inadequate infrastructure, expensive market access, unfavourable agro-climates, lack of irrigation and weak, unstable governments had blocked the spread of new technologies. Beyond the general diagnosis of why the Green Revolution had not occurred in sub-Saharan Africa was the belief that livestock were understudied, and that African animal disease and rangeland management problems were unusually difficult. These considerations confirmed the view that a new research approach to livestock and livestock systems was needed in sub-Saharan Africa.

The role of the Rockefeller Foundation

The Rockefeller Foundation traced its global agricultural influence to Dr Norman Borlaug's wheat programme in Mexico in the 1940s. The Foundation believed that 'international cooperation in any field of science ... would contribute towards a common pattern of global living' (Chandler, 1992, pp. 2–3). In addition to its role in CIMMYT, the Foundation had funded the establishment of IRRI, and was a logical organization to advance agricultural research institutes in sub-Saharan Africa.

The Rockefeller Foundation was active in the creation of ILRAD and ILCA, commissioning a series of meetings and reports, and later signing the initial memorandum of agreement with the Government of Kenya for ILRAD, on behalf of CGIAR. The Foundation further convened a series of conferences between 1968 and 1970 that led to the task force that set the basis for what became ILCA.

The Beck and Tribe reports

Discussions of an African livestock institution had begun as early as 1963[7]. At that time, IRRI

had been established, CIMMYT was nascent and complementary needs for livestock research were recognized. In 1966, a paper in the *Proceedings of the National Academy of Sciences USA* noted the 'need for the establishment at an early date of a major research centre located in the tropics devoted to tropical diseases of animals' (Pritchard *et al.*, 1972, p. 368). A US Presidential Panel on the World Food Supply recommended the establishment of international centres for research on animal production and diseases in the humid and arid tropics, with 'at least one centre devoted primarily to research on epizootic diseases' (President's Science Advisory Committee, 1967: Vol. 1, p. 93). Donors were reluctant because of the potential high costs.

In 1968, a Rockefeller Foundation conference in Bellagio on East African rangelands recommended the establishment of an 'International Range Land Institute' (Longhurst and Heady, 1968). In 1970, the Ford Foundation proposed an 'International Centre for Rangelands Research and Development in Africa', with the goal of increasing 'the yield of animal protein (meat and milk) and other animal products from such rangelands to its maximum economic level, while carefully monitoring all such programmes of management and development' (Robin and Brown, 1970). The ambition of this Ford Foundation proposal appeared smaller than that from the Rockefeller Foundation; the proposal reassured readers that 'with no capital spending and no capital assets beyond its office furniture and equipment, the Centre can be terminable at any time' (Robin and Brown, 1970, p. 3). The specific title of the Ford Foundation proposal – an 'International Centre for Rangelands' – revealed the bias of the international partners in the decade before the founding of ILCA and ILRAD towards animal production on extensive grasslands and against smallholder mixed farming.

The Beck report

In 1971, a Rockefeller Foundation-sponsored mission, led by Professor Glenn Beck[8] and including scientists with wide African experience, wrote what became known as the Beck report. The Beck report explored the possibility of an 'African Livestock Center' and suggested one institution with a central headquarters in Kenya, working through a 'network of associated African research stations'. The new centre would have two 'thrusts' – a 'livestock production research laboratory' in West Africa, working at sites in Niger and in Nigeria to cover a range of agroecological conditions; and a proposed 'International Laboratory for Animal Disease Research in Africa' in East Africa with a 'program in ECF and trypanosomiasis' (Beck, 1971, pp. 28–29). The new institution would have one board and one Director General, with associate directors at the East Africa and West Africa sites.

The new centre would have the goals of 'improving the social and economic welfare of pastoralists' and of increasing the contribution of livestock to African GDP by inducing technical change to increase meat production per animal, lift offtake rates, optimize production systems and reduce losses to animal disease (Beck, 1971, p. 34).

In light of these goals, an initial task of the new centre was declared as (Beck, 1971, p. 35):

> A study of livestock production systems of Africa is an area of high priority. New research is likely to have most impact if planned within the context of these production systems. An Analysis and Planning Unit would be required from the inception of the Centre for this purpose. This would involve surveys and data analysis covering sociology, range ecology, water resources, animal production, economics and marketing.

The Beck report (Beck, 1971, p. 27) further defined the role of what became ILCA:

> The most important function of the Centre would be to assemble a multidisciplinary team of scientists to develop research programmes designed to solve the basic production and socio-economic problems that are serving as constraints to livestock development.

Beck proposed specific research domains in 'range and pasture studies', 'animal production studies' (including such problems as 'causes of low reproductive performance and high calf mortality') and animal disease studies covering 'parasitism, streptothricosis, and fascioliasis' (Beck, 1971, p. 38).

The Tribe report

More detail about a potential second institution was required following the Beck report, and this

was provided by a mission led by Professor Derek Tribe. The Tribe report (Tribe *et al.*, 1973, p. 1) focused on systemic and multidisciplinary approaches in making its recommendations:

> In particular, there is a need for more detailed study of animal production systems of tropical Africa before existing knowledge can be fully utilized or future research priorities defined. This work must give full consideration to those aspects of biology, economics and social anthropology that relate to animal production.

The Tribe mission advocated several activities – research, capacity building, advice at different levels and development of a knowledge base of 'all relevant information on animal production in tropical Africa' – in close '... cooperation with existing institutions in Africa ... Its essential role should be complementary, cooperative and catalytic' (Tribe *et al.*, 1973, p. 28).

The Tribe report gave a comprehensive and ambitious overview of what ILCA would become and recommended that '... an International Centre for the development of animal production in Africa should be established immediately'.

The limited history of international agricultural research institutes made it difficult for donors to reach a consensus on the decentralized, network model recommended by the Tribe report. Discussions about a second livestock institute in Africa therefore continued, partly under the influence of an earlier view of the need for both an 'ILRAD' and a second institute, working on production (Pino, 1970).

By the beginning of 1973, there was a consensus among potential donors that Africa would host two international centres of livestock research. Initial prospects for merging them on one campus had not been realized – not necessarily for scientific reasons but rather due to politics and timing – and within a few years two new campuses would exist, one in Nairobi and the other in Addis Ababa.

Despite the forcefulness of the Tribe report, the Rockefeller Foundation chose not to invest in ILCA, considering it too risky, and ultimately invested in what became ILRAD. The Rockefeller Foundation's early experience was influential in creating two institutions because of its focus on 'isolable problems' such as raising rice and wheat yields rather than focusing on agricultural production systems. It was generally believed that success was more likely if ILRAD were to focus on one or two diseases, and on one problem, that of immunization. If ILCA were to come into being as a centre to study livestock systems, then ILRAD should logically focus on livestock disease. The evident synergy between animal production and animal disease led the enabling committee for the establishment of ILCA to conclude that ILCA and ILRAD should be integrated from the start, although this ultimately did not happen for 20 years.

That the centres were established at the same time, one seeking the laboratory solutions for two animal diseases and the other analysing production systems, underlined two issues. First was the prevailing optimism that science could make a fundamental contribution to livestock production and related agricultural problems in Africa. Second was the view that African livestock research structures were inadequate to solve problems of livestock disease and management.

Establishment of ILRAD

The Rockefeller Foundation, on behalf of CGIAR, began work with the Government of Kenya to establish ILRAD. Bruce MacKenzie, the then Minister of Agriculture of Kenya, co-drafted a letter with John F. McKelvey of the Rockefeller Foundation for President Jomo Kenyatta to send to Robert McNamara, the then President of the World Bank. The letter recommended that ILRAD be established in Kenya; this ultimately allowed CGIAR to appoint an enabling committee, financed by the Rockefeller Foundation, for the establishment of ILRAD in Kenya. An agreement was signed in 1973 between the Government of Kenya and the Rockefeller Foundation (Gray, 1984).

Establishment of ILCA

ILCA was established by the signing of a memorandum of understanding between the Ethiopian Minister of Agriculture and CGIAR in February 1973. The first Director General of ILCA, Jean Pagot, arrived in Ethiopia in September 1974 and construction began on the new centre soon after.

The International Laboratory for Research on Animal Diseases

ILRAD was established in 1973 and inaugurated in 1978 as a new centre with independent facilities and staff.

Priorities

One initial vision of ILRAD was to focus only on a vaccine for theileriosis, commonly known as East Coast fever (ECF), partly because it was believed that no existing facility could create such a vaccine (Pritchard 1991, interview)[7]. The proposed single disease focus raised questions from the Rockefeller Foundation and the United Nations Development Programme (UNDP), given the potential competition with existing efforts. Research at the East African Veterinary Research Organization (EAVRO), funded by the UNDP, had concentrated on ECF, and scientists there had been the first to grow *Theileria parva*, the causative agent, in tissue culture. The choice was ultimately made to focus ILRAD's mission on two problems – trypanosomiasis and ECF.

The limited mandate of two diseases at IL-RAD simplified the definition of research. Although the questions about ILRAD's mandate had been resolved, other problems remained. One was that the global outlook of CGIAR derived from a US or European worldview and hence was at times detached from the countries where the centres worked (Fitzgerald, 1986; Anderson *et al.*, 1991). A second was relationships with other research institutions in East Africa.

Documentation from a meeting in Rome in 1971 suggests other considerations in expanding ILRAD's initial mandate. One was the view that an ECF vaccine would soon be available commercially: 'One half or perhaps three fourths of the research towards vaccine production has been accomplished but to complete the final stages of this research will probably require five to ten years' (McKelvey, 1971, pp. 285–286). ECF vaccine development was clearly seen as a 'short-term programme' and trypanosomiasis research as a 'long-term problem'. Indeed, some felt that a 10-year time frame for the development of an effective vaccine against trypanosomiasis was 'conservative' (Anderson *et al.*, 1991).

The choice of two mandate diseases did not close the question of how to attack them. There had been extensive discussion in the Bellagio meetings about ILRAD's initial priorities. Ultimately, the decision was made that its initial emphasis would be on haemoprotozoan parasites and immunological aspects of African animal diseases[9]. A third disease, cysticercosis, was considered for ILRAD's initial programme and rejected[10]. Underlying the choice of the two diseases, the first paragraph of ILRAD's founding memorandum of understanding with the Government of Kenya began with a reference to 'basic research'.

A second issue at ILRAD's founding was translation of research results into commercial applications. There was discussion about what an ECF vaccine would cost, who would pay, whether it would be more cost-effective than dips and whether it would be commercially viable.

Both ECF and trypanosomiasis were diseases that could possibly be controlled through new molecular techniques involving similar scientific skills, even if ECF was the 'short-term problem' and trypanosomiasis the 'long-term problem'. Earlier research on the causative agents of the two diseases, tick-transmitted apicomplexans of the *T. parva* spp., and tsetse-transmitted kinetoplastids of the species *Trypanosoma brucei*, *Trypanosoma congolense* and *Trypanosoma vivax*, respectively, had shown that, while it was possible to immunize livestock against reinfection with that specific immunizing strain, immunity was not conferred to other strains of trypanosomes or *Theileria* spp. This inevitably meant that ILRAD would have a different mandate from the other early centres, which were primarily mandated to conduct applied and adaptive research. ILRAD, too, had an adaptive and applied mandate, but it also had basic research to do, notably establishing immunity against parasites and the mechanisms causing its failure. Disease control would be – indeed, still is – a long-term and ambitious goal, and would leave ILRAD and ultimately ILRI vulnerable to new priorities in how 'science for development' should be conceived.

McKelvey[11] believed that:

> ... to focus sharply on one, possibly two,
> diseases East Coast fever and African animal

trypanosomiasis, and on one problem, immunization techniques, to combat the diseases would afford greater chance of success than to range widely over many problems of cattle production in Africa. The Rockefeller Foundation successes in the medical sciences, combating yellow fever, for example, and in the agricultural sciences, maize and wheat improvement, reinforced this belief.

Research capacity was strong in East Africa. African institutes, such as EAVRO and the University of Nairobi, plus foreign universities and colonial programmes, had made significant research investments. Donor agencies, in particular the British Overseas Development Administration and the UNDP, were keen on a regional East African institution, and assisted in forming a research network serving Kenya, Tanzania and Uganda. This communitarian ideal soon faded with the differing political systems of the three nations; matters reached the point where it was expedient to communicate bilaterally with Kenya over ILRAD. This simplified the initial decision to locate ILRAD at Muguga under the auspices of EAVRO (McKelvey, 1991).

East African trypanosomiasis research and control had started around the turn of the century and had been strengthened in 1946 with the formation of what would become the East African Tsetse and Trypanosomiasis Research and Reclamation Organisation (EATTRO), at Tororo in Uganda, and EAVRO, based at Muguga, Kenya. Research was redirected equally at 'entomology, protozoology, biochemistry and medical and veterinary studies' (Onyango, 1971). While EATTRO's work had faltered for lack of resources, new external funds had revived it to some extent (Clarke, 2007) and ILRAD's work would clearly impinge upon the mandate of EATTRO.

The timing of ILRAD's foundation was also fortunate in terms of advances in immunology and molecular biology, which promised a revolution in vaccine development. Advances in recombinant DNA technology and DNA sequencing, alongside other technologies, allowed closer study of parasites and host immune systems, and of the genomes of parasites and hosts, and the invention of new tests for characterizing parasites and diagnosing infections. As we shall see in the thematic chapters, especially those in Part I,

the field impact of those advances was mixed in the two ILRAD mandate diseases.

Protozoan and helminthic diseases affect millions of people and animals in the developing world, implying that a targeted investment in their control could have a significant impact on human and animal health with potential spillover effects from scientific advances into control of malaria. The challenge, however, was formidable. Unlike bacteria and viruses, unicellular protozoa and the cells of worms resemble the cells of their human and animal hosts; these pathogens have accordingly developed sophisticated mechanisms to evade attack by host immune systems.

Parasitology emerged relatively late as a scientific discipline and, by the early 1970s, was about to undergo profound change. There was a recognition that modern biology, especially molecular biology, could make an important contribution to parasitology. This interest in parasitology was to some extent prompted by colonialism, which had seen livestock diseases as threats to the profitability of colonial investments (Lyons, 1992).

Approach to trypanosomiasis control at ILRAD's founding

In 1895, David Bruce identified *T. brucei* as a causative agent of animal trypanosomiasis. In 1903, Bruce identified tsetse-transmitted *Trypanosoma gambiense* as a causative agent of human trypanosomiasis. In 1906, Robert Koch showed that aminophenyl arsonic acid (atoxyl) could cure trypanosomiasis in people, albeit at the risk of blindness. These findings, as well as subsequent advances in understanding of tsetse and trypanosome taxonomy, trypanosome host range and virulence, and identification of less toxic trypanocidal drugs, underpinned the strategies used in colonial Africa to control epidemic human trypanosomiasis – diagnosis and treatment, vector control, and spatial separation of host and vector.

Imposition of these historical strategies on human populations throughout humid and semi-humid Africa, while dehumanizing (Headrick, 2014), had led by 1940 to a decline in human trypanosomiasis and improved human health. Despite a resurgence of human trypanosomiasis

during the post-colonial period because of the breakdown in control, the human disease is now contained in most regions and the World Health Organization (WHO) projects that it is possible, with appropriate control measures, to eliminate the human disease as 'a public health problem' by 2020 (www.who.int/trypanosomiasis_african/en/; accessed 21 January 2020).

While human African trypanosomiasis is now a less serious health risk in Africa, African animal trypanosomiasis (AAT) is still quite important. AAT is endemic throughout the tsetse habitat, which encompasses the humid and semi-humid regions of Africa, a landmass covering about one-third of the continent. AAT causes high mortality in cattle and other domestic livestock and excludes cattle-based agriculture from all but the fringes of the tsetse habitat where tsetse and trypanosome challenge are relatively low; even there, animal agriculture requires tsetse control and the application of trypanocidal drugs and can still incur substantial production losses. Exotic breeds of livestock that had been selected for growth rate and milk and meat production tended to develop more acute forms of AAT than indigenous African breeds, and this usually limited the use of such exotic stock where tsetse was endemic unless trypanotolerant breeds could be introduced.

Much of ILRAD's mandate was to discover new ways of controlling AAT, with a focus on vaccination. It was clear from the inception of ILRAD that the development of an efficacious AAT vaccine would be difficult because bloodstream-stage African trypanosomes were known to have remarkably high antigenic variation. However, there was evidence to suggest that animal infective 'metacyclic' trypanosomes derived from tsetse, and the first bloodstream-stage parasites that they generated, might express a common antigen that could be targeted by a vaccine (summarized by Gray, 1970, pp. 113–116). Thus, molecular characterization of trypanosome surface coat antigens, and analysis of their diversity within and between strains, species and differentiation stages of trypanosomes, was an immediate focus at ILRAD, and was paralleled by deeper analysis of the bovine immune system, and by the investigation of immune responses to putative AAT vaccine antigens and to trypanosome infections. These scientific developments renewed hope that a trypanosomiasis vaccine

might be found and were influential in ILRAD's early priorities[12].

The state of knowledge of the animal trypanosomiases at the time of ILRAD's founding was good. The comprehensive review of Mulligan and Potts (1970) had described vector biology and behaviour, pathogenesis of the disease in animals and clinical aspects of disease management, in addition to measures for control of the disease in livestock, and there was extensive field knowledge of the disease across sub-Saharan Africa. One outstanding gap of the Mulligan and Potts book was the field of trypanotolerance, which become a major ILCA/ILRAD theme in the late 1970s.

Approach to ECF control at ILRAD's founding[13]

ECF is a fatal bovine disease caused by the protozoan parasite *T. parva*. The disease occurs in 12 countries in eastern, central and southern Africa where the vector, the brown ear tick (*Rhipicephalus appendiculatus*), is found. ECF causes major economic losses by affecting both dairy cows and young Zebu cattle among pastoralists and on ranches. It is among the most serious constraints to cattle productivity in the countries in which it is found.

At the time of ILRAD's founding, ECF had been managed with acaricides, but this treatment was expensive and not always successful. An alternative was for farmers to keep local cattle breeds, which tended to be more disease resistant but were less productive than exotic breeds, especially for dairying. It was widely accepted that vaccination against ECF would be the most attractive control option, and development of a vaccine was a founding aim of ILRAD.

Work to develop an ECF vaccine had begun in the 1960s at EAVRO, located in Muguga, Kenya, under the auspices of the East African Community. At about the time of ILRAD's establishment, a vaccination procedure was being developed at EAVRO. The infection-and-treatment method (ITM) was an immunization procedure against ECF involving inoculation of live sporozoite forms of *T. parva*, usually in the form of a semi-purified homogenate of *T. parva*-infected ticks, combined with simultaneous treatment
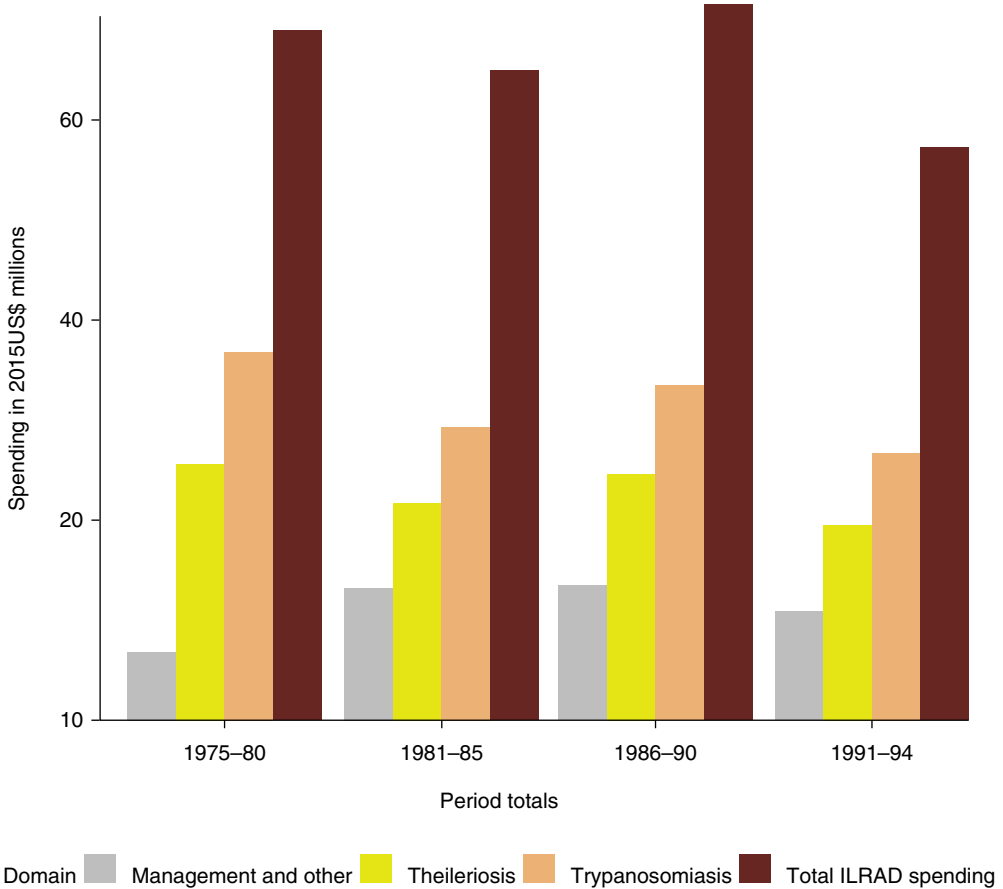
Fig. I.5. ILRAD spending by research domain and period, 1975–1994. Total ILRAD spending, 1975–94, of $262 million in 2015 US$. (Data from ILRAD Annual Reports, various years).

with a dose of a long-acting formulation of oxytetracycline. Production and delivery of this live ECF vaccine was complicated, expensive and time consuming, and at the end of the 1970s, there were doubts as to whether the ITM process would be commercially viable.

Despite uncertainties about the commercial possibilities of ITM, it was recognized that acaricide treatments had their own shortcomings, including cost and sustainability given the need for repeated applications. ILRAD therefore focused on the immunopathology of theileriosis and began the years of work in its laboratories, and with East African partners, that eventually led to the commercial introduction of the ITM 'Muguga cocktail' vaccine in several East African countries between 1998 (Tanzania pastoral sector) and 2012 (Kenya dairy sector).

Resources

Figure I.5 summarizes ILRAD's spending over its life as an independent centre. ILRAD began with a complement of perhaps 50 international scientists in the 1970s (CGIAR/TAC, 1981, Table 1, p. 23)[14]. Its annual budget (in 2015 US$) averaged US$11.5 million between 1975 and 1981 (the year of ILRAD's initial external review). In the early years of ILRAD, the numbers of scientists by discipline (CGIAR/TAC, 1981, Table 2, p. 26) were (of a total of 38): parasitology, seven; cell biology, six; immunology, nine; molecular biology, two; biochemistry, seven; and pathology, seven. We estimate that ILRAD spent nearly 60% of its research commitments on trypanosomiasis and related immunological work and the balance

on ECF; and, further, that ILRAD spent about one-sixth of its real budget on management and administration over its lifetime. ILRAD investment in systems, economics and policy was limited to trypanotolerance work before 1987, when its veterinary epidemiology unit commenced. ILRAD spending on systems, economics and policy was less than 3% of its lifetime total.

Institutional evolution

The first external evaluation of ILRAD (known at the time as a quinquennial review (QQR) (CGIAR/TAC, 1981) praised the centre's science[15]. It stated:

> ... the Panel is unanimously satisfied with the very rapid progress achieved by ILRAD in building up a first-class research tool, with the remarkable advances made in the scientific knowledge of trypanosomiasis and theileriosis and with the high quality of the scientific leadership.

While proposing no change in ILRAD's disease mandates, the panel recommended changes in management and priorities, including organizing research themes into projects, doing more on trypanotolerance, building a greater presence in West Africa, and establishing five new subprojects on trypanosomiasis and another five on ECF.

Throughout the 1980s, research on ECF moved at a faster pace than trypanosomiasis research, as had been expected at ILRAD's foundation. Already, however, ECF vaccine development was behind earlier ambitious timescales. Nevertheless, by 1989, a review group recommended the establishment of a Project Area on vaccine formulation. A vaccine against trypanosomiasis proved more intractable.

The second external programme review of ILRAD

The second external programme review of IL-RAD (CGIAR/TAC, 1986a) again praised the laboratory's work. It found scientific advances[16] in studying the two diseases. It expressed continued hope for 'immunological solutions' to trypanosomiasis and ECF, although it recognized that prospects for a trypanosomiasis vaccine were fainter. While the second external

programme review (EPMR) noted a lack of field impact during 1986, it expected that such an impact would occur within the next 5 years based on what had been achieved scientifically in the first decade.

The second external programme review of ILRAD did not recommend major changes in priorities. It rejected major new work on heartwater, a tick-borne disease caused by *Ehrlichia ruminantium*. It referred to collaboration with ILCA in the context of the Joint ILRAD/ILCA Trypanotolerance Programme but did not recommend changes in institutional collaboration or structure. While the second EPMR stated that new priorities on trypanosomiasis or ECF should be funded from existing resources, ILRAD management sought additional funds for the study of chemotherapy against trypanosomiasis and for research on trypanotolerance (CGIAR/TAC 1986a, p. 4 of letter from ILRAD Board Chair to the Technical Advisory Committee (TAC) Chair).

Given the limits of funding and the changes in CGIAR priorities, developing ILRAD's capacity to assess the research impact was important. Accordingly, in 1987, ILRAD established a small socio-economic and epidemiology programme, whose goal was to estimate the economic impact of trypanosomiasis and ECF and to evaluate the potential impact of their control. This programme soon became a leader of ILRAD's research, and its successors have been a highly productive part of ILRAD/ILRI over the past 30 years (see Chapter 3, Chapter 5 and Chapter 6, this volume).

The third external review of ILRAD

The third external review of ILRAD (CGIAR/TAC, 1993a) further acknowledged the quality of the institution's work. It urged widening ILRAD's mandate to apply its findings from molecular biology and immunology to other diseases and to do more capacity development. It set a deadline of five years for a theileriosis vaccine. It recommended that immunology research on trypanosomiasis be restricted to four candidate antigens before 'any new ones are isolated' (CGIAR/TAC, 1993a, p. ii). It suggested that ILRAD do 'a modest expansion' of research on other tick-borne diseases. While recommending no major change in ILRAD's mandate, it recognized the need for new investment in a vaccine development facility (CGIAR/TAC, 1993a, p. iii). This third external
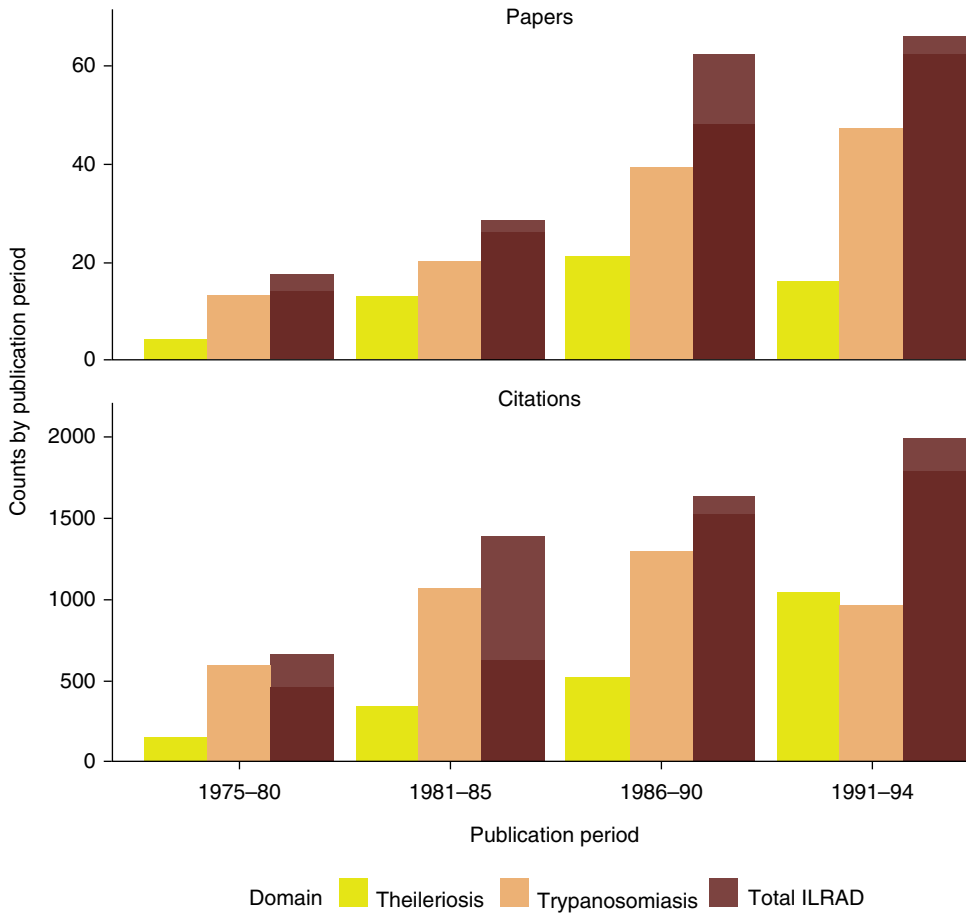
Fig. I.6. ILRAD publications by research domain and period, 1975–1994. Sample size of 632 papers. (Data from www.scopus.com and www.scholar.google.com).

review of ILRAD did not endorse a merger of ILCA and ILRAD, but it did encourage better co-ordination between ILCA and ILRAD across sub-Saharan Africa.

Achievements

The start-up costs of building facilities, appointing scientists and developing a programme meant that initial progress at ILRAD was slow. These start-up costs soon made the projected 5–10-year period to develop a vaccine against AAT unrealistic, a finding that was confirmed by the first ILRAD external review (CGIAR/TAC, 1981). Scientific achievements during ILRAD's initial 15 years were none the less significant, as shown by the many papers published by ILRAD

scientists and partners and as confirmed by three positive external reviews of the laboratory's work.

Figure I.6 shows the numbers of the principal ILRAD papers in two fields – trypanosomiasis and ECF – plus the total. ILRAD's chief achievements in its early period were in diagnostic and other methods, as summarized in Fig. I.6, and in the fields of genetics, immunology and pathology. The thematic chapters in Part I of this volume review the scientific and development impact of that work.

Achievements for the two major ILRAD diseases (see Chapters 1–6, this volume) were:

- The successful continuous cultivation of *T. brucei in vitro* (Hirumi and Hirumi, 1989; Hirumi *et al.*, 1977).

- Advances in the diagnosis of trypanosomiasis (Paris *et al.*, 1982; see see Chapters 2 and 3, this volume).
- Advances in understanding the genetics of *T. brucei* and *T. vivax* in (see Chapters 2, this volume).
- Improvements in the management of AAT in the absence of a vaccine (see Chapters 2 and 3, this volume).
- Parasitology and immunology of trypanosomiasis and theileriosis (Baldwin *et al.*, 1986); despite the eventual failure to produce a successful vaccine against AAT, major global advances in bovine immunology and immunopathology were made at ILRAD (see Chapter 4, this volume).
- The successful example of the long tradition of research on the economic aspects of controlling tsetse and trypanosomiasis, to which ILCA/ILRAD/ILRI work has contributed in part over many years (see Chapter 3, this volume). This began with Hans Jahnke's path-breaking work (1974, 1976, 1982), continued through the African Trypanotolerance Livestock Network (ILCA/ILRAD, 1988; Itty, 1992), the summary of Swallow (2000), and the detailed investigations by Shaw (2004, and 2015, for example). This work has allowed the definition of control models and has provided valuable advice to extension services on the application of those models.
- Advances in cultivation of *T. parva* (1970s and 1980s), continuing the work of EAVRO.
- Understanding of the biological mechanisms of trypanotolerance (Murray *et al.*, 1982; ILCA/ILRAD, 1988; Rowlands and Teale, 1994).
- Understanding of the behaviour and control of the ECF vector, the brown ear tick (*R. appendiculatus*) (see Chapter 10, this volume).
- Understanding of tsetse fly (*Glossina* spp.) behaviour and control (see Chapters 2 and 3, this volume).
- Definition of the epidemiology of trypanosomiasis and theileriosis (Perry and Hansen, 1994, and Norval *et al.*, 1992, on theileriosis; see Chapters 5 and 6, this volume).

- Novel field and participatory epidemiology. The focus of ILRAD's work was almost exclusively laboratory based from 1975 until the merger with ILCA in 1995. Two significant exceptions were the ATLN on trypanotolerant animals, which started in 1977, and field epidemiology on ECF, which started in 1986 (see Chapters 2–6, this volume, for discussions of this field work).
- Development of partnerships with national programmes in Kenya and Ethiopia.

Capacity development

Training of scientists and technicians became an immediate ILRAD contribution, given the time needed for research results. Moreover, creating a well-trained alumnus was important if ILRAD was to extend its research findings across Africa. Accordingly, technicians received bespoke training in partnership with the Kenya Agricultural Research Institute and the University of Nairobi. Technicians from East Africa were trained, with ambitions to extend opportunities to francophone and anglophone West Africa. Courses on theileriosis, trypanosomiasis and immunology were offered to associates and veterinary graduates. ILRAD alumni ultimately made major contributions to investigations of trypanosomiasis and bovine immunology (see Chapters 2–4, this volume).

The International Livestock Centre for Africa

The CGIAR Task Force's site recommendation was for Addis Ababa, Ethiopia, or Yaoundé, Cameroon, with the former being the apparent preference because Ethiopia had the largest cattle population in Africa and a 'wide range of ecological conditions' according to the Tribe report (Tribe *et al.*, 1973, p. 45). Further advantages of Ethiopia were its emergence as a hub for international institutions and the fact that hosting both ILRAD and ILCA in anglophone countries would have been politically unacceptable. ILCA was established in 1974 in Addis

Ababa, Ethiopia, with the first phase of its campus inaugurated in 1980.

Priorities

ILCA had a similar genesis to ILRAD – the idea of applying science to agriculture, in a public institution, with wide international collaboration, and with the expectation of stable core funding. ILCA's founding premise was that solutions to Africa's livestock problems existed, but productivity had not grown because of a 'failure to integrate the biological, economic and sociological components of research and development programmes' (Tribe *et al.*, 1973, p. 1). The Tribe report stated (p. 31):

> Technical answers are available to many of the specific problems facing livestock development in Africa. The major constraint lies rather in the difficulty of introducing change into existing socio-economic systems, combined with inexperience in adapting technologies to suit local conditions.

The initial job of ILCA became one of assembling multidisciplinary teams to study physical and economic constraints to livestock development. A basic choice of ILCA's mandate was to work only on ruminants and only in sub-Saharan Africa. Some work on camels began in the early 1980s and had significant capacity development effects, but the original ruminant mandate of ILCA and ILRAD changed little until the 1995 merger into ILRI.

ILCA was quite different from ILRAD. It worked on many problems where ILRAD worked on only two. It focused on creating new field knowledge, and on mapping existing information, instead of creating new laboratory knowledge, by reviewing literature, by evaluating development projects and by conducting new surveys (Tribe *et al.*, 1973, p. 192). ILCA grew out of systems thinking and out of work recognizing the importance of indigenous knowledge, as opposed to the laboratory approach of ILRAD.

The Tribe report proposed (p. 31):

> Having established broad frameworks for systems studies ... a more analytical phase will soon follow, which will both identify areas of specific ignorance which deserve priority

attention in future surveys and research, and suggest new or amended systems of animal production... Such techniques and systems will almost certainly require validation and further investigation, either at the Centre itself or within a cooperative programme at national stations, so that a constant interplay can be expected between research and development planning.

The initial work was diagnostic, developing a 'problem analysis' as a basis to formulate improvement packages at the farm level, undertake more intensive studies, experiment on components and assess alternative systems. Accordingly, sub-Saharan Africa was divided into three broad agroclimatic zones, first by Beck and later by ILCA scientists – arid, humid and highland – which were the sites of ILCA's initial systems research. Multidisciplinary teams, based in Nigeria, Ethiopia, Kenya and Mali, subsequently prepared systems surveys in four agro-climates[17]:

- The middle highlands (near Debre Zeit) and upper highlands (near Debre Berhan) of Ethiopia, where mixed crop–livestock farming was dominant.
- The subhumid zone in north-central Nigeria, around Kaduna, to cover mixed crop-and-livestock farming in the humid and subhumid regions.
- The semi-arid zones in Botswana, north-central Mali (near Niono) and later in south-western Niger, to cover agropastoral systems in the arid and semi-arid rangelands; and the semi-arid pastoral zone in Kajiado County, Kenya, known as the Maasailand study area.
- The humid zone of south-western Nigeria, near Ibadan.

Resources[18]

ILCA spent about US$374 million (in constant 2015 US dollars) from 1975 to 1994 (Fig. I.7). ILCA spent about US$16.9 million annually from 1975 to 1987 (the latter is the date of the second EPMR) and another US$22.0 million annually from 1988 to 1994. ILCA's real spending over its lifetime was about 43% more than that of ILRAD in its lifetime. One reason was that ILCA had a broader scientific mandate than ILRAD. A second was that the Tribe report (Tribe
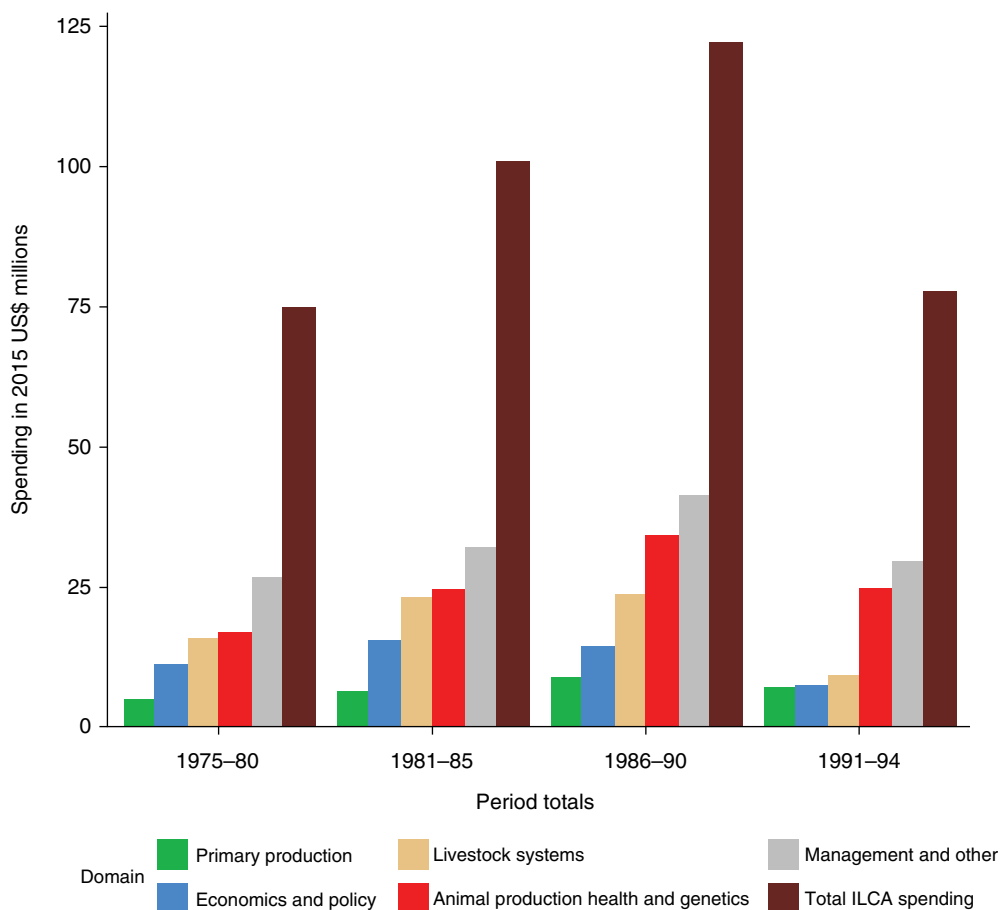
Fig. I.7. ILCA spending by research domain and period, 1975–1994. Total ILCA spending of US$374 million in 2015 US$. (Data from ILCA Annual Reports, various years.)

et al., 1973, pp. 1 and 102) had proposed a decentralized structure at ILCA; ILCA therefore created subcentres at Kaduna, Ibadan, Bamako and Nairobi, in addition to the three Ethiopian sites at Addis Ababa, Debre Zeit and Debre Berhan, thus increasing its total costs compared with those of ILRAD with its one Nairobi site.

Scientific spending was about 77% of ILCA's total from 1975–1994, of which 12% was devoted to capacity development; the balance was spent on management, administrative and support services. ILCA lifetime spending shares by domain were: (i) livestock systems, 19% (much of which was at sites outside Ethiopia); (ii) economics and policy, 13%; (iii) primary production, 7%; (iv) animal genetics, health and production, 27%; (v) capacity development, 12%; and (vi) management and administration,

23%. There were no important differences in those shares over subperiods of ILCA's 20 year existence. A crude attribution of ILCA's spending by country is: Ethiopia, 70% of the total from 1980–94; Ibadan, Nigeria, 3%; Kaduna, Nigeria, 5%; Niono and Bamako, Mali, 10%; Nairobi, Kenya, 10%; and the sum of other Africa countries plus occasional work in Asia, Latin America and the Caribbean, 1%[19].

Institutional evolution

The findings of ILCA's QQR covering the period 1975–1981 and issued in 1982 (CGIAR/TAC, 1982) differed sharply from those of ILRAD. The panel concluded that ILCA's research was of poor quality and its management was worse.

The QQR recommended that ILCA move away from 'systems description' and towards component analysis. The panel argued that the identification of constraints had been done and that the logical next step was to develop technical options to overcome these constraints. These were especially important as early research had showed that, contrary to the erroneous assumptions of the founding Tribe report, introduced technologies offered no significant advantages over traditional methods given the economic and ecological constraints facing producers (Gryseels and Anderson, 1983, for highland Ethiopia; Cossins and Upton, 1987, and Cossins and Upton, 1988a,b, for the Borana rangelands in southern Ethiopia; Wilson *et al.*, 1983, Wilson, 1986, and Wagenaar *et al.*, 1986, for central Mali).

ILCA's research gradually evolved to focus on component technical changes to release system constraints. These included the following:

- Highlands (Debre Zeit and Debre Berhan, Ethiopia): cross-bred cows for dairying, single-oxen traction, simple mechanization to improve the drainage of waterlogged soils, and establishment of a forage gene bank in 1983.
- Subhumid (Kaduna, Nigeria): making better use of indigenous feeds, establishment of 'fodder banks' of leguminous pasture for dry-season grazing, crop rotations with cereals and legumes, and nutrient cycling alternatives with crop residues and animal manures with work on both large and small ruminants.
- Semi-arid (Niono, Mali; Niger; Kenya; Ethiopia): selective harvesting and handling of crop residues to improve livestock nutrition and soil management, water and grazing management, and on-farm fattening of ruminants.
- Humid (Ibadan, Nigeria): alley cropping with leguminous fodder trees and trypanotolerant stock, which focused mainly on small ruminant production (ILCA, 1979a,b).

The second phase of ILCA – roughly 1981–1987 – saw a strengthening of the central research units, including the Livestock Economics Unit, the Small Ruminant and Camel Group, and the Forage Agronomy Section. There was an expansion of the Livestock Productivity and Trypanotolerance Group, which formed part of the ATLN jointly coordinated by ILCA and ILRAD. The network established study sites under different levels of tsetse challenge and trypanosomiasis risk in West Africa (Côte d'Ivoire, the Gambia, Togo and Zaire) and East Africa (Ethiopia and Kenya).

The second EPMR of ILCA (CGIAR/TAC, 1987) was again quite critical of ILCA's performance. In fact, the second EPMR was drafted but withheld from publication by TAC until the new ILCA management could prepare a 'long-term strategy as a basis for setting of short and medium-term priorities' (CGIAR/TAC, 1987,

Table I.1. ILCA priorities around the time of its first formal strategy in 1987.

Field	Budget shares, 1988–1993	Publication shares, 1975–1994	Citation shares, 1975–1994
Cattle	27	40	44
Small ruminants	18	21	32
Animal traction	17	4	10
Feed and animal nutrition	14	37	5
Trypanotolerance	13	19	15
Economics and policy	11	13	32

Publication shares are numbers of ILCA publications by field, divided by the total number of all ILCA publications in all fields; citation shares are numbers of citations of ILCA publications by field, divided by the total of citations of ILCA publications in all fields. Publication and citation shares add up to more than 100 because multiple citation classes per publication occur often.
Sources: Budget shares for 1988–1993 were calculated from data in the 1993 EPMR (CGIAR/TAC, 1993b, p. 68). Publication and citation shares were calculated from the Scopus and Google Scholar databases for the 406 published papers (publications database updated through March 2020) in which at least one member of ILCA staff participated as an author of any rank (e.g. first author, third author, etc.).
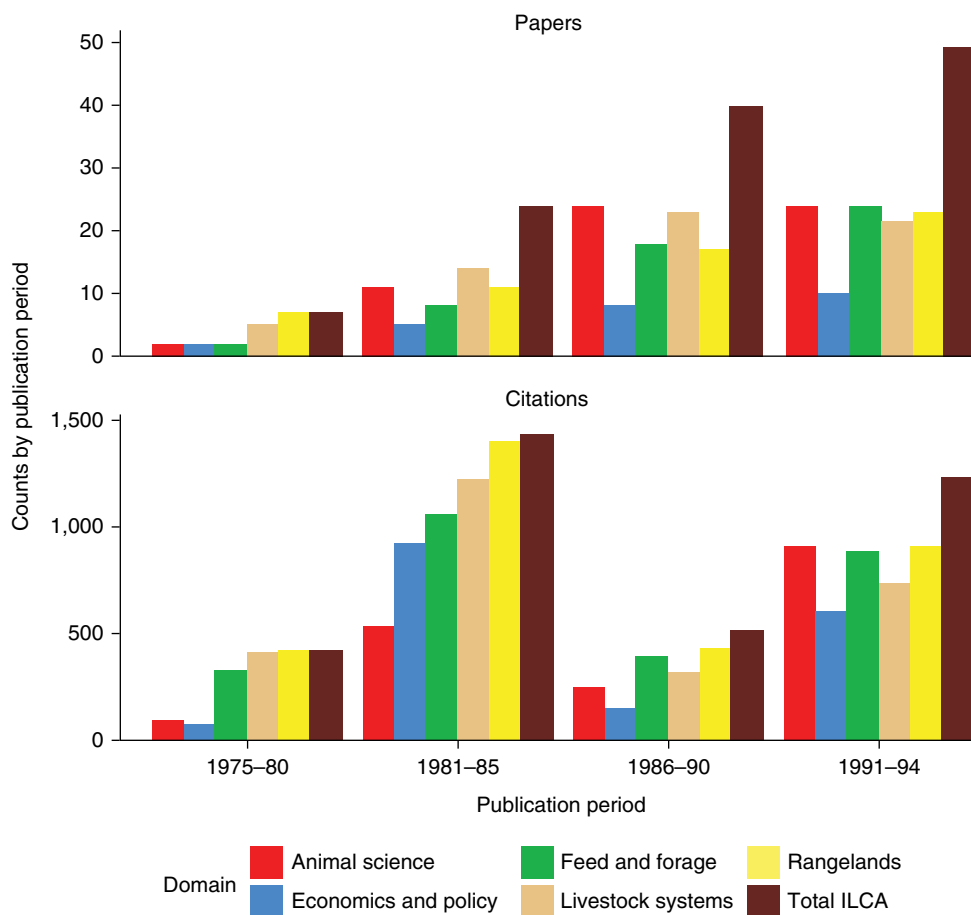
Fig. I.8. ILCA publications by research domain and period, 1975–1994. Sample size of 406 papers. (Data from www.scopus.com and www.scholar.google.com.)

p. 10). The second EPMR did not recommend that the centre change its mandate, which remained limited to sub-Saharan Africa and to ruminants. The review did insist that ILCA 'should focus its research activities ... and avoid spreading its resources too thinly' (CGIAR/TAC, 1987, p. 10).

A fourth senior management team arrived at ILCA in November 1986. It prepared a scientific strategy in 1987 (Table I.1). The strategy organized its work into six 'thrusts': three 'commodity thrusts' – cattle milk and meat, small ruminant meat and milk, and animal traction – and three 'strategic thrusts' – animal feed, trypanotolerance, and livestock policy and resource use. This structure and strategy remained in place until the merger with ILRAD in 1995.

Achievements

Figure I.8 summarizes the chief achievements of ILCA in its 20 years. A bibliometric analysis, using the Scopus publications and Google Scholar databases, was done as described in Box I.2.

These achievements were as follows[20]. Animal genetics and health:

- Contributions with ILRAD and national partners in elucidating the genetic and physiological basis of trypanotolerance in African livestock and identifying conditions in which those stock could be more productive (ILCA/ILRAD, 1988; Rowlands and Teale, 1994).

Publications as a measure of scientific impact apply to many research projects because the latter produces knowledge that may never have been translated into economic output. Examples of such knowledge are understanding soil nutrient management on small farms or mapping vector behaviour across farming environments. While it is possible to attribute costs to research programmes, the problem of estimating benefits to outputs from those programmes has typically proven intractable in most of the work done at ILRI and its international partners in livestock research.

One solution to the problem of assigning benefits to knowledge outputs is to estimate the numbers of papers published and citations per paper using 'bibliometrics' tools (Aria and Cuccurullo, 2017). A related tool is Altmetric (www.altmetric.com/; accessed 13 March 2020), which uses a briefer period of analysis but takes a broader view of the form of scientific impact as it includes social media, which bibliometrics generally does not. Papers and citations are a measure of scientific productivity and an – admittedly imperfect and partial – indicator of the potential economic gains from research. In the Prefaces to each part of this volume, we present analyses of published papers and citations with the purposes of estimating the relationship between scientific output and research cost and of situating ILRI's published outputs in the African and global contexts.

- An analytic review of the determinants of the reproductive performance of African Zebus (Mukasa-Mugerwa, 1989).

Primary production:

- Identification of potential technical changes in grazing and water management (Borana and Maasailand), in alley farming with leguminous trees (humid west-central Africa), in sown forages (subhumid west-central Africa) and in herd and flock management (semi-arid Mali), the integration of livestock into mixed farms through semi-arid and subhumid Africa, and research on the role of women in pastoral and mixed agropastoral farming systems.
- Extended knowledge of the range ecology in East Africa and across the continent (ILCA, 1975).

- Complete novel feed quality and animal nutrition research (Reed *et al.*, 1988, 1990), which later led to a classification of nutritional toxicology in forage legumes (Reed, 1995).
- Building the forage gene bank and herbage seed unit (see Chapters 12 and 13, this volume).

Livestock systems:

- Characterization of the principal animal production systems of sub-Saharan Africa (Jahnke, 1982).
- Complete innovative systems studies of grazing (Mali, Kenya, lowland Ethiopia) and mixed systems (Kaduna, Ibadan, highland Ethiopia).
- Explaining the successes and failures in pastoral development in poor countries, with a focus on sub-Saharan Africa (Sandford, 1983a) and many papers in the African Livestock Policy Analysis Network (ALPAN) and Overseas Development Institute (ODI) Pastoral Networks.
- Analysis of the resources, constraints and potential for livestock water in sub-Saharan Africa (Classen *et al.*, 1983; King, 1983; Sandford, 1983b).
- Explanation of the evolution of African mixed farming systems in terms of land use and technology choice (McCown *et al.*, 1979; McIntire *et al.*, 1992).

Related scientific impacts were: predictions of system evolution from the climate change literature, particularly warnings about the more rapid conversion of grazing systems into mixed farms in East and West Africa (see Chapter 15, this volume); and on the effect of population growth on tsetse infestation (see Box I.1).

Much of ILCA's scientific legacy was in characterizing African livestock systems and in making predictions of system evolution, particularly about the more rapid conversion of grazing systems into mixed farms in East and West Africa (see Chapter 15, this volume).

Systems evolution

Beginning with the work of Hans Jahnke on *Tsetse Flies and Livestock Development in East Africa* (Jahnke, 1976) and continuing with Jahnke's milestone book (Jahnke, 1982) on *Livestock Production Systems and Livestock Development in*

Tropical Africa, ILCA scientists and partners described the evolving role of animals in African grazing and mixed farming systems. Prominent works in the early history of ILCA included studies on pastoralism and on the role of water in livestock development (Sandford, 1983b). Work on farming systems across sub-Saharan Africa by ILCA, or in collaboration with ILCA, included Pingali *et al.*, (1987) on agricultural mechanization and McIntire *et al.* (1992) on crop–livestock integration. A major piece in the area of land management was the work by Powell *et al.* (1995) on livestock and nutrient cycling in mixed farming areas. The impact of these books was to describe the constraints to technical change and to set the physical, demographic, economic and agronomic boundaries with which higher productivity could be achieved in the principal mixed crop–livestock systems of Africa.

Systems characterization

As discussed in Chapter 15 (this volume), initial systems studies consisting of field surveys and data analysis led by ILCA, with varying collaboration with national and international institutions, defined the principal constraints to animal production. These included low dry-season feed quantity and quality, inadequate water supplies, and competition between people and calves for limited milk supplies in arid pastoral systems. Animal diseases, poor feed quality and low soil fertility were barriers to higher productivity in humid and subhumid zones. Availability of animal draught power, high mortality of young stock, liver fluke in sheep, inefficient water conservation and utilization, and inadequate supplies of protein supplements were noted in highland zones.

The main scientific accomplishments were as follows:

- Characterization of mixed farming systems in semi-arid central Mali (Wilson, 1986), the Inner Delta of the Niger River in semi-arid central Mali (Wagenaar *et al.*, 1986), in subhumid central Nigeria (von Kaufmann *et al.*, 1986), and two sites in the highlands of Ethiopia (Gryseels and Anderson, 1983).
- Characterization of grazing systems in Kenya ('Maasailand', Kajiado County, Kenya; Bekure *et al.*, 1991) and in southern Ethiopia ('Borana'; Coppock, 1994).

- Advances in forage agronomy in Ethiopia, Nigeria and Mali, related to the systems studies, based on a combination of on-station and on-farm trials (Kang *et al.*, 1990; Powell *et al.*, 1995).
- Defining the research inputs needed to raise productivity of animal traction among smallholders in Ethiopia and Mali, including the adaptation of a broad-bed maker for vertisols in central Ethiopia.
- Estimating the trade-off between meat and milk production in grazing systems in Kenya, Ethiopia, the Gambia (Agyemang *et al.*, 1993, 1997), Mali (Wagenaar *et al.*, 1986) and Botswana (Cartwright *et al.*, 1982).
- Elucidating the interactions between small ruminant parasitology and leguminous trees in alley farming systems for humid West Africa (Kang *et al.*, 1990).
- Creating the first ley farming model in the lowland tropics of sub-Saharan Africa (von Kaufmann *et al.*, 1986), which integrated *Stylosanthes hamata* cultivars into fodder banks for cattle.

Trypanotolerance

The joint ILRAD/ILCA African Trypanotolerant Livestock Network (ATLN) began in 1979 after background studies in sub-Saharan Africa. By 1986, under the leadership of John Trail at ILCA and Max Murray at ILRAD, it had analysed data on tsetse group and challenge level, livestock species, and type and management regime from 11 sites in seven countries of humid and subhumid West and Central Africa (ILCA, 1994, pp. 69–75). Important results were found on the genetics, diagnosis, pathology and management of trypanotolerant livestock under varying conditions of trypanosomiasis challenge, as summarized in ILCA/ILRAD (1988).

The principal landmarks in trypanotolerance research, done jointly by ILCA and ILRAD in collaboration with national and international programmes in sub-Saharan Africa, were as follows:

- Understanding the genetics and pathology of trypanotolerance (ILCA/ILRAD, 1988; Rowlands and Teale, 1994; also Chapters 2, 3 and 4, this volume).
- Developing a comprehensive model – genetics, vector control and disease management –

for using trypanotolerant stock (Rowlands and Teale, 1994).

• Devising the first empirical benefit–cost analyses of the combined use of trypanotolerant animals and chemotherapy based on reliable productivity in several situations in sub-Saharan Africa (Itty, 1992).

Forage gene bank and herbage seed unit

ILCA created the forage gene bank in Ethiopia in 1983. From an early stock of some 10,000 accessions in 1986, the collection had grown to over 18,600 in 2017. An herbage seed unit was established in 1989 to enhance forage use in sub-Saharan Africa, given the evident fact that seed was a constraint to adoption of new forages.

The scientific impact of the forage gene banks, including those at ICARDA and CIAT, has been strong (Amri *et al.*, 2018, for ICARDA; Schultze-Kraft and Peters, 2017, for CIAT; Labarta *et al.*, 2017 for CIAT; Lynam and Byerlee, 2017 for CIAT; see Chapter 12, this volume). Scientific impacts included: (i) an understanding of the distribution and biology of tropical forages; (ii) germplasm management in relation to production constraints, such as establishment; and (iii) use of modern genetic tools to elucidate phylogenetics.

Feed quality and nutrition research

ILCA reported:

> Studies on the nutritive value of feeds covered not only traditional forages but also crop residues and foliage and seeds of browse trees. A major research area was in identifying polyphenolic compounds in crop residues and browse and determining their effects on feed intake and utilisation. ... Assessments of the nutritive value of browses was largely directed at determining the content and effects of polyphenolic compounds in different browse species and accessions.
> ILCA (1994, pp. 146 and 149).

Related work on forage agronomy, including grasses and legumes, was done at several sites in Nigeria (von Kaufmann *et al.*, 1986; ILCA, 1994, pp. 121–124), Ethiopia (Kahurananga, 1987) and Mali (ILCA, 1994, pp. 56–58). ILCA also made significant advances in knowledge of ruminant nutrition under tropical conditions, notably by showing the effects of phenolics in the digestibility of roughages, in quantifying the value of crop residues in cereal and legume improvement programmes (Reed *et al.*, 1988), and in later work on the toxicology of phenolics in tropical legumes (Reed, 1995).

Merger of ILRAD and ILCA into ILRI, 1995

Discussions in the early 1970s considered and rejected the option of one institution, although it was widely believed that the two centres would eventually merge. The QQR of ILCA (CGIAR/TAC, 1982, p. 5) considered the relevance of a 'change in the relationship of ILCA and ILRAD' but saw no need for a 'change in the structural relationship between the two centres' (CGIAR/TAC, 1982, p. 69). The second EPMRs, respectively, of ILRAD (CGIAR/TAC, 1993a) and ILCA (CGIAR/TAC, 1993b) agreed that the two should not be joined, although this view soon changed.

The second EPMR of ILRAD (CGIAR/TAC, 1993a) was generally positive about ILRAD's work in its first two decades. While praising the research of ILRAD, it took a cautious approach about the probability of success with a vaccine against trypanosomiasis; it did advocate, however, a production facility for an ECF vaccine. It recommended that the lessons from research on theileriosis and trypanosomiasis be applied to new diseases such as heartwater and anaplasmosis. It said that ILRAD should gradually extend its work outside sub-Saharan Africa. The report did not recommend a merger between ILRAD and ILCA.

The second EPMR of ILCA (CGIAR/TAC, 1993a) was again critical of the quality of ILCA's research and management. The review, unlike the second EPMR of ILRAD, argued that ILCA's mandate should be narrowed, given the difficulty of managing such a complex institution across several subregions of sub-Saharan Africa. The second EPMR of ILCA again rejected a merger, while agreeing to 'appropriate collaborative projects' between ILCA and ILRAD (CGIAR/TAC, 1993b, pp. ii and x).

Following the 1993 EPMRs of ILRAD and ILCA, the TAC undertook another global priority setting exercise in 1992–1993 (CGIAR/

TAC, 1994). It compared the CGIAR's research investment to the value of production of the major food commodities. This analysis suggested more resources for resource management, policy research and germplasm conservation. Following the TAC priority exercise and taking note of CGIAR investment in livestock research and of the second EMPRs of ILCA and ILRAD, TAC agreed that the centres should remain separate while expanding 'ecoregional programmes' to join crop-and-livestock work in a systematic way.

Despite TAC's views against a merger, as expressed in the second EPMRs and in the priority setting exercise, external opinion was building in favour of a merger for programmatic and managerial reasons. An external assessment of animal agriculture in sub-Saharan Africa (Winrock

International, 1992) argued for tighter research focus in ILCA with the implication that this could be achieved by incorporating the animal health work of ILRAD.

A CGIAR Steering Committee on Livestock Research was formed in 1993 to 'identify priority activities for international livestock research, which would be managed through a single institution and be constrained by the current proportion of CGIAR resources allocated to livestock' (ILCA, 1994, pp. 2–3). The steering committee subsequently recommended the creation of a new, consolidated centre. CGIAR approved the steering committee recommendation at its meeting in October 1993. CGIAR later requested a Rockefeller-appointed task force (an 'implementing agency') to develop
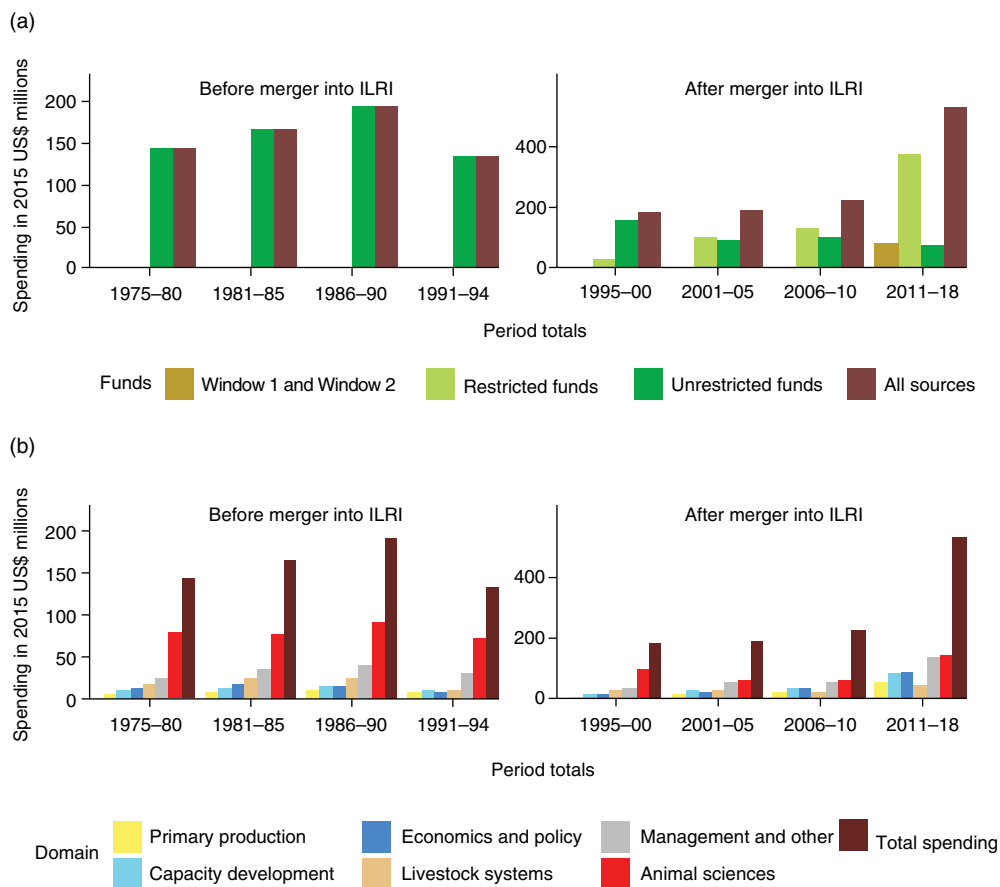
Fig. I.9. ILRI spending by source of funds and period (a) and by research domain and period (b) 1975–2018. Lifetime (1975–2018) spending of US$1753.2 million, in 2015 US$ millions. (Data from ILRI Annual Reports and Financial Reports, various years.)

a unified strategy for global livestock research to be conducted within CGIAR by the merged ILRAD and ILCA. This implementing agency in 1994 developed a medium-term strategy and a strategic plan for the new CGIAR global livestock research institution – ILRI, which was legally established in September 1994 and began work in January 1995.

New priorities at the merger

The nascent ILRI shifted from an exclusive focus on sub-Saharan Africa to a global one under a rapid projected growth in budget. The indicative medium-term plan for ILRI (CGIAR/TAC, 1994a, p. 30) projected that ILRI staff would expand from 88 scientists (100% in sub-Saharan Africa) in 1994 to 107 scientists (81% in sub-Saharan Africa, 11% in Asia, 5% in Latin America and the Caribbean (LAC), and 3% in West Asia and North Africa (WANA) by 1998. Starting from a combined 1994 (ILCA and ILRAD) nominal budget of US$24.8 million, CGIAR projected that ILRI's budget would grow by 25% to 1998 (CGIAR/TAC, 1994a: Table 5).

Despite optimistic budget projections at the launch of ILRI, the merger coincided with a fall in budget from an annual average of US$36.4 million (constant US$2015) in 1988–1994 to an average of US$31.5 million in 1995–2001. The 1995–2001 core budget fell from 89% of the total from 1995 to mid-year 1998 to 69% from mid-year 1998 to 2001. The falling trend in unrestricted resources continued until 2011 when core budget was eliminated across all centres (Fig. I.9a).

The ILRI 2000–2010 Strategy (ILRI, 2000, p. 68) forecast regional shares to be: sub-Saharan Africa 64%, LAC 6%, WANA 2%

and Asia 28%, in a projected 2010 budget of US$47 million. The budget targets for the first decade of the 21st century were met, but projected regional shares for 2010 were not achieved; the great majority of ILRI's budget in the years 2000–2010 was spent in sub-Saharan Africa, as had always been the case for ILCA and ILRAD, and the Asia staff never exceeded 5% of the total.

Species mandate

TAC's commentary on the first EPMR of ILRI (CGIAR/TAC, 2000) only advised ILRI to consider work on non-ruminants, seeking impact on small producers in Asia while using results, where relevant, from its ruminant research. The 2000–2010 Livestock Strategy (ILRI, 2000, p. 68) forecast a non-ruminant share of 10% for the 2010 budget (in a projected total of US$47 million), but this was not achieved. The share of swine and poultry research in ILRI papers grew from roughly zero in the mid-1990s to a cumulative share of about 3% by 2016. Research on non-ruminants consisted mainly of poultry pathology in the first decade after the merger with later work on poultry genetics, the immunology and pathology of African swine fever (ASF), food safety risks related to non-ruminants and value chain analytics.

Scientific priorities

The merger and the more restrictive budget meant a change in priorities. Rough estimates of the priorities of ILCA and ILRAD before the merger can be created, from budget data and from publications and citations data (Table I.1)[21]. Subsequent ILRI priorities (Table I.2) are some-

Table I.2. ILRI planned budget by CGIAR allocations, 1999–2003. (From ILRI, 2000, Table 2.)

Field	Shares, % of 1999–2003 planned budget
Improving productivity (total)	58
Germplasm	9
Production systems	49
Protecting the environment	12
Saving biodiversity	7
Improving policies	9
Strengthening national agricultural research systems	15

what difficult to compare on spending because of changes in institutional structure and spending reporting but can be compared more easily on output metrics, such as papers and citations. Figure I.9(b) shows ILRI spending in the principal fields of 'animal sciences', 'economics and policy', 'systems', 'feed and the environment', 'capacity development' and 'other' over its entire history.

Resources

The ILRI Medium-term Plan 1998–2000 proposed budgets in terms of CGIAR resources allocation categories at the time. It declared post-merger priorities in terms of 'products', including the following:

- Ruminant genetics (mapping the bovine genome; identifying areas of the mammalian genome that control trypanosomiasis).
- Ruminant health (laboratory culture for growing trypanosomes *in vitro*; immunity work on ECF; genetic map of *T. parva*; community trypanosomiasis control in Ethiopia; better estimates of the economic impacts of trypanosomiasis and tick-borne diseases).
- Ruminant feed resources (distributing materials to the national programmes; identifying more productive forages through selection; analysing the use and quality of crop residues).
- Crop–livestock systems (characterizing the major African systems; quantifying nutrient exchanges among crops, animals and soils; reducing range degradation).
- Strengthening collaboration with national programmes (training; bibliometrics; collaborative research).
- Regions outside Africa projected to grow from about 20% of the research portfolio in 1996 to about 30% in 2000.

An estimate of priorities after the merger can be derived from the ILRI Medium-Term Plans (e.g. ILRI, 2000), the first EPMR of ILRI (CGIAR/TAC, 2000), the second EPMR of ILRI (CGIAR/TAC, 2008) and from publications after 1994. Table I.2 shows ILRI's projected budget after the merger.

Reorientation of ILRI after 2000

In the early part of this century, ILRI underwent four transformations. First, it began to explicitly address poverty, which had not been a major research theme before 2000, largely in response to donor demands for more immediate impact and to join the spirit of the recently announced Millennium Development Goals. The goal of research grew beyond higher productivity – it became the broader development goal of 'better lives through livestock'. Landmark books by Perry *et al.* (2002) and Thornton *et al.* (2002) established empirical relationships among agricultural environments, livestock production, animal health and poverty.

Second, there was a shift from laboratory-based animal science working on genetics and immunopathology to field-based animal science focusing on veterinary epidemiology with new programmes in food safety, zoonoses and emerging infectious diseases. At the same time, the work of the institute expanded to include research on swine, poultry and previously understudied diseases such as ASF, contagious bovine pleuropneumonia (CBPP) and contagious caprine pleuropneumonia (CCPP). Work in this century on zoonoses, food safety, and transboundary diseases became prominent and replaced much of the earlier laboratory work on a trypanosomiasis vaccine and on trypanotolerance.

Third, was the emergence after 2000 of a new field – the interactions between livestock and climate change. This field had been a small share of the ILCA/ILRAD portfolio and of the ILRI portfolio before the turn of the century. Since about 2000, research on climate change has become a fairly large share of the institute's work, and papers in this field have been among the most cited of ILRI's outputs.

A fourth shift was towards becoming a service provider. In 2002, ILRI began to host the Biosciences eastern and central Africa (BecA)-ILRI Hub whose purpose was to become a biosciences centre of excellence for East and Central Africa. As such, the BecA-ILRI hub would provide capacity development services for regional scientists in the biosciences related chiefly to agriculture and the environment.

Part of the shift towards service provision was a new orientation to work directly in

development projects. Budget shifts, beginning in the mid-1990s and accelerating until about 2010, were associated with a change from core (untied) resources to special projects (tied) resources. These changes in total funding and in its composition induced a move away from longer-term research, for example on vaccines, parasitology and genetics, to more short-term research and to more engagement in development projects in the hope of short-term benefits. Part III of this book, with chapters on systems research and policy, evaluates the effects of the shift in orientation from research to development.

A millennial change related to shifts in portfolio was in information and communication technology (ICT). ICT has also, of course, been transformational with regard to science and allows communications among scientists and research that would have been impossible recently. Examples are lowered costs of collaboration with partners in Africa and on other continents and lowered costs of scientific analysis, such as gene sequencing of plants, animals and pathogens. These lowered costs have allowed more efficient collaboration and increased the scientific productivity of research spending. The scientific impact of modern ICT has been high at ILRI and its partners by allowing more rapid analysis of data and communication of results. The direct development impact related to ILRI's use of ICT is unknown, but broader development impacts are obviously large.

The reform of CGIAR

The gradual reduction of core funding (Fig. I.9a) that had begun around the time of the merger, continued in the first decade of the new century, and culminated in 2011 with the elimination of core funding. The reform of CGIAR, beginning in about 2011, reversed the trend of declining overall funding but at the cost of a complex and burdensome systemic change that changed the allocation and composition of funding and the structure and type of research.

A second major change in 2011 was the advent of the CGIAR research programmes (CRPs). These organized much of CGIAR research into 16 programmes, each being a multicentre consortium (in most cases with non-CGIAR partners). The former core funding was now channelled through the CRPs as programmatic funding. Although the CRPs had been designed on the assumption that 50–60% of the funding would be provided as programmatic funding with the balance being from bilateral projects, this never happened, and the programmatic funding declined from about 40% of ILRI's budget in 2012 to about 20% in 2018. Bilaterally funded projects now make up most of the portfolio of the CRPs. Seven programmes were commodity based, three focused on environment and natural resource management, three dealt with agricultural systems in different agroecological zones, one dealt with policies, institutions and markets, one with agriculture, nutrition and health and one supported the 11 gene banks in CGIAR.

ILRI was engaged in seven CRPs. It led a CRP on Livestock and Fish, with WorldFish, CIAT and ICARDA as partners, and was a partner in Climate Change, Agriculture and Food Security (CCAFS), Agriculture for Nutrition and Health (A4NH), Policies, Institutions and Markets (PIM), Dryland Systems, Humidtropics and Genebanks. While the CRPs were effective at fostering collaboration, the transaction costs of being engaged in many CRPs were high for ILRI and for the other centres.

A second phase of the CRPs started in 2017, with a reduced number (12 plus three platforms – Big Data, Excellence in Breeding and Genebanks). The need to reduce transaction costs, coupled with the observation from an independent review (CGIAR/ISPC, 2014) that CGIAR livestock research was dispersed across many CRPs, led to the consolidation of livestock research. Livestock work was concentrated in one Livestock CRP, led by ILRI, from 2017. ILRI was still engaged in CCAFS and A4NH and has selective involvement in PIM and the three platforms. As the CRPs were designed as long-term programmes, it is too soon to judge their development impact, although the first evaluation of the Livestock and Fish CRP was generally positive.

ILRI's second-generation research extended its work on animal disease, especially in veterinary epidemiology, although it abandoned field work on trypanotolerance in the later 1990s and did less on identifying constraints through the earlier systems studies. At the same time,

Table I.3. Principal achievements of ILRI research, 1975–2018.

Domain/sub-domain	Field/system	Era	Achievements
Animal health and genetics			
Cattle genetics	Bovine genome	1990s–present	Mapping of the bovine genome (Barendse *et al.*, 1997; see Chapter 1, this volume)
			Genetics of African pastoralism (Hanotte *et al.*, 2002)
			Genetic structure of cattle breeds (Bovine HapMap Consortium, 2009).
Genetics of trypanotolerance and trypanosomiasis	Subhumid and humid Africa	1990s–present	Quantitative trait loci controlling trypanotolerance in N'Dama and Borana (Hanotte *et al.*, 2003; see Chapters 1–3, this volume)
			Genetics of the infection response to *Trypanosoma congolense* (Noyes *et al.*, 2011)
			Genes controlling resistance to trypanosomiasis in mice (Kemp *et al.*, 1997)
			Cloning Boran cattle (Yu *et al.*, 2016)
Diagnostic methods	Diagnostics; *in situ* phenotyping tools	2000s	Use of SNP tools for *in situ* characterization of smallholder livestock
			Description of African bovine genome
Sheep genetics	Sub-Saharan Africa; highland Ethiopia	Recent	Genetic history of African sheep and full genetic characterization of Ethiopian sheep
			Inter-breed differences in resistance to endoparasites
Yak genetics	Mongolia and Russia rangelands	2000s	Molecular characterization of yak genomes
Genetics of ASF	Sub-Saharan Africa	2000s	Genome sequencing of ASF (Bishop *et al.*, 2015)
	Swine pathology including ASF		Has very high development potential
Control of trypanosomiasis	GIS methods for mapping control methods: trypanocides, tsetse control, and trypanotolerant animals		Trypanocide resistance in West Africa (Affognon *et al.*, 2009; Clausen *et al.*, 2010)
	Sources of trypanocide resistance; control of resistance		
Vector biology	Tick dynamics	1980s–present	Less emphasis on tick and tsetse biology after merger
			Acaricide resistance, (see Chapter 10, this volume)
			Possible field impact through tsetse control (Leak, 1999)
			Ticks (see Chapter 10, this volume)
			Population growth and tsetse dynamics (Reid *et al.*, 2000)
Veterinary epidemiology	LGA, LGH, LGT, MRA, MRH, MRT	1995–present	Problems of scale, policy changes and technical changes (see Chapters 5–7 and 9, this volume)

ECF ITM		1970s–present	
	Identification of the polymorphic immunodominant molecule of *Theileria parva*		See Chapter 6 (this volume)
			Potential vaccine development
CBPP and CCPP			Potential vaccine development
Peste des petits ruminants			High development potential of a thermostable vaccine (Mariner *et al.*, 2017)
Heartwater control	LGH, MRH	1990s	See Chapter 5 (this volume)
Highly pathogenic avian influenza	Diagnostic and surveillance tools	2000s	Mariner *et al.* (2014)
Zoonoses and emerging infectious diseases	Global analysis of 13 zoonotic diseases	2010s	Policy, capacity, priority setting and control methods (Grace *et al.*, 2012; see Chapter 8, this volume)
Food safety	Surveys of main risks; identification of risk profiles and prevention methods		Policy, capacity and priority setting (Grace *et al.*, 2012; see Chapter 9, this volume)
Rift Valley fever	Economic analysis of control options	2010s	See Chapters 5 and 7 (this volume)
	Mapping of disease	2010s	Rich and Wanyoike (2010)
Economics of animal health and disease	Modelling economics of parasitic diseases	1990–present	Perry and Randolph (1999)
Primary production			
Forage gene bank	Global tropics (LGA, LGT, MRA, MRH, MRT, MIA, MIH, MIT)	1995–present	Materials collected, characterizations partly completed and wide distribution
	Sub-Saharan Africa, WANA, LAC		More than 70,000 accessions in ILRI, CIAT and ICARDA forage gene banks
			More than 60% of collections characterized on morphology
			New information generated on conservation and production characteristics
Herbage seed unit	Global tropics (LGA, LGT, MRA, MRH, MRT, MIA, MIH, MIT)		More than 138,000 samples distributed
Multidimensional crop research	India and Ethiopia, MRA, MRH, MRT, MIA, MIH, MIT	1999–present	Quality factors identified in pearl millet, sorghum and maize (see Chapter 14, this volume)
			Used in Indian national breeding programmes
			Importance of new multidimensional model for cereals selection and breeding.
			Finding variation in crop residue quality; near-infrared spectroscopy methods
Planted forages	Sub-Saharan Africa; South Asia; tropical LAC		Forage development strategies produced (see Chapter 13, this volume)
			Wide uptake of forages by commercial farmers in LAC

Continued

Table I.3. Continued.

Domain/sub-domain	Field/system	Era	Achievements
Livestock systems, economics and policy	LGA, LGT, MRA, MRH, MRT, MIA, MIH, MIT	1990s–present	Baltenweck *et al.* (2003)
			Nutrient cycling and allocation (Powell *et al.*, 1995)
	East Africa		Understanding complementarities between wildlife and domestic stock
	Arid/semi-arid Niger, LGA, MRA	1990s and 2000s	Hiernaux and Ayantunde (2004); Hiernaux *et al.* (2009)
			Grazing management
			Geography of crop–livestock interactions.
Humid zones	Alley farming	Abandoned in 2000s	Plant yields, animal nutrition and nutrient cycling
Subhumid zones	Borana and Kaduna	Abandoned in 1990s	
Kenya coast	Mombasa dairying (MRT)	1990s and 2000s	Nicholson *et al.* (1999)
Highlands	Kenyan dairy policy (MRT, MRH)		See Chapter 17 (this volume)
	East Africa poverty mapping (MRT, MRH)		See Chapter 17 (this volume)
	Ethiopia dairy experiments (MRH)		See Ethiopia dairy impact studies discussed in Chapter 17 (this volume)
Kenya index-based livestock insurance	Arid, semi-arid Kenya (LGA)	2009–present	Created analytic, empirical and operational basis of an index-based livestock insurance instrument (Chantarat *et al.*, 2013)
Global environment			
Crop yield and environmental indices	Maize yield modelling	2000–present	Climate change impacts on maize in Africa and LAC (Jones and Thornton, 2003)
	MarkSim model	2000–present	Software to generate daily climate data in sub-Saharan Africa and LAC,
Climate change	Livestock technology and policy	2000–present	Characterization, policy guidance and estimates of mitigation and adaptation effects; see Chapter 16 (this volume)
			Livelihood transitions between cropping and herding.
			Identification of climate and livestock productivity relationships (see Chapter 16, this volume).
			Identification of mitigation and adaptation options.

ASF, African swine fever; CBPP, contagious bovine pleuropneumonia; CCPP, contagious caprine pleuropneumonia; ECF, East Coast fever; GIS, geographic information system; ITM, infection-and-treatment method; LGA, livestock/grazing/arid; LGH, livestock/grazing/humid; LGT, livestock/grazing/tropical highlands; LAC, Latin America and the Caribbean; MIA, mixed, irrigated, arid/semi-arid; MIH, mixed, irrigated, humid/subhumid; MIT, mixed, irrigated, temperate; MRA, mixed, rainfed, arid/semi-arid; MRH, mixed, rainfed, humid/subhumid; MRT, mixed, rainfed, temperate; WANA, West Asia and North Africa; SNP, single-nucleotide polymorphism.

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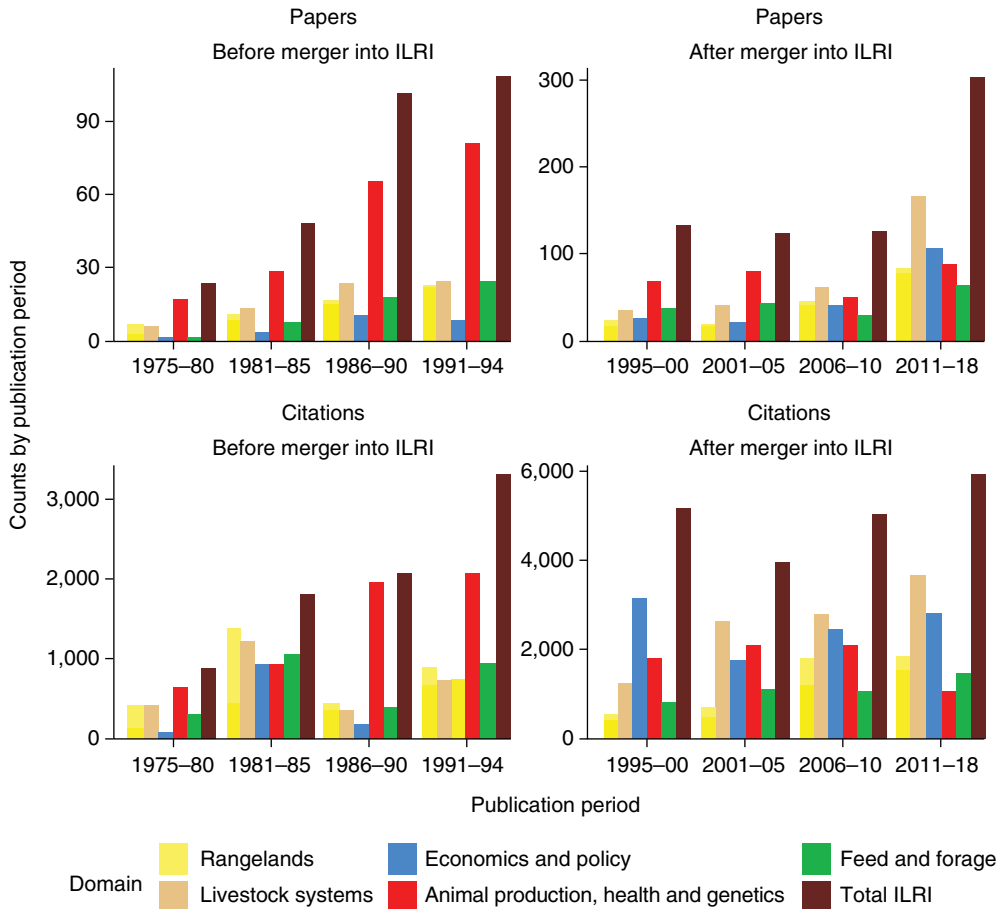
Fig. I.10. ILRI publications by research domain and publication period, 1975–2018. Sample size of 4,367 papers. (Data from www.scopus.com and www.scholar.google.com).

ILRI became a global centre and posted scientists to Latin America, East Asia and India. The Latin American programmes and several Asian programmes were short lived. The principal sustained effort outside sub-Saharan Africa was the programme on multipurpose crops at ICRISAT in Hyderabad[22]. ILRI created a model of 'livestock as a pathway out of poverty', doing less on production constraints and more on large-scale systems analysis and on the animal link to climate change.

Achievements, 1975–2018

We organize the discussion of ILRI's principal scientific achievements as outlined in Table I.3,

by the three parts of this volume: (i) animal genetics, production and health; (ii) primary production; and (iii) livestock systems, including economics and policy, climate change and gender (Fig. I.10).

ILRI's scientific spending was about 77% of its total from 1995 to 2018, of which about 11% was devoted to capacity development. Spending by scientific domain over ILRI's lifetime has been: (i) livestock systems, 10%; (ii) economics and policy, 11%; (iii) primary production and the environment, including climate change, 6.4%; (iv) animal genetics, health and production, about 39%; (v) capacity development, 11%; and (vi) management, administration and technical support, 23%.

Animal genetics, production and health

Trypanosomiasis and trypanotolerance

Our best estimate of trypanosomiasis spending is US$234 million (US$5.3 million annually), which is approximately 13% of the ILCA/ILRAD/ILRI total from 1975 to 2018 (see Preface to Part I, this volume). That investment led to many notable achievements:

- Characterization of the pathology of trypanosomiasis, trypanotolerance and *Theileria* and description of related immunological problems (see Chapters 2–4, this volume).
- Definition of molecular markers for trypanotolerance (see Chapter 2, this volume).
- Identifying genes controlling resistance to trypanosomiasis in mice (Kemp *et al.*, 1997).
- Describing the genetics of infection response to *T. congolense* (Noyes *et al.*, 2011).
- Showing the steps in cloning Boran cattle (Yu *et al.*, 2016).
- Establishment of protocols for cultivation *in vitro* of bloodstream stages of *T. brucei* and subsequently *T. congolense*.
- Recognition that trypanosome strain complexity and surface coat antigenic variation precludes development of an effective conventional vaccine that targets the immunodominant coat antigens.
- Developed a comprehensive suite of monoclonal antibodies that identified the major bovine T-cell subpopulations, immunoglobulin isotypes, phagocytic cell populations, several bovine lymphocyte antigens (BoLAs; also called major histocompatibility complex (MHC) antigens, and the circumsporozoite coat of *T. parva* sporozoites used in host-cell invasion.
- Development and maintenance *in vitro* of clones of bovine CD4^{+} and CD8^{+} T-cells that facilitated analysis of monoclonal antibody specificity, investigation of *T. parva* antigenic diversity, and *T. parva* peptide–BoLA complexes that induce *T. parva* strain- and host MHC-specific protective immunity.
- Elucidation of host immune responses that control the frequency, magnitude and duration of African trypanosome (and *T. parva*)

parasitaemic episodes in cattle and in Cape buffalo.
- Trypanocides and vector resistance to trypanocides; field studies in Ethiopia, other East African nations, and in West Africa, which developed cost-efficient models of trypanocide use.
- Definition of the epidemiology of trypanosomiasis (see Chapters 5 and 6, this volume).

No realistic overall economic analysis is possible of trypanosomiasis and trypanotolerance research at ILCA/ILRAD/ILRI. None the less, this work has produced economic benefits in several areas:

- Generating information about the profitability of trypanotolerant stock – economic analysis done in the ATLN (a joint effort of ILCA and ILRAD) showed internal rates of return ranging from 15 to 53% (see Chapter 3, this volume; Itty, 1992) at seven subhumid and humid sites of sub-Saharan Africa.
- Producing information about drug resistance and optimal drug treatment regimens under various levels of tsetse and trypanosomiasis challenge.
- Work led by partners, gathering information valuable for targeting tsetse and trypanosomiasis control by disease pressure and type of treatment.

Theileriosis (see Chapters 5, 6 and 10, this volume)

The closest estimate we can make of theileriosis spending is US$181 million (US$4.1 million annually), which is approximately 10% of the 1975–2018 total for ILCA/ILRAD/ILRI (see Preface to Part I, this volume). This investment resulted in:

- Genetic characterization of *T. parva* strains.
- Publication of a landmark book (Norval *et al.*, 1992), which has become the global reference on the epidemiology of theileriosis.
- The sequencing of the *T. parva* genome (Gardner *et al.*, 2005). This was the second apicomplexan to be sequenced and was essential in screening for cytotoxic T-lymphocyte antigens.
- An understanding of tick distributions and their determinants, allowing cheaper and

more effective vector control through acaricides and grazing management.

- Models of vector distribution that allowed better targeting of vector controls (Duchateau *et al.*, 1997).
- Application of molecular technologies to improve the scientific understanding of ticks and tick control, including capacity development for a new generation of scientists.
- Further development of the ITM method of vaccinating cattle against ECF, as discussed in Chapter 6 (this volume). Chapter 6 of this volume presents a model of ITM use in Kenyan cattle, stratified by production system. Results from that model show benefit:cost ratios to ILRAD/ILRI research in the range of 1.6–16.5 under justifiable assumptions about vaccine adoption and mortality avoided and with use of actual data on output prices and quantities.
- There are two other results of ILRI research on ECF for which economic analysis is impossible but which probably produced development benefits: (i) influencing the government of Ethiopia about the risk of *R. appendiculatus*, which led to a change in Ethiopian policy on live cattle imports from Kenya; and (ii) development of sustainable tick control strategies for field application in most of the East African countries where ECF is present.

Achievements in other fields of animal genetics and health (see Chapters, 5–9, this volume)

The closest estimate we can make of spending on animal genetics, production and health other than projects clearly labelled as 'trypanosomiasis' or 'theileriosis' is US$261 million (US$6 million annually), which is approximately 15% of the 1975–2018 total.

- Creating a genetic linkage map of the bovine genome (Barendse *et al.*, 1997).
- Analysing the genetics of African pastoral cattle (Hanotte *et al.*, 2002).
- Elucidating the genetic structure of cattle breeds (Bovine HapMap Consortium, 2009).
- Presenting the genetic history of African sheep and full genetic characterization of Ethiopian sheep.

- Identifying inter-breed differences in resistance to endoparasites in small ruminants.
- Creating and developing the Domestic Animal Genetic Resources Information System (DAGRIS), a web tool for indigenous farm animal genetic resources (Ayalew *et al.*, 2003; Hanotte *et al.*, 2010).
- Using single-nucleotide polymorphism (SNP) tools for *in situ* characterization of smallholder livestock.
- Estimating the relationships between poverty and livestock in a spatial framework (Barendse *et al.*, 1997; Perry *et al.*, 2002).
- Modelling the economics of parasitic diseases (Perry and Randolph, 1999).
- Long-term support to participatory epidemiology and participatory disease surveillance in Kenya, including its use in control of avian influenza and Rift Valley fever. Later efforts developed global capabilities in the management of zoonoses, through participatory epidemiology techniques in Egypt, Indonesia, Nigeria and Pakistan. ILRI has published a landmark review (Grace *et al.*, 2012), which is now a global reference on the subject.
- Innovative work on food safety in sub-Saharan Africa and South-east Asia, notably on aflatoxins, including publication of a major book on Africa (Roesel and Grace, 2014; Chapter 9, this volume).
- Achieving thermostability in the existing peste des petits ruminants virus vaccine (Jones *et al.*, 2016; see Chapter 7, this volume).
- Defining a model of CBPP (Mariner *et al.*, 2006; Jores *et al.*, 2013; see Chapter 7, this volume).
- Analysing acaricide resistance in ticks (see Chapter 10, this volume) and trypanocide resistance in trypanosomes (see Chapter 3, this volume).
- Advances in the genetics and epidemiology of several important transboundary diseases (see Chapter 7, this volume), notably for ASF, including:

  - Isolation and genetic characterization of CBPP and ASF with better understanding of related disease dynamics and of immunity in African breeds and European breeds.
  - Developing a new vaccine challenge model for CCPP, improved diagnostics for

CBPP and ASF, and using synthetic biology to identify vaccine candidates.
- Modelling of the dynamics of ASF, CBPP and rinderpest, and investigating reservoirs of ASF and rinderpest and the role of carriers in ASF.

Primary production

The best estimate we can make of spending on 'primary production' – broadly defined as work on primary production of four broad types – rangeland production systems, forage diversity, planted forages, multidimensional crops – is US$111 million (US$2.5 million annually), which is approximately 6.4% of the 1975–2018 total. Achievements in the field of primary production are covered in Part II (see Chapters 11–14, this volume):

- Completing landmark studies of grazing systems in Mali, Niger, Ethiopia, and Kenya (see Chapters 11, 15 and 16, this volume).
- Elucidating the competition between domestic livestock and wildlife in East Africa (see Chapter 11, this volume).
- Expanding the forage gene bank, involving the collection and characterization of nearly 20,000 accessions, and distributing approximately 18,600 accessions and distributing some 138,000 samples to more than 180 countries (see Chapter 12, this volume).
- Contributing modestly to the development of improved forage cultivars for tropical smallholders, while adding much more to the characterization of forage options for diverse tropical farming systems.
- Completing work on multidimensional crops (cereals, legumes and oilseeds), with important global results in research methods and in distribution of materials to national and regional programmes (see Chapter 14, this volume).
- Estimating the development impact of planted forages for smallholders, notably fodder banks in the West African subhumid systems (see Chapter 13, this volume).

Livestock systems, the global environment and gender

An upper bound estimate of ILRI lifetime spending on livestock systems has been about US$177

million, or 10% of the 1975–2018 total of US$1.75 billion. This spending double counts some work done in the 'primary production' domain, specifically on rangelands systems, but this has been unavoidable. Achievements from this spending include:

- Characterizing the principal grazing and mixed livestock systems in sub-Saharan Africa (Wilson *et al.*, 1983; von Kaufmann *et al.*, 1986; Wilson, 1986; Bekure *et al.*, 1991; McIntire *et al.*, 1992; Coppock, 1994; Hiernaux and Ayantunde, 2004).
- Defining nutrient cycling functions in mixed and grazing systems (Powell *et al.*, 1995; Buerkert and Hiernaux, 1998; Giller *et al.*, 2011).
- Estimating crop–livestock interactions across continents (Baltenweck *et al.*, 2003).
- Delineating the relationships between livestock and poverty (Thornton *et al.*, 2002; Randolph *et al.*, 2007).
- Completing characterization of a mixed farming and grazing system in semi-arid western Niger where rural poverty and land degradation are acute (Hiernaux and Ayantunde, 2004; Hiernaux *et al.*, 2009).

Livestock and the global environment

ILRI's limited investment in global environmental research has been very productive in this century and the institute is now a world leader in this area. Achievements include:

- Mapping livestock systems – scope, productivity, potential for growth and relationship to income poverty – refinement of greenhouse gas emission estimates by systems (Seré *et al.*, 1996; Kruska *et al.*, 2003; Robinson *et al.*, 2011).
- Analysing the interaction between livestock and the global environment (Reid *et al.*, 2000; Thornton *et al.*, 2009; Herrero *et al.*, 2013).
- Quantifying the greenhouse gas emission mitigation potential of tropical livestock systems (see Chapter 16, this volume).
- Significant contributions to understanding policy measures to mitigate climate change or to adapt to its effects in livestock systems (see Chapter 16, this volume).

- Under the leadership of CIAT, identifying sources of biological nitrification inhibition in *Brachiaria* spp. (Subbarao *et al.*, 2006, 2009).

Economics and policy

ILRI lifetime spending on economics and policy research has been about US$198 million since 1975, or 11.3% of the 1975–2018 total of US$ 1.75 billion. ILCA/ILRAD/ILRI research has contributed to the understanding of policy determinants and applications (see Chapter 17, this volume), especially on grazing systems, water development and management, and public finance. Achievements include:

- Contributing to the global movement to reduce policy barriers to growth of African agriculture (see Chapter 17, this volume).
- Providing the analytic base and advice (Kaitibie *et al.*, 2010) for the reform of Kenyan dairy marketing, producing national benefits in net present value terms of US$230 million (see Chapters 9 and 17, this volume).
- Description of policy responses to the rapid expansion of global livestock trade beginning in the 1990s (Delgado *et al.*, 1999).
- Developing the analytic and operational basis of an index-based livestock insurance policy, which is now in commercial use in eight counties of Kenya (Chantarat *et al.*, 2013; and, most recently, Jensen *et al.*, 2019); a major achievement of the IBLI work is the collection and publication of unusually rich household data and many high-quality papers, over several years, without which policy making is impossible.
- Estimating the rate of return to research and development costs of the broad-bed maker tool (Rutherford *et al.*, 2001; Rutherford, 2008; see Chapter 15, this volume) in Ethiopia.
- Advancing the introduction of a gender perspective into programmes across CGIAR, which forced changes in the design and conduct of research programmes that lessened the bias against the economic potential of women, which is particularly acute in the livestock sector given the importance of animal production to women's wealth and income.

Impact Analysis

The thematic chapters in Parts I–III of this volume analyse the impact of international livestock research in the areas led by ILRI and its partners, including other centres working on livestock.

Each chapter first presents an executive summary, which is a concise non-technical statement of the principal problems, scientific impacts and development impacts and, where information was available, an estimate of expenditures at ILRI and its predecessors in the given field. The chapters continue with a review of the history of research at ILRI and its collaborators, of the main achievements, and an analysis of how those achievements were translated into scientific and development impact.

Each chapter answers some common questions:

- What were the research problems?
- How relevant were those problems? For example, did ILRI and its predecessors work on the scientific problems with the highest potential scientific and development returns?
- What were the principal scientific achievements?
- What were the principal development achievements?
- What were the principal capacity development achievements?

In answering these questions, each chapter presents a history of the research and its principal findings. Each history examines the results of ILRI and its predecessors, with this concentration being obviously more thorough in the chapters on trypanosomiasis, ECF, ticks, zoonoses and other themes that were rarely or never studied by other IARCs. There is also an analysis of the problems studied – for example, animal health, farming systems characterization, primary production, livestock and climate change, animal genetics, bovine immunology, the control of trypanosomiasis, the behaviour and control of ticks, forage crop improvement and others – as constructed from the publications of the institutions and of collaborators. Each section presents briefly the resources invested – money, scientists and sites – where it has been possible to reconstruct the financial and staff data in adequate detail.

The book broadly defines two types of impact:

- *Scientific impact*, as indicated by papers, citations and specific achievements as shown in Box I.2.
- *Development impact*, as indicated by net *ex post* economic benefits of given technologies (e.g. the ITM vaccine against ECF and the broad-bed maker tool in highland Ethiopia), of policy reforms promoted by ILRI (e.g. the Kenya dairy market), by poverty effects (the numbers of people lifted out of poverty) and capacity development effects.

Limitations of Citation Indices

Publications databases, such as Scopus, Google Scholar, and Web of Science, have common limitations. The metadata submitted to journals are sometimes incomplete or in various formats. The algorithms used to generate the databases are naturally imperfect, and their outputs are not always completely comprehensive or accurate. The databases do not always cover all journals. Some papers, even from high-impact journals, escape the search algorithms. An important shortcoming of the Scopus databases used in this volume is that they give a biased underestimate of citations of many older ILCA and ILRAD books (e.g. Wilson, 1986, on livestock in central Mali; von Kaufmann *et al.*, 1986, on mixed grazing and livestock systems in central Nigeria; ILCA/ILRAD, 1988, on livestock in tsetse-affected areas) and even some of the most important ILRI works (Norval *et al.*, 1992; Perry *et al.*, 2002; Thornton *et al.*, 2002) These forms of sampling bias affect the evaluation of impact of ILRI work over time and with respect to other scientific centres.

Citation scores can also be influenced by: (i) the age of the paper: older papers obviously tend to accumulate more citations; (ii) field effects: some domains have higher citation scores than others, e.g. mathematics and computer science have fewer citations than molecular biology because the latter tends to have more references per paper; (iii) the type of paper: methodological papers tend to have the highest citations, e.g. Lowry *et al.*, (1951), describing a method to measure protein has more than 250,000 citations

to date and Farrell's (1957) paper on the measurement of productive efficiency has more than 21,000 citations; (iv) the frequency of some keywords, which vary over time with new research technologies, e.g. earlier papers would have fewer hits on 'DNA sequence' and related terms; less obvious is the fact that expressions related to income and wealth ('poverty', 'poor') rarely appeared in ILRI published work before 2000; and (v) double counting of papers among research domains – for example, many papers will hit on 'trypanosomiasis' and on 'bovine immunology'.

Construction of Search Expressions

A database of some 4367 ILCA/ILRAD/ILRI papers was extracted from Scopus, Google Scholar and CGSpace for the period 1975–2018[23]. Citation counts from Scopus were supplemented with counts from Google Scholar for papers that did not appear in Scopus or were obviously undercounted there. The bibliometrix software of Aria and Cuccurullo (2017) was used to generate master lists of search terms from the database. A clustering technique was then applied to the master lists to identify correlations among search terms and to create aggregate expressions from the clusters. The code and data can be found at www.ilri.org/dataportal/impact/bibliometrix.

The analysis of impact uses four models:

- **Literature reviews** by field (e.g. bovine immunology, forage crops, zoonoses, economic and policy research), including analyses of citations. 'Literature' is usually limited to reviewed papers but includes at times other formats, such as newspaper articles, conference papers and social media.
- **Meta-analyses of research and project data**; these are limited because the data are sometimes incomplete or poorly reported, or the experiments were themselves not properly designed for impact analysis.
- **Cost–benefit analyses**; these are few and most are *ex ante*, not *ex post*; even in the Organisation for Economic Co-operation and Development (OECD) countries, with much

more comprehensive information on the conduct and effects of research, individual cost–benefit analyses of livestock commodity or system research are much less common than those for crops despite the economic importance of animal products. There are few African examples of individual commodity or livestock systems research that lend themselves to cost–benefit analysis.

- **Project evaluations of the effectiveness/efficiency/sustainability types**, such as are done in the development banks and in FAO. Such evaluations could be used to measure both scientific and development impact. Project evaluations were, until the past decade, of limited use in the CGIAR context for several reasons. First, most of the centres' budgets were unrestricted until about 2005, making attribution of specific spending infeasible. Second, even where it is possible to attribute results to spending from a given project, results frameworks have rarely been done in a standardized manner, as they are in the development banks. Even when project evaluations are done to scientific standards, the criteria cannot be summed to estimate an aggregate return to a research problem, scientific field or institution.

Acknowledgements

Notes

[1] Spending data for ILCA, ILRAD and ILRI are shown at www.ilri.org/dataportal/impact/finance

[2] A Standing Panel on Impact Assessment (SPIA) 2016 review calculated the following shares of International Agricultural Research Centre (IARC) livestock research spending from 1990 to 2015: ILRI, 91.7%; CIAT; 4.2%; ICARDA, 1.1%; CIP, 0.1% and other (not attributed to a single centre) of 2.8% (Jutzi and Rich, 2016: p. 14, Table 2) in a total of US$948.5 million (current dollars).

[3] Trail *et al.* (1979a,b) were the first major reviews of trypanotolerance and the foundations of the innovative field work of the ATLN. These reviews were a collaborative effort of ILCA, ILRAD, the United Nations Environment Programme (UNEP) and the FAO.

[4] A short summary of CIAT and ICARDA livestock research, based on background papers from CIAT and ICARDA scientists at www.cgspace.com.

[5] To be followed in 1967 by the International Centre for Tropical Agriculture (CIAT, 1973) in Colombia and the International Institute for Tropical Agriculture (IITA) in Nigeria.

[6] J. George Harrar was an agricultural scientist who worked on the original Rockefeller Foundation programme in Mexico and subsequently became president of the foundation.

[7] Pritchard, in an interview (24 February 1991), traced discussions about a forerunner to ILRAD to 1963, following his attendance at a forum that considered a livestock centre for research.

[8] The formal title of the Beck report is 'An International African Livestock Centre: Task Force Report', 15 October 1971.

[9] Influenced by Elvio Sadun, who was designated as founding Director General but died before he assumed the post.

[10] ILRAD's Board of Trustees considered work on African swine fever in 1979 but rejected the idea.

[11] Personal communication to ILRAD's Peter Gardiner in 1991.

[12] It is important to recognize the legacy of EAVRO in developing the infect-and-treat 'Muguga cocktail' ECF vaccine, later taken up by ILRI. This is discussed in Chapter 6 (this volume).

[13] Material in this section is taken from Chapter 6 (this volume) on 'The Management and Economics of East Coast Fever'.

[14] All categories – core scientists, visiting scientists, post-doctorates and research associates – are included. The 1981 quinquennial review of ILRAD noted that the 'number of core scientists is unusually low' (CGIAR/TAC, 1981: p. 26).

[15] The names of the external evaluations of ILRAD and ILCA changed from time to time. The first external evaluation of ILRAD (and likewise of ILCA) was called a 'quinquennial review' (QQR). The second external

evaluation of ILRAD (CGIAR/TAC, 1986a) was called the second 'External Programme Review' and was conducted in parallel to the 'External Management Review' (CGIAR/TAC, 1986b) of ILRAD. The second external evaluation of of ILCA (CGIAR/TAC, 1987) was called the first 'External Programme and Management Review' (EPMR). The third external evaluation of ILRAD (TAC/CGIAR, 1993a) was called the third 'External Programme and Management Review', as was the third external evaluation of ILCA (CGIAR/TAC, 1993b).

[16] These advances are discussed in Chapters 1 and 2 (this volume).

[17] See Chapter 15 (this volume) on 'African Livestock Systems Research'.

[18] Spending is in 2015 US$, unless otherwise stated; any small amounts of ILCA or ILRAD spending before 1975 were added to the 1975 spending.

[19] Data on scientific fields and staff locations are shown in www.ilri.org\dataportal\impact\finance.

[20] ILCA (1994) is a history of ILCA, as written by Paul J.H. Neate; Thornton and Odero (1998) is a compendium of ILCA/ILRAD/ILRI impact studies in various stages of completion to 1998.

[21] ILCA had no formal written strategy for more than a decade after its founding.

[22] ILRI-led research at ICRISAT's Hyderabad, India, headquarters has made significant contributions to estimating the relationships among greenhouse gas emissions and biomass (see Chapter 16, this volume) and to quantifying the feed value of stover in multidimensional crops (see Chapter 14, this volume).

[23] Another 340 papers were published in 2019, but they are excluded from this database because citations data would be incomplete.

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Preface to Part I: Research Spending and Publications on Animal Genetics, Production and Health

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This preface first reviews the estimated spending in the principal fields corresponding to the ten chapters in the domains of animal genetics, production, and health. It then sketches 'scientific impact' as a function of publications and citations of the International Livestock Centre for Africa (ILCA), International Laboratory for Research on Animal Diseases (ILRAD) and International Livestock Research Institute (ILRI) extracted from the Scopus and Google Scholar databases using search keywords relevant to the four fields (Aria and Cuccurullo, 2017).

Research Spending

Data from the financial and annual reports of ILCA, ILRAD and ILRI were used to compile a spending database for 1975–2018. Current spending for each year and institution was assigned to scientific domains using spending detail by project, by scientists' fields of expertise and, sporadically, from cost accounting by the institutions. Current annual spending in US$ was converted to constant annual spending in 2015 US$ using the global manufacturers' unit value (MUV) index.

ILRI and its predecessors, ILCA and ILRAD, made major investments in animal health and genetics (Fig. PI.1)[1]. ILCA and ILRAD scientists working on animal genetics, production and health of all types – notably trypanosomiasis,

trypanotolerance, theileriosis, most commonly known as East Coast fever (ECF), intestinal parasites and, recently, transboundary diseases – committed real spending on animal genetics, production and health of some US$334 million (in 2015 US$) in the 20 years before ILRI, or 50% of the total of the two predecessors to ILRI. Lifetime spending (1975–2018) on animal health and genetics was some US$676 million, or roughly 39% of the total of US$1.75 billion. The mean of real annual spending over the lifetime of ILCA/ILRAD/ILRI was roughly US$15 million. The shares of spending on animal genetics, production and health fell after the mid-1990s; during the period 2011–2018, this share was 42% of the 2011–2018 total of US$529 million as ILRI diversified into other research domains.

Trypanosomiasis

The closest estimate we can make of trypanosomiasis spending is US$234 million (US$5.3 million annually), which is approximately 13% of the total from 1975 to 2018. A paper in the trypanosomiasis field cost about US$334,000 and generated about 77 citations per US$ million. The mean number of citations per trypanosomiasis paper was 26, the median was 15, and the top ten individual papers generated 19% of all citations of ILRI papers in that field (Fig. PI.2a, b). Most ILRI papers (1975–2018) had few
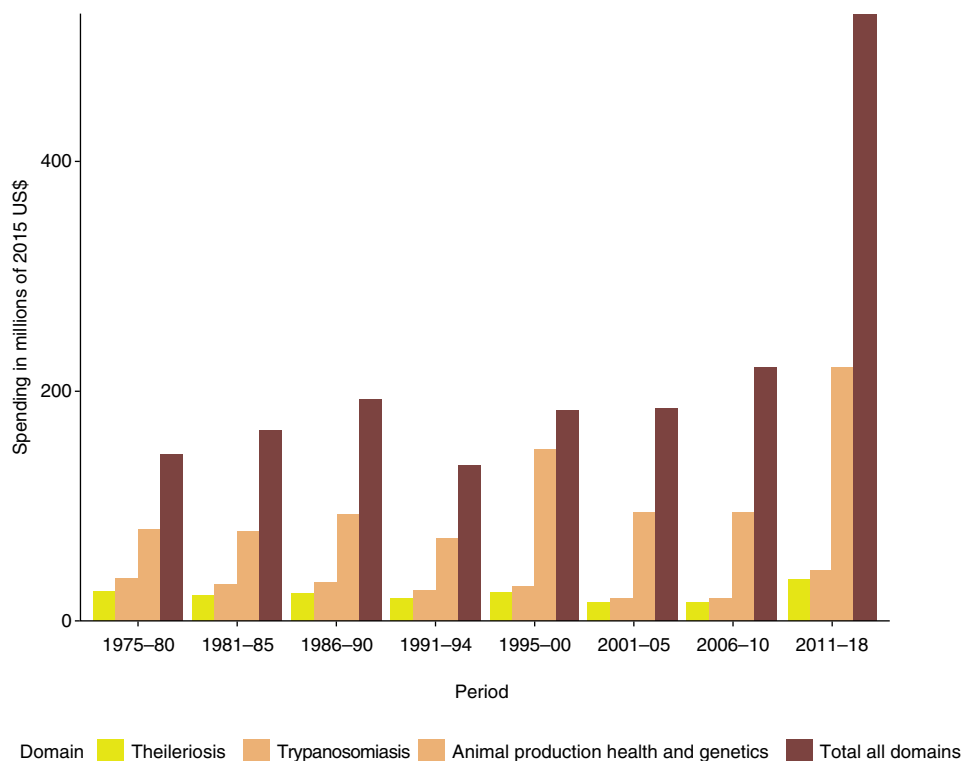
Fig. PI.1. The decreasing importance of ILRI spending on theileriosis and trypanosomiasis, 1975–2018. Data from ILRI Annual Reports and Financial Reports, various years. Total, all domains spending (1975–2018) of US$1753.3 million, in 2015 US$ millions.

citations; for example, 85% had fewer than 41 citations, a share similar to that of global papers on the subject (87%). Trypanosomiasis papers were 16% of all ILRI papers and 17% of all citations. A coarse estimate of ILRI's lifetime contributions to research on animal trypanosomiasis, including work on the tsetse fly vector, is roughly 7% of global papers and 8% of global citations. It is notable that ILRAD and the International Trypanotolerance Centre (ITC) created the modern field of trypanotolerance research, which had been neglected before the creation of ILRAD (Fig. PI.2c); ILRI and its two predecessors contributed 68% of global papers and 91% of global citations in this field (see Chapters 2–5, this volume).

The major papers on trypanosomiasis are older and tend to report advances in methods and in understanding of the basic mechanisms of trypanosomiasis. Highlights include the work of Hirumi and Hirumi (1989) on cultivation *in vitro* of *Trypanosoma brucei*, of Murray *et al.* (1977) and Paris *et al.* (1982) on diagnostic techniques, of Murray *et al.* (1982) on host susceptibility and trypanotolerance, and of Baldwin *et al.* (1986) and Clevers *et al.* (1990) on bovine immunology. Subsequent work focused on estimating the economic burden of trypanosomiasis, on control methods, on understanding and managing trypanotolerance, on projecting the future of the disease. Swallow's (2000) review of trypanosomiasis and African agriculture illustrated the difficulties of estimating the impacts of this disease by summarizing the variability in such basic parameters as morbidity, mortality and calving rates associated with trypanosomiasis. The model of Reid *et al.* (2000) projected that the tsetse fly vector would continue to cover wide areas of sub-Saharan Africa at least until 2040 despite
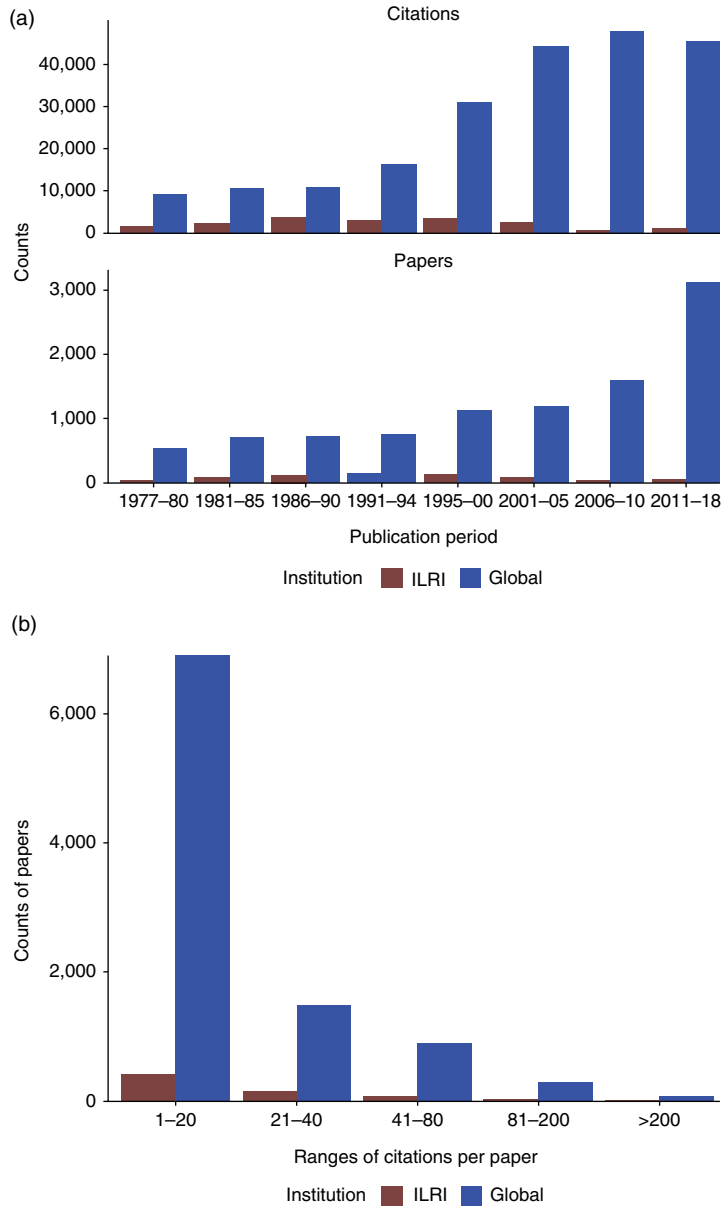
Fig. PI.2. (a) The decreasing ILRI share of global publications on trypanosomiasis, 1977–2018. ILRI sample = 691 papers; global sample = 9,681 papers. (b) Frequency of citations of ILRI and global publications on trypanosomiasis, 1977–2018. Merged ILRI and global sample size = 10,372 papers. (c) Domination of the field of trypanotolerance by ILRI papers, 1977–2018. ILRI sample = 127 papers; global sample = 185 papers. (Data from www.scopus.com/.)

(c)

Citations

Papers
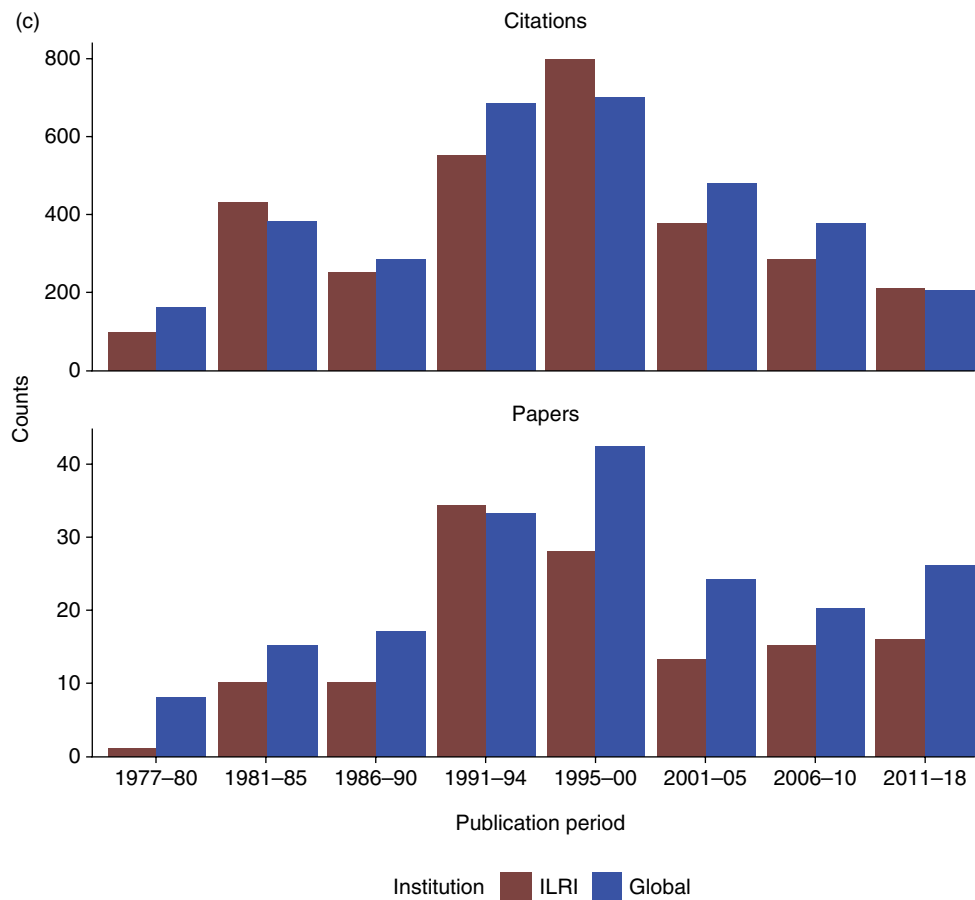
Fig. PI.2. Continued.

dramatically higher rural population density and cropping intensity. The field work reported in Chapters 2 and 3 showed the difficulty of managing trypanosomiasis by controlling vectors with insecticides and by treating infected animals with drugs in the absence of a vaccine.

Theileriosis

The closest estimate we can make of theileriosis spending in the total is US$181 million (US$4.1 million annually), which is approximately 10% of the 1975–2018 total. A paper in the ECF field cost about US$384,000 and generated about 64 citations per US$ million. The mean number of citations per ECF paper was 25, and the median was 14 (Fig. PI.3a, b).

ECF papers were 11% of all ILRI papers and 11% of all citations of ILRI papers. The top ten papers generated 16% of all ILRI papers in the field of ECF. A coarse estimate of ILRI's lifetime contributions to theileriosis research, including work on the tick vector, is roughly 13% of global theileriosis papers and 19% of global theileriosis citations.

Most of the major epidemiology (e.g. Norval *et al.*, 1992, and the work cited in Chapters 5 and 6, this volume) involved the study of *Theileria parva*. Notable advances were made in elucidating the genetics of *Theileria* spp., leading eventually to the sequencing of *T. parva* (Gardner *et al.*, 2005) and of *T. annulata* (Pain *et al.*, 2005). A particular innovation in ILRAD/ILRI epidemiology on theileriosis was the initial development of bioeconomic models of ECF
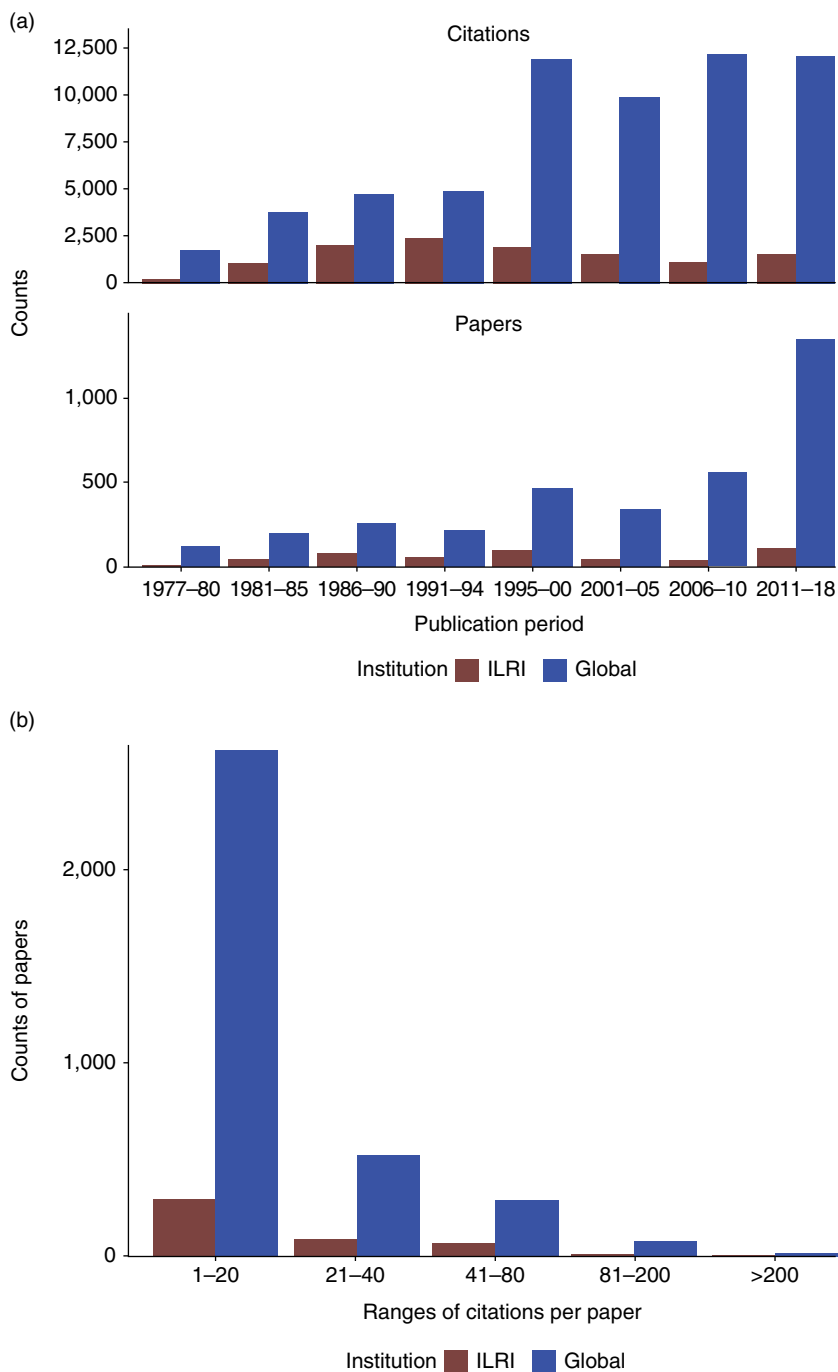
Fig. PI.3. (a) ILRI and other publications on theileriosis and related problems, 1977–2018. ILRI sample = 471 papers; global sample = 3510 papers. (b) Frequency of citations of ILRI and other publications on theileriosis and related problems, 1977–2018. Merged ILRI and global sample size = 3,981 papers. (Data from www.scopus.com/.)

(Mukhebi *et al.*, 1992), integrating field data collection into geographic information systems (GIS) data derived from remote sensing and other sources.

Immunology

Spending on immunology cannot be clearly distinguished from other fields given that it was always integrated into trypanosomiasis and ECF investigations and given that ILRAD/ILRI scientists worked across disciplines. ILRI produced 894 papers on some aspect of immunology, with a mean number of citations per paper of 23 and a median of 14 (Fig. PI.4a, b). Immunology papers were 20% of lifetime ILRI papers and 20% of citations. The top ten ILRI immunology papers produced 10% of ILRI lifetime citations in immunology. A rough estimate of ILRI's lifetime contributions to research on immunology involving human and animal trypanosomiasis and theileriosis is roughly 20% of global papers and 24% of global citations.

The failure to develop an effective vaccine against trypanosomiasis should not prevent recognition of the wide scientific impact of the immunology and immunoparasitology work of ILRAD in its 20 years of life (see Chapter 4, this volume). Although the contribution of published ILRI work to the global effort on animal immunology has weakened noticeably after the mid-1990s, as immunology became a lower priority in the views of ILRI management, those earlier contributions remain important to this day.

Genetics, food safety, transboundary diseases and zoonoses

Spending on the wide domain including animal genetics, food safety, transboundary diseases and zoonoses cannot be quantified accurately. The closest estimate we can make of spending on animal genetics, production and health other than projects clearly labelled as 'trypanosomiasis' or 'theileriosis' is US$261 million (US$6 million annually), which is approximately 15% of the 1975–2018 total. We created an 'other problems' category with keywords for 'zoonoses', 'food safety', 'Rift Valley fever', 'African swine fever', 'peste des petits ruminants' and for several mycoplasmas. The mean of citations per 'other problems' paper was 25 and the median was ten. 'Other problems' papers were 29% of all ILRI papers and 26% of all ILRI citations (Fig. PI.5, b).

The keywords for the genetics field were limited to recent terminology because of the obvious possibility of including practically all papers based on laboratory work. For example, the keyword 'sequencing' in the context of DNA/RNA analysis appears in fewer than 20 papers before the year 2000 but appears frequently after that year. Given the explosive growth in modern genetics, we decided not to estimate a share of ILRI papers in global publications, but it would evidently be quite small given the modest research investment made by ILRI over its lifetime in the genetics subfield. Despite contributing a small share of global publications in animal genetics, ILRI has several landmark papers in that domain, as shown in Chapter 1 (this volume), notably on the history and structure of the bovine genome and on the genetics of trypanotolerance. Swine and poultry genetics have only become more important at ILRI over the past decade, following with a long lag the addition of pigs and poultry to ILRI's mandate in 1995.

The remarkable expansion of ILRI's work on food safety, zoonoses and transboundary diseases in this century, as shown by the spending and bibliometrics data, has not produced a measurable economic rate of return, but it is likely that it will do so soon (see Chapters 7–9, this volume).

One measure of major ILRI scientific contributions is the share of ILRI papers in the top 5% of citations in a given field, compared with the share of all papers – ILRI plus global – in the top 5% (Fig. PI.6). This subsample was limited to papers having at least ten citations. ILRI's global leadership in studies of *Theileria* spp. and of bovine immunology are notable using this metric. The ILRI share of all trypanosomiasis papers was about 9%; the ILRI share of papers in the top 5% of citations was about 6%. The corresponding shares of ILRI papers in the *Theileria* field were 16% and 12%, respectively; the shares were 21% and 13%, respectively, for immunology papers. The heterogeneity of the 'other problems' field made it unrealistic to calculate the place of ILRI papers in the distribution of global publications.

(a)

Citations

Papers

Counts

Publication period

Institution ■ ILRI ■ Global

(b)

Counts of papers

Ranges of citations per paper

Institution ■ ILRI ■ Global
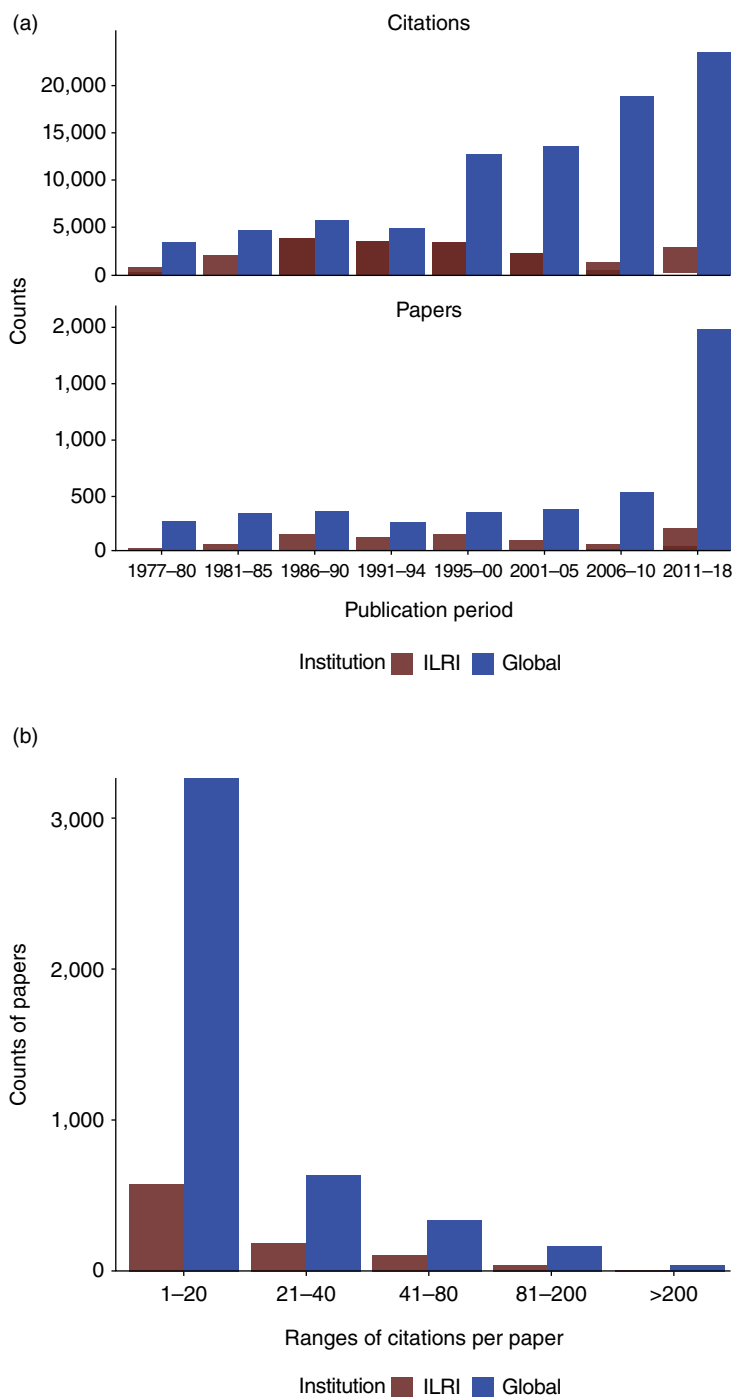
Fig. PI.4. (a) The domination of ILRI papers in global livestock immunology until recently, 1977–2018. ILRI sample = 894 papers; global sample = 4,428 papers. (b) Frequency of citations of ILRI and other publications in immunology, 1977–2018. Merged ILRI and global sample size = 5,322 papers. (Data from www.scopus.com/.)
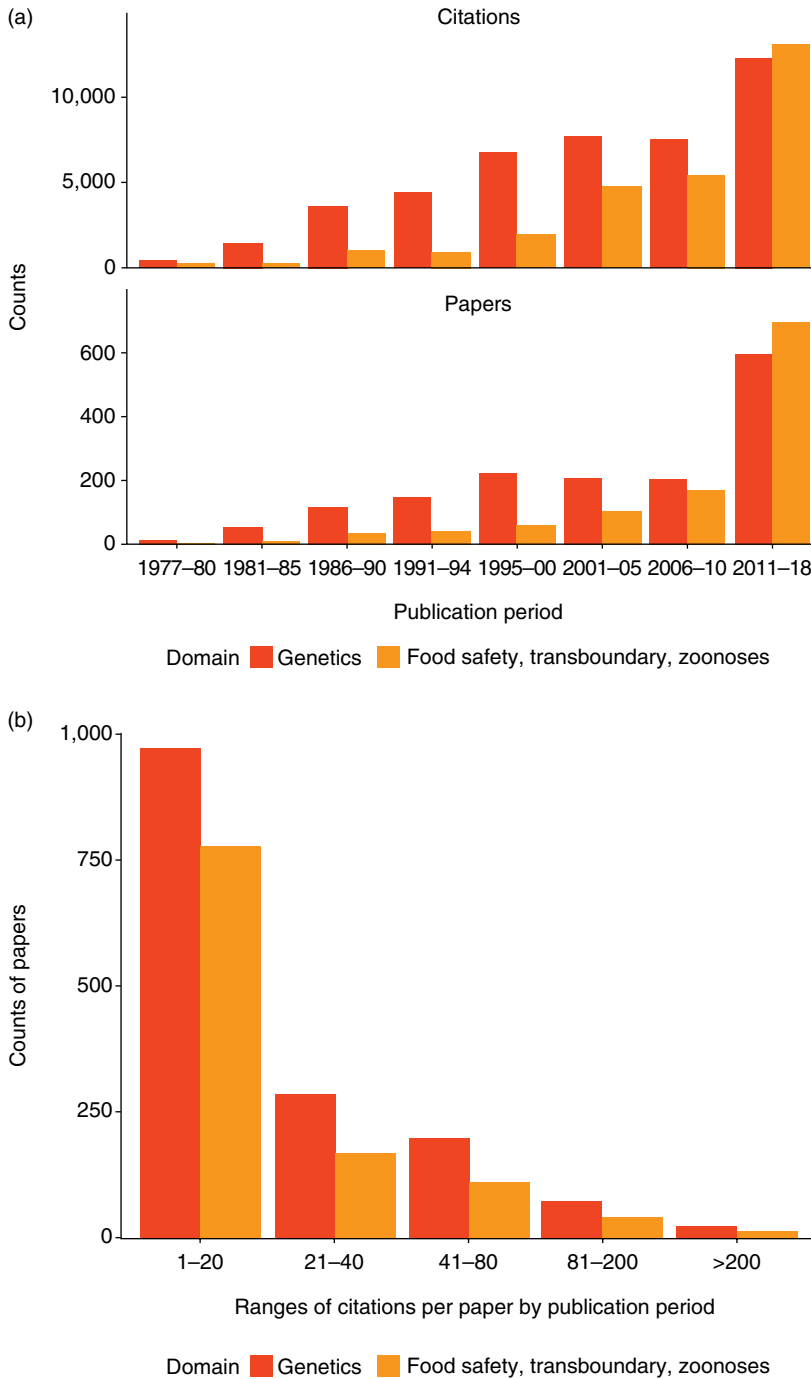
Fig. PI.5. (a) The rapid increase in ILRI papers on animal genetics, food safety, transboundary diseases, zoonoses after the ILCA/ILRAD merger, 1977–2018. Genetics sample = 1,544 papers; food safety, transboundary, zoonoses = 1,108 papers. (b) Frequency of citations of ILRI publication on animal genetics, food safety, transboundary diseases and zoonoses, 1977–2018. Merged sample size = 2,652 papers. (Data from www.scopus.com/.)
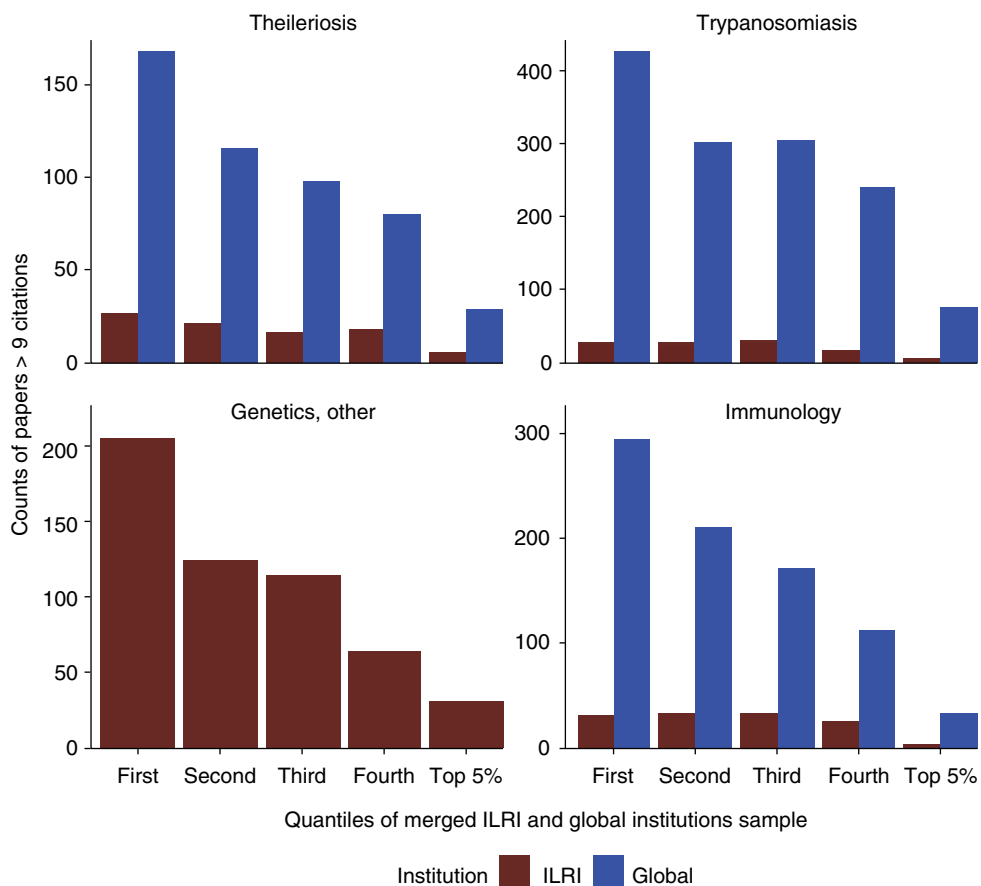
Fig. PI.6. Frequency of citations of ILRI and global institutions in animal health research by quantile, 1976–2018. Sample size = 11,430 papers having at least ten citations. (Data from www.scopus.com.)

Note

[1] Spending data from the International Center for Tropical Agricultural (CIAT) and the International Center for Agricultural Research in the Dry Areas (ICARDA) were not available and are not included in this discussion.

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1 Livestock Genetics and Breeding

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Contents

Executive Summary

Five challenges informed the historical choices of research priorities in livestock genetics and breeding at the International Livestock Research Institute (ILRI). The first challenge was to develop vaccines against two protozoan parasites causing African animal trypanosomiasis and theileriosis (East Coast fever), which led to novel work on cattle genetics. The second challenge, related to the first, was the need to understand trypanotolerance, the genetic ability of some animals to tolerate infection with the trypanosome parasite that causes trypanosomiasis in cattle. The third challenge, which came much later, was understanding the genetics of environmental adaptive attributes (especially diseases and climate challenges) in African livestock and their potential contribution to improving livestock productivity. The fourth challenge, on which ILRI's predecessor, the International Livestock Centre for Africa (ILCA), began work in 1992, was exploiting the potential of the genetic diversity of indigenous African livestock (ILCA, 1992). The fifth challenge was amassing research data on the comparative performance of breeds and genotypes (purebreds and cross-breds) in different production environments to inform cross-breeding programmes.

ILRI's contribution in the global context

The initial work of the International Laboratory for Research on Animal Diseases (ILRAD) concentrated on the genetic aspects of pathology and immunopathology of two major diseases of livestock: African animal trypanosomiasis and theileriosis. ILRI's characterization of animal genetic resources (AnGR), including work on diversity studies, trypanotolerance in cattle and endoparasite resistance in small ruminants, has since created unprecedented levels of awareness in national programmes of the uniqueness and potential of these genetic resources. The greater attention paid to indigenous livestock genetic resources led to more informed interventions to conserve and use these resources. The increased visibility resulted largely from research results, tools and methods by ILRI and its partners. The 'awakening' that ensued has enabled the national agricultural research systems (NARS) of Africa and Asia to play significant roles in expanding the characterization of their native livestock, and this has accelerated the coverage of many livestock populations across these continents.

While ILRI's substantive entry into designing on-farm breeding strategies is more recent, the progress already achieved has demonstrated promising possibilities for setting up working

models that can be used for data and informed breeding programmes leading to long-term genetic improvements within breeds and in cross-bred livestock populations.

According to altmetrics, by 2019, ILRI had contributed to 27% of the global research outputs on African livestock genetics and is a substantial contributor to the Scopus database on African animal genetics in general and on endoparasite resistance in particular. ILRI's classification of African cattle and small ruminant breeds remains a widely used standard reference. Some of the top-cited papers include: Clevers *et al.* (1990) on the bovine antigen structure (97th percentile in Scopus); Barendse *et al.* (1997) on the genetic linkage map of the bovine genome (97th percentile); Hanotte *et al.* (2002) on the genetic history and structure of African livestock (98th percentile); Hanotte *et al.* (2003) on mapping the quantitative trait loci (QTLs) controlling trypanotolerance in an N'Dama × Boran cross; Pain *et al.* (2005) on the comparative genetics of *T. annulata* and *T. parva* (97th percentile); and the Bovine HapMap Consortium (2009) on a genome-wide survey of variation in single-nucleotide polymorphisms (SNPs) and the genetic structure of cattle breeds.

Scientific impacts

ILRI's research findings on the genetics of disease resistance and genome mapping are widely recognized. The institute has made significant contributions to the discovery of candidate genes responsible for the phenotypic variation in livestock diseases and for phenotypic and genetic characterization of indigenous livestock using neutral markers. Together, these contributions have helped unravel the genetic history and geography of African livestock (cattle, sheep, goats, camelids and chickens), and have made significant contributions to our understanding of Asian livestock (yak, camelids, banteng, chickens, cattle, sheep and goats). Many publications of this research are highly cited globally, and the tools and methods are now used across Africa, Asia and other parts of the world.

Livestock genetics and breeding

ILRI delivered 'firsts' in many areas of livestock genetics and breeding. ILRI scientists identified molecular mechanisms and markers for defining trypanotolerant cattle types – polymorphisms that differentiate breeds such as the trypanotolerant N'Dama from non-trypanotolerant African Zebu types. They identified candidate chromosomal regions by mapping second-filial generation (F_2) N'Dama × Boran resource families, and subsequently candidate genes in pathways responding to infection with the causative parasite, *Trypanosoma congolense*, through genetic and expression analysis. This work examined variation in products of the major histocompatibility complex (MHC) loci, biochemical variants of a variety of gene products, and both mitochondrial and nuclear DNA polymorphisms. This work described a strategy for the discovery of candidate genes responsible for phenotypic variation in trypanotolerance, paving the way for subsequent expression analysis, *in vitro* testing of candidate pathways, genome mapping and population genetic work. Anticipating that identification of causative trypanotolerant genome mutations in cattle would come to light shortly, as such mutations had already been identified in wild species, ILRI led the cloning of the first African indigenous transgenic livestock by somatic cell nuclear transfer using primary embryonic fibroblasts. Tumaini (Kiswahili for 'hope') is the result – a Kenyan Boran bull born on ILRI's research facility in Nairobi. This cloning success has opened up the possibility of genetically engineering African livestock using foreign genes for desired traits (such as disease resistance) through genome editing at the fibroblast level followed by somatic cell nuclear transfer.

Genetic characterization and history of livestock

ILRI delivered the first comprehensive classification of African cattle breed and strain groups, including the status of their risk of extinction, and the first and most compelling reconstruction of the genetic history of indigenous African cattle. One of the papers (Hanotte *et al.*, 2002), published in *Science*, won a CGIAR Science Award as 'Outstanding Scientific Article' in 2003 and remains a key reference on the genetic history of African cattle, ranking in the 98th percentile in Scopus citations in its field to March 2020. Similarly, ILRI described the first complete molecular characterization of Mongolian and Russian yak populations, supporting their

distinct genetic entities for conservation and breeding programmes, including the first molecular validation of cattle introgression into the yak genome. Using these novel approaches, ILRI scientists and collaborators made the first report of multiple introduction routes of chicken on the African continent (terrestrial and maritime) and documentation of a directional gene flow from domestic chickens into free-ranging wild red junglefowl. Similarly, ILRI and its collaborators developed a comprehensive genetic history of African sheep and classified Ethiopian sheep breeds. ILRI also validated the first set of molecular markers for the genetic characterization of camelids and undertook the first molecular characterization and classification of Kenyan dromedary breeds. These are now papers of reference for the history of the dromedary, revealing the dynamics of their domestication and cross-continental dispersal. Similarly pioneering was the finding of Ethiopia as one of the centres of genetic diversity (and potentially of domestication) for domestic donkeys in the Horn of Africa.

Breeding technologies

Of direct relevance to millions of farmers across Africa (and Asia), ILRI made the first application of SNP technology to identify genotypes *in situ* in smallholder systems (disclosing what genotypes farmers currently have) and to estimate genotype differences among a diverse range of genotypes kept by these farmers. ILRI has also demonstrated the feasibility of making genetic improvements through within-breed selection in village poultry systems.

Development impacts

Much of ILRI's work has had policy and development impacts in animal genetics and breeding. Elucidation of the genetic uniqueness of indigenous livestock and the special adaptive attributes of certain breeds have provided critical evidence of the potential of indigenous livestock, which has catalysed actions for their conservation and use in Africa and Asia. In the absence of breed-level livestock census data, breed survey tools developed by ILRI are being applied by countries to estimate populations and trends in individual indigenous breeds. More recently, an

innovation platform of the Dairy Genetics East Africa (DGEA) project helped identify business opportunities in the dairy value chain (heifer production, semen production and field delivery), which are now operational. The DGEA project provided compelling evidence that innovative application of genomic and associated technologies can be transformative.

ILRI has made global contributions to the development of economic valuation tools to inform the prioritization of breeds and resource allocations for conservation programmes and the Global Strategy on Animal Genetic Resources for Food and Agriculture led by the Food and Agriculture Organization of the United Nations (FAO). ILRI also established and continues to maintain the Domestic Animal Genetic Resources Information System (DAGRIS) as a research and development tool providing access to much-needed information and data for researchers and development practitioners.

Capacity development

ILRI has built significant capacity in livestock genetics and breeding through its master's and doctoral trainings as well as through its mentorship of practising scientists in collaborative projects and group training courses. While livestock genetics and breeding research remain comparatively weak throughout Africa, ILRI's capacity strengthening efforts, made through graduate training, secondments, group training and advisory services, have created a cadre of high-level experts in African countries who are generating new outputs in livestock genetics and breeding.

ILRI has supported at least 200 Bachelor of Science students, 70 Master of Science students, 65 doctoral students, 35 visiting scientists and postdoctoral fellows, and 150 short-term trainees in genetics, breeding and related fields. Many of the beneficiaries of these capacity strengthening efforts are driving the livestock genetics research agenda across the sub-Saharan continent, with some now internationally recognized experts in their own right.

Partnerships

Partnerships with national programmes have been the basis of nearly all research at ILRI.

Other than the resource populations used in genetics of disease resistance – the N'Dama cattle herd, the Red Maasai and Dorper sheep flocks, the Galla and Small East African goat flocks, and the mouse lines in ILRI's laboratories – all of ILRI's genetics and breeding research was based on animals owned by NARS institutions or farmer-owned animals accessed through NARS collaboration. ILCA and ILRAD worked closely with the International Trypanotolerance Centre (ITC) in The Gambia and the Centre International de Recherche-Développement sur l'Elevage en zone Sub-humide (CIRDES/ILRI/ITC, 2000) in Burkina Faso. ILRI's work has also benefitted from collaboration with universities and national programmes in the Global North (Europe, North America and Australia), in Asia (China and Korea), and in Latin America (Brazil). FAO has been a critical partner of ILRI, especially through engagement of ILRI experts in formulating the Global Plan of Action for Animal Genetic Resources, for example, by contributing to the development of tools, protocols and guidelines for characterizations across the globe.

Introduction

Scientific understanding of African and Asian livestock has improved remarkably since ILRAD and ILCA were established in 1973–1974. At that time, countries classified livestock by species with limited reference to breeds, strains or types (Payne, 1970). The only widely applied within-species distinction was that made among indigenous types, exotics and crosses between the two. Exotic animals were uniquely and consistently identified as distinct breeds and further classified into output- or commodity-specific types – dairy, meat or wool – reflecting the fact that long-term within-breed genetic improvement had successfully produced these specialized European breeds.

While the works of Epstein (1971) and Mason (1988) on classification of African livestock were cited, indigenous livestock continued to be lumped together as though they were a uniform genetic group. Impressionistic accounts of indigenous 'breeds' suggested – indeed, emphasized – that their productivity was low compared with European livestock. The indigenous animals were generally considered less worthy of attention

than the exotics, and many efforts were made to 'upgrade' them, the vision then being that they would gradually transition into 'grade livestock' and eventually into pure exotic types. This was widely considered to be the main strategy for improving livestock productivity in Africa and Asia. From the 1950s and 1960s through to the late 1970s, the word shenzi, which is Kiswahili for uncivilized, uncultured, uncouth or even filthy, and its equivalents in other parts of Africa were commonly used in reference to indigenous livestock.

At the species level, national livestock statistics continued to be presented at the level of native or indigenous versus exotics and crosses. While some results across the continent showed that the productivity of local types could be improved under better management, the baseline was still so limited that the importation of exotic breeds was seen as the means to breed more productive livestock (Blench, 1997). The few successful European settler farms using European breeds, although usually based on economically unrealistic management practices (Dunbar, 1970), seemed to validate such a strategy.

Endowed with more resources than was previously available for livestock research and development on the continent and guided by more forward-looking research agendas informed by stakeholder consultations, ILCA and ILRAD were able to put together well-trained teams and agricultural research and development programmes with the ability to mobilize and apply available and emerging scientific tools. ILCA and ILRAD programme priorities in their early days, from the 1970s and to the early 1980s, had one thing in common: a focus on understanding context. In relation to genetics and livestock improvement, ILCA's entry point was understanding the performance of different livestock genotypes (indigenous, exotics and crosses) in different production systems. ILRAD's focus in this domain was more specific: confirming indigenous breeds that were reported to be able to survive and produce under trypanosomiasis challenge (i.e. possessing the trypanotolerance trait). These initial priorities developed over time into major programme initiatives over three decades – the AnGR programme, which included molecular genetic characterization, and the genetics of disease resistance programme, focusing on trypanosomiasis and endoparasites.

While not 'complete' by any measure, much more is known today about indigenous livestock in developing countries; many breeds and strains have now been identified with specific attributes and some anecdotal claims are now supported with data.

ILRI has contributed significantly to documenting diversity among populations within species, providing evidence to match genotypes to environments, and unravelling the genetics underpinning observed differences, including in adaptive attributes anecdotally referenced in earlier reports. In major ways, ILRI research has provided the evidence now used widely in 'calls for action' for the conservation of the unique genetic diversity found in indigenous livestock, and these results are now informing conservation strategies.

Genetic improvement of indigenous livestock

The rate of progress made in *understanding* indigenous livestock – and the role that ILRI has played in this – is much greater than that in the genetic *improvement* of livestock in Africa (and Asia). There are at least two major and interrelated reasons why genetic improvement of local African and Asian breeds has received comparatively little attention: (i) the decades-long perception that these breeds are inferior to exotic breeds; and (ii) the original (and persisting) belief that cross-breeding is an effective and sustainable shortcut to productivity improvement, with inadequate considerations given to the important role of indigenous livestock adaptations to their environments. This continues to be the case, even after studies have shown that time and capital invested in selection within local breeds can, and does, eventually lead to adapted and profitable populations (FAO, 2013). Even where attempts have been made in recent decades to pay attention to local breeds, informed by the results of genotype characterization, the primary focus of such initiatives has been to conserve and use local animals as they are, with very little investment in selective breeding.

The few attempts made to genetically improve indigenous breeds through various nucleus breeding schemes (and other approaches) have tended to be short-term atomized projects with no opportunity to demonstrate tangible genetic progress. The end result is that local breeds have remained uncompetitive, especially because the metrics used for comparisons have focused on productivity as measured in terms of quantities of milk, meat, eggs, growth rate, etc., with little reference to the economics of production under different production constraints, such as disease, poor feeds and excessive heat. The lack of performance and pedigree recording in developing countries, which has been a major driver of the success of breeding programmes in the Global North, has compounded the problem. In the absence of robust recording systems, the 'eye-balling' and memory approach used in traditional livestock systems does not have the same discriminatory power to deliver the required selection differentials and accuracies, especially in view of the large environmental noise that is typical in smallholder systems. Continued inferior economic performance of local breeds reduces farmers' interest in those breeds, and they become threatened with extinction (Rege, 2008).

At the time of ILRI's founding, two mutually reinforcing actions were needed in developing-country situations: (i) to increase the economic performance of indigenous animals, with more output and/or less cost; and (ii) to conserve livestock breeds not yet supported by market forces. While the early work of ILRI provided useful information on genotype comparisons under different production environments, ILRI's direct and explicit entry into the area of livestock genetic improvement is more recent (starting in 2000). This work is taking advantage of recent developments in the areas of genomics and information and communication technologies to speed up the pace of genetic improvements in, and for, smallholder livestock systems.

This chapter summarizes ILRI's work in livestock genetics and breeding, with a focus on scientific and development impacts since the establishment of ILCA and ILRAD. The chapter is organized in the following sections: (i) characterization of livestock genetic resources; (ii) genetics of disease resistance/tolerance, focusing on trypanotolerance in cattle and endoparasites in small ruminants; (iii) genetic improvement strategies; and (iv) strengthening the capacity of NARS to conduct and use this work. Figure 1.1
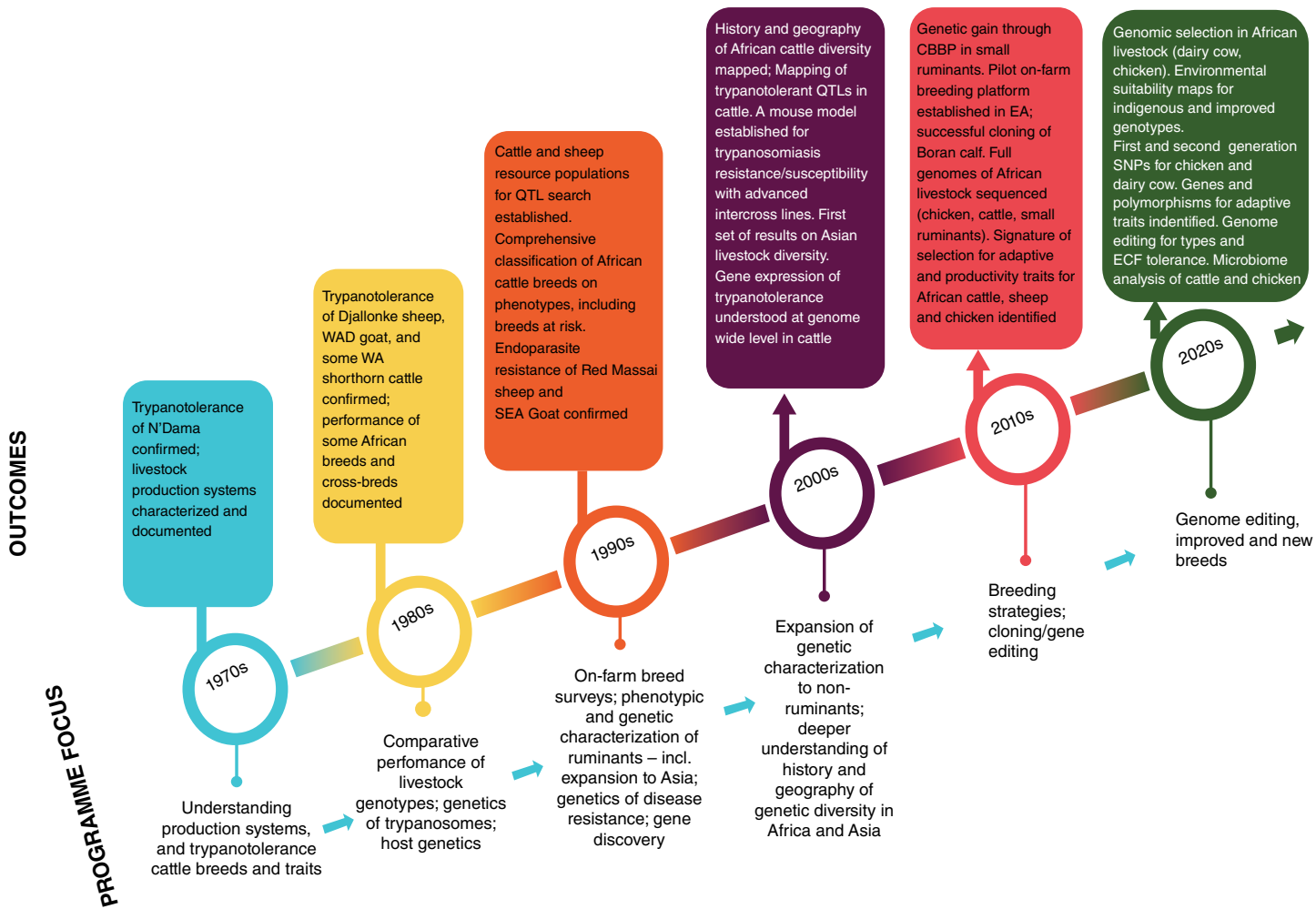
Fig. 1.1. Evolution of the ILRI genetics portfolio, 1970s to 2020. EA, East Africa; ECF, East Coast fever; CBBP, community-based breeding programme; SEA, Small East African; WA, West African; WAD, West African Dwarf.

summarizes the past and present outcomes and impacts of ILRI's genetics programme portfolio since the mid-1970s and ILRI's projected future focus in this area.

Characterization of Animal Genetic Resources

The developing regions of Africa and Asia have rich reservoirs of AnGR. Until the 1990s, information on the genetic diversity of this reservoir was lacking, limiting development of livestock conservation and use strategies. Characterization of AnGR – the distillation of all available knowledge, both published and unpublished, that contributes to the reliable prediction of genetic performance in defined environments – includes measurable/observable performance as well as the underlying genetic diversity, whether related to the observable performance or not. Work to characterize AnGR includes defining both the genetic attributes of a population possessing a unique genetic identity and the environment to which it is adapted or known to be partially adapted (Rege, 1992). While breed evaluation and comparison (based on phenotypic information) is an important aspect of characterization that provides information on performance (including adaptation), genetic characterization refers to the description of attributes that involve specific DNA sequences. The conservation of AnGR entails actions designed to prevent loss of the genetic distinctiveness of different species, subspecies, breeds or populations due to concerns that existing phenotypes, genetic integrity and local adaptations need to be maintained. It is, however, increasingly recognized that in the face of environmental change the conservation of adaptability and the processes sustaining and providing diversity might be of greater general importance than a focus only on conserving specific local adaptations. Knowledge, including local indigenous knowledge, of population differentiations and the temporal and spatial extent of gene flows is therefore essential to management decision making. This section highlights both direct and indirect ILRI contributions to the characterization of African and Asian AnGR over the past four decades.

Phenotypic characterization and breed surveys

Early work in phenotypic characterization of indigenous breeds and their crosses with exotic types formed the foundation of what later evolved to become animal genetics and breeding at ILRI. This work initially focused predominantly on production traits – growth, milk yield and reproductive traits. The only substantive work on adaptive traits (in the broad sense) in the 1980s was the work on trypanotolerance – the ability of some livestock breeds and strains to survive and produce under trypanosomiasis challenge (Trail *et al.*, 1979b; ILCA, 1979; see Chapters 2 and 3, this volume). Trypanotolerance was important due to the high livestock productivity losses associated with trypanosomiasis. These huge losses effectively curtail the use of livestock across vast regions of Africa that are infested by the tsetse fly, which transmits the disease-causing trypanosome parasites to the animals when the flies take a blood meal. The first continent-wide effort to characterize African AnGR was spearheaded by ILCA starting in 1992 (Rege and Lipner, 1992), and this set the stage for continental AnGR characterization efforts, eventually covering all the major livestock species of Africa and later expanding into Asia. The initial phase of this research was aimed at developing, in collaboration with NARS and FAO, baseline information on Africa's livestock – the number of breeds, sizes of populations, their indicative performance and their typical traditional production environments.

Tools and methods for conducting breed surveys

Previously, a major limitation to the phenotypic characterization mission was the lack of methods for conducting breed surveys and phenotypic characterization. In collaboration with FAO and other partners, ILRI scientists made a major contribution to this initiative by developing new instruments for breed surveys. They developed random cluster and transect survey methods for estimating herd/flock structures and partitioning species-level population statistics into breed-level census data for use in determining the risk status of ruminant breeds. They also published breed survey guidelines

(Rowlands *et al.*, 2003; Ayalew *et al.*, 2004) for use throughout Africa and Asia.

Classification of African livestock populations

Another notable contribution by ILRI and partners has been the comprehensive classification of African livestock populations through breed surveys and phenotypic characterization. ILRI spearheaded the first continent-wide initiative to characterize African AnGR starting in 1992 (Rege and Lipner, 1992). ILCA's systematic breed surveys led to the first comprehensive classification of African cattle (Rege *et al.*, 1994a,b,c; Aboagye *et al.*, 1994; Rege, 1999a). This set the stage for what were to become major continental AnGR characterization efforts. These efforts involved many international and national stakeholders and linked with a global plan under development by FAO 'to preserve the ancestral gene pool of domestic animals in the developing world'. This work built on breed evaluation activities that ILCA was already undertaking in collaboration with NARS under a Cattle and Small Ruminant Thrusts initiative and expanded the scope to encompass breed surveys focusing on identification, quantitative and qualitative description of breeds and the natural habitats and production systems to which they were adapted.

The first efforts focused on cattle. The first major description of African domestic cattle had been prepared by Doutressoulle (1947), while Epstein (1971) carried out the most comprehensive review of the era before ILRAD. Attempts had previously been made to construct outlines with the aid of archaeological (Epstein and Mason, 1984; Muzzolini, 1983; Clutton-Brock, 1989) and other (Blench, 1993; Doutressoulle, 1947; Epstein, 1971) evidence.

The first papers (Trail *et al.*, 1979a,b; Shaw and Hoste, 1987) surveyed the distribution of trypanotolerant cattle of West and Central Africa. Subsequent efforts by Rege *et al.* (1994a,b,c), Aboagye *et al.* (1994), Rege (1999b) and Rege and Tawah (1999) represented the most systematic classifications of African cattle and cattle populations, and included production systems, characteristics and extinction risk. This continental survey confirmed that phenotypically humped cattle – the 'non-native' Zebu cattle of Africa – constituted the majority of African cattle. Subsequent molecular work demonstrated that African Zebu cattle are ancient hybrids of African *Bos taurus* with *Bos indicus* of historical Asian origin. Contemporary African cattle populations were assigned to four broad categories: the humpless *B. taurus*; the humped African Zebu, distributed widely in Africa; *B. taurus* × *B. indicus* derivatives (sanga), found mainly in eastern and southern Africa; and sanga × Zebu types (termed the 'zenga'), such as the Fogera and Horro of Ethiopia and the Nganda of Uganda. The taurine (humpless) type has two subgroups – longhorns (*B. taurus longifrons*) and shorthorns (*B. taurus brachyceros*) – both of which were (and still are) restricted to West and Central Africa. While the longhorns are represented by two breeds only – the N'Dama and the Kuri – the shorthorn subgroup has numerous representatives (Box 1.1). The survey revealed that sub-Saharan Africa is home to a total of at least 145 cattle breeds/strains comprising two taurine longhorns, 15 taurine shorthorns, 75 Zebu (*B. indicus*), 30 sanga, eight zenga, nine 'recent' breeds derived from interbreeding of indigenous breeds/strains located in close proximity to each other and six systematically created composite breeds. Of the 145 breeds identified from these studies, using the FAO's classification, 47 (about 32%) were considered to be at risk of extinction. Of the breeds identified as at risk of extinction, six were in the 'rare' category, ten were 'vulnerable', another ten were 'endangered' and 15 were 'critical'. A total of 22 breeds previously recognized on the continent were determined to have become extinct in the past century. This number excluded some populations that were considered to have lost individual identities due to admixtures involving two or more originally distinct breeds.

The European (commercial) taurine breeds and their cross-breds were also found in many parts of the continent, but their populations then, as today, were relatively low compared with the indigenous breeds. Taking a cue from these surveys, NARS scientists in many countries, working independently or in collaboration with ILRI, started to undertake similar on-farm surveys and detailed studies of individual breeds. Examples include Mekonnen *et al.* (2012) working on Horro cattle; Tawah and Rege (1996a,b) on Gudali and white Fulani cattle; Tawah *et al.* (1997) on Kuri cattle; and Rege *et al.* (2001),

Box 1.1. The taurine cattle of West Africa.

The review of West African taurine breeds sought to determine the extent to which those breeds are endangered and to inform conservation decisions. The reviews addressed origin, distribution, population statistics, habitat, management and production systems, description, adaptability, disease resistance and performance characteristics.

West African taurine cattle breeds include the hamitic longhorns (*Bos taurus longifrons*) and the shorthorns (*Bos taurus brachyceros*). Only two longhorn breeds are found in West Africa – the N'Dama and the Kuri. The shorthorn population is much more varied and their breeds/strains are known by a variety of names, depending largely on their location, including Muturu (Liberia and Nigeria), Lagune (Benin, Côte d'Ivoire and Togo), Ghana shorthorn, Baoulé (Burkina Faso and Côte d'Ivoire), Somba (Benin and Togo), Bakosi, Bakweri, Doayo and Kapsiki (Cameroon), Lobi (Burkina Faso and Côte d'Ivoire), Manjaca (Guinea Bissau) and Logone (Chad). However, it is not clear whether all of these populations are different enough to deserve different names (this classification challenge pointed to the need for genetic diversity studies, which were to follow). With the possible exception of Kuri cattle, which live in a special environment where tsetse flies have not been recorded, these breeds have developed in tsetse-infested areas and are thought to have developed various degrees of trypanotolerance. The N'Dama is the best known, most numerous and most widely spread of the trypanotolerant breeds, with a total of nearly 5 million head spread throughout West and Central Africa. However, the population of all West African shorthorns is only around 2 million head, and several breeds, including the Muturu and Lagune, are at risk of extinction, mainly due to cross-breeding (especially with Zebus), to neglect and to reduction of pastoral lands as human population pressure increases.

Mwacharo and Rege (2002) and Mwacharo *et al.* (2006a) on East African Zebu. A clear pattern of the different phenotypic characteristics and distribution of different types of African cattle populations emerged from these studies.

Breed characterization soon thereafter became a major area of livestock research. Most of these initiatives were conducted by ILRI in collaboration with NARS (Rege and Lebbie, 2000), or were inspired or directly influenced by the work of ILRI. The work expanded to sheep and goats (Farm Africa/ILRI, 1996; Warui, 2008; Abegaz *et al.*, 2013; Taye *et al.*, 2016) and thereafter to chickens (Halima *et al.*, 2007; Dana *et al.*, 2010; Dessie *et al.*, 2012) and camels (Ishag *et al.*, 2010; Tandoh *et al.*, 2018).

Molecular genetic characterization

When ILRAD and ILCA merged in 1995, the ILCA Animal Genetic Resources programme and the ILRAD Genetics of Disease Resistance programme were already organizing a global programme on molecular genetic diversity of livestock. The large phenotypic variation observed among African populations of cattle, sheep and goats was used to formulate the hypotheses that formed the basis of the genetic diversity studies. As was the case with phenotypic characterization, the first major set of ILRI-led molecular diversity studies started with African cattle. A concerted effort was initiated in 1995 to collect biological samples for DNA extraction for this purpose. Coinciding with the emergence and increasing application of a wide range of genetic markers, these studies attracted many scientists to the power of 'neutral' molecular markers in unravelling genetic structure and estimating diversity in livestock populations.

By 1993, scientists had developed and tested a panel of short sequence repeat markers and methods for global use in genetic diversity studies of different livestock species (Brezinsky *et al.*, 1993a,b,c; Kemp *et al.*, 1992, 1995). As such, ILRI was a major contributor from the start to the FAO-coordinated 'Molecular Domestic Animal Diversity' – which identified and published panels of markers to be used globally for genetic diversity studies of different livestock species (FAO, 1993) – and to the secondary guidelines developed (ISAG/FAO, 2004); the FAO marker panel included many of those developed and tested by ILRI. These markers and methodologies catalysed significant investments in AnGR characterization in Africa using a variety of markers. The co-development of the 30-microsatellite marker panel, related capacity development efforts, and the wider domestication and use of these methods has led to accelerated and high-quality characterization of a large number of indigenous livestock breeds in Africa and Asia. This has

consequently led to increased understanding of genetic diversity and thus informed conservation efforts, including regional gene banks, Sheko semen banks in Ethiopia, Ankole semen banks in Uganda and local/indigenous chicken germ-cell banks in ILRI Kenya, among other efforts.

First genetic history of cattle in Africa, linking livestock to human history

Utilizing the tools and methods developed, ILRI scientists established the genetic relationship of more than 31 breeds of African and Asian cattle and reconstructed the first genetic history of cattle in Africa (Hanotte *et al.*, 2002), linking livestock to human history and providing a glimpse into the distant past of the peoples and civilizations of Africa and Asia. The major cumulative result of this work has been the knowledge base of the history and geography of the genetic diversity of domestic livestock of Africa and Asia.

Taken together, these studies led to the conclusion that the earliest cattle of Africa were of taurine *B. taurus* type. Subsequent waves of migrations of humped Zebu (*B. indicus*) animals then reshaped the genomic landscape of African cattle (Bradley *et al.*, 1994; Hanotte *et al.*, 2002; Freeman *et al.*, 2004). African and European cattle seem to be more closely related and quite distinct from Indian cattle, the relatively large divergence providing evidence for two separate domestication events, presumably of different subspecies of the aurochs, *Bos primigenius* (Loftus *et al.*, 1994). Today, the African continent is uniquely rich in cattle diversity, with an estimated 145–150 African cattle breeds or populations recognized (Rege, 1999b; Mwai *et al.*, 2015). Importantly, it is now well established that African cattle carry a taurine maternal ancestry originating from the Near East taurine domestication centre(s), while the possible genetic contribution of the now-extinct African auroch (*B. primigenius opisthonomous*) remains unclear (Epstein, 1971; Bonfiglio *et al.*, 2012; Decker *et al.*, 2014). The pattern of introgression of the Zebu genome across the southern, eastern and north-western parts of sub-Saharan Africa has been well documented using autosomal and Y-chromosome-specific microsatellite loci (Bradley *et al.*, 1994; Hanotte *et al.*, 2000a; Freeman *et al.*, 2004).

African cattle inhabit more than five distinct major agroecological zones. Overall, Zebu cattle are common in the arid and semi-arid northern Sahelo-Sudanian zone, as well as in the eastern part of the continent, including the highlands, whereas taurine cattle today form the majority of the herds in the subhumid and humid regions of West Africa, which are heavily infested with tsetse fly. Sanga are predominant in the western region of Central Africa, around the Great Lakes region, and in the southern part of the continent. The highest genetic diversity is among African Zebu and sanga cattle (Kim *et al.*, 2017). No pure indigenous *B. indicus* cattle occur on the African continent. These findings have informed strategies for genetic characterization and have direct and important implications for AnGR conservation and use, as they point to population location phenotypes and uniqueness.

Genetic history and geography of African sheep

Indigenous African sheep genetic resources have been classified into two main groups, fat-tailed and thin-tailed sheep. The fat-tailed sheep are the most widely distributed, being found in a large part of North Africa (from Egypt to Algeria) and in eastern and southern Africa (from Eritrea to South Africa). The thin-tailed sheep are present mainly in Morocco, Sudan and West Africa. Historically, African sheep were domesticated outside of Africa. They share a common ancestry with European and Asian sheep. Archaeological information supports separate introductions and dispersion histories for the African thin-tailed and fat-tailed sheep. The first sheep entered Africa via the Isthmus of Suez and/or the southern Sinai Peninsula between 7500 and 7000 BP. They were likely of the thin-tailed type. Fat-tailed sheep entered Africa through its north-eastern part and the Horn of Africa. Mitochondrial DNA analysis supports a common maternal ancestral origin for all African sheep, while autosomal and Y-chromosome DNA analysis indicates a distinct genetic history for African thin-tailed and fat-tailed sheep, and the main ancestral population of southern African fat-tailed sheep probably originated in East Africa (Muigai and Hanotte, 2013).

Genetic history and geography of African chickens

ILRI has made a major contribution to the body of knowledge of African chicken origin and present-day diversity (e.g. Lyimo *et al.*, 2014). Sociocultural, linguistic, archaeological and historical data together suggest a complex history of present-day African chicken populations. Introductions evidently occurred via land and sea routes followed by several subsequent dispersal routes across the continent (Mwacharo *et al.*, 2013b). Molecular genetic studies support the origin and migration models for African domestic chickens and suggest centres of origin in Asia, including South Asia and South-east Asia. Studies have consistently found that indigenous chickens are uniquely adapted to their local agroecologies and are distinct from commercial broiler and egg layer lines (Bettridge *et al.*, 2018). More localized studies have been used to test specific hypothesis on origins. For example, results of a study reported evidence for a dual geographical and genetic origin for the indigenous Malagasy chickens, specifically, their relationship to Asian breeds and, more particularly, to Indonesian chickens (Razafindraibe *et al.*, 2008). However, a subsequent in-depth study (Herrera *et al.*, 2017) has reported findings suggesting a much stronger relationship between Malagasy and East African chicken populations, putting an interesting spin on the earlier link of the genetic origin due to an important functional genetic trait – susceptibility/resistance to viral (avian influenza) infection (Razafindraibe *et al.*, 2008). Using autosomal microsatellite markers, Mwacharo *et al.* (2013b) identified three distinct autosomal gene pools (I–III) in eastern African chicken populations, possibly representing genetic signatures of separate events in the history of the continent that relate to the arrival and dispersal of village chickens and humans across the region. Earlier, analysis of mitochondrial DNA indicated a probable Indian subcontinent origin for the commonest haplogroup and a maritime introduction for the next commonest one from South-east and/or East Asia (Mwacharo *et al.*, 2011). These findings not only support ancient historical maritime and terrestrial contacts between Asia and East Africa but also indicate the presence of large maternal genetic diversity in the region,

which could support genetic improvement programmes. It is anticipated that further continent-wide studies combining archaeological, ancient and/or modern genetic information are likely to shed new insights on the history of chickens in Africa, as well as globally.

Genetic history and geography of the African dromedary

The dromedary has a higher initial diversity relative to the native distribution of its wild ancestor on the Arabian Peninsula and to the brief coexistence of early-domesticated and wild individuals compared with other livestock, which show a long history of gene flow with their wild ancestors. Mburu *et al.* (2003) reported results not supporting the classification of the indigenous Kenyan dromedary into four distinct breeds based on socio-geographical criteria; instead, their results pointed to only two separate genetic entities, the Somali population on the one hand and a group including the Gabbra, Rendille and Turkana populations on the other. Extending this work to Africa and Asia, phylogenetic analyses of ancient and modern dromedaries suggest a history of restocking from wild relatives from the south-east coast of the Arabian Peninsula following domestication (Almathen *et al.*, 2016). The results suggested that the classic models of domestication from multiple centres and from wild conspecific individuals in isolation may not be applicable to the dromedary. Molecular genetic analyses have revealed a relative lack of genetic differentiation among dromedaries living in different areas; this is a possible legacy of ancient trading routes converging at Mediterranean ports where goods, including the packing animals carrying them, were exchanged (Almathen *et al.*, 2016).

Establishment of a joint laboratory with CAAS in Beijing and expansion into Asia

Understanding the genetic diversity of domestic stock requires attention to Asia both because of the importance of Asia in the history of many African livestock populations and because of Asia's endowment with livestock genetic diversity. Thus, ILRI's early sampling strategies for genetic diversity studies included coverage of strategic areas in Asia and included more than

just reference populations for African livestock species; the coverage included species not farmed in Africa, such as water buffalo, yak, banteng and Bactrian camels. Work in Asia was significantly strengthened when, starting in 2005, ILRI established a joint laboratory in Beijing with the Chinese Academy of Agricultural Sciences (CAAS) to support livestock and forage genetic resources work. Subsequent funding enhanced the quality of science and capacity in AnGR for Bangladesh, Sri Lanka and Vietnam, among other countries, allowing the wider application of FAO's panel of genetic markers. The ILRI-CAAS Joint Laboratory significantly increased ILRI's presence in, and impact on, the Asian continent. Although quantitative estimates were variable, the results across all species began to draw attention to the uniqueness of various local populations or 'breeds' not just in Africa but also across Asia, such as yak (Jianlin *et al.*, 2002; Xuebin *et al.*, 2005; Qi *et al.*, 2010), camelids (Jianlin *et al.*, 2000, 2004); banteng (Nijman *et al.*, 2003) and cattle (Dorji *et al.*, 2003). Going beyond its intended role, the joint laboratory and its associated capacity working with other laboratories enabled China, in 2018 during the African swine fever outbreak, to put in place polymerase chain reaction (PCR)-based diagnostics to support disease surveillance. Specifically, sequencing analysis of a 417 bp region of the *B646L/p72* gene of the virus helped trace the outbreak to the Georgian strain of the virus in Russia and Eastern Europe (Wang *et al.*, 2018).

ILRI's genetic characterization as a catalyst for international interest

ILRI's efforts in molecular characterization catalysed significant investments in this area, while beginning to provide genetic links to populations of other regions using a variety of markers to study subsets of populations, ranging from single countries to groups of countries in a subregion of the continent to the whole continent. Indeed, as part of ILRI's entry into Asia, its genetics programme activities were among the first to move ILRI's work into Asia and to strengthen its work on cattle (Okomo *et al.*, 1998; Hanotte *et al.*, 2000b; Hanotte *et al.*, 2002; Hassen *et al.*, 2007; Ndumu *et al.*, 2008; Kugonza *et al.*, 2011; Kim *et al.*, 2017; Taye *et al.*, 2018), sheep (Gizaw

et al., 2007; Muigai *et al.*, 2009; Muigai and Hanotte, 2013), goats (Chenyambuga *et al.*, 2004; Tarekegn *et al.*, 2018), chickens (Mwacharo *et al.*, 2007; Razafindraibe *et al.*, 2008; Mwacharo *et al.*, 2011; Dessie *et al.*, 2012; Wragg *et al.*, 2012; Desta *et al.*, 2013; Mwacharo *et al.*, 2013a,b; Bettridge *et al.*, 2018; Park *et al.*, 2018) and camelids (Jianlin *et al.*, 2000; Mburu *et al.*, 2003; Jianlin *et al.*, 2004; Almathen *et al.*, 2016), applying a range of markers, starting with the first-generation DNA markers (restriction fragment length polymorphisms, minisatellites, microsatellites and mitochondrial DNA).

Demonstrating the unique attributes of indigenous livestock has provided a strong rationale for conservation and use of indigenous animals. Other scientific outcomes included improving the body of knowledge of the origin and diversity of African cattle (Hanotte *et al.*, 2002), sheep (Muigai and Hanotte, 2013) and chicken (Mwacharo *et al.*, 2006b; Mwacharo *et al.*, 2013a), grossly expanding the knowledge base of the history and geography of the genetic diversity of the domestic livestock of Africa and Asia. These 'pathfinder' studies triggered subsequent studies (Decker *et al.*, 2014), which analysed an expanded cattle data set worldwide (134 breeds), showing ancient African cattle to have been first domesticated in the Fertile Crescent of the Middle East and then brought to Africa by migrating peoples thousands of years ago. Today, the study of the genetic diversity of livestock at the molecular level has developed into an active area of research, with African results receiving considerable new attention by the scientific community.

ILRI's genetics and breeding work on African cattle included many 'firsts', such as comprehensive classification of breed/strain groups, including their status of risk of extinction (Rege *et al.*, 1994a,b,c) and reconstruction of their genetic history (Hanotte *et al.*, 2002). Other 'firsts' included: the complete molecular characterization of Mongolian and Russian yak populations, supporting their distinct genetic entities for conservation and breeding programmes (Xuebin *et al.*, 2005); molecular validation of cattle introgression into the yak genome (Jianlin *et al.*, 2002; Qi *et al.*, 2010); reports of multiple introduction routes of chicken on to the African continent (terrestrial and maritime) (Mwacharo

et al., 2013a,b); a comprehensive genetic history of African sheep (Muigai and Hanotte, 2013) and a classification of Ethiopian sheep breeds (Gizaw *et al.*, 2007); documentation of a directional gene flow from domestic chickens into free-ranging wild red junglefowl, calling attention to interpretation of genetic data applied to a genetic approach to the conservation of the red junglefowl (Thakur *et al.*, 2018); the molecular characterization of the dromedary, which reclassified the four traditional Kenyan dromedary breeds (Somali, Turkana, Rendille and Gabbra) into two genetic entities, the Somali and a second group comprising the Gabbra, Rendille and Turkana populations (Mburu *et al.*, 2003); validation of the first set of molecular markers for the genetic characterization of camelids (Jianlin *et al.*, 2000); the paper of reference for the history of the dromedary, revealing the dynamics of domestication and the cross-continental dispersal of the dromedary (Almathen *et al.*, 2016); and the finding of Ethiopia as one of the centres of genetic diversity (and potentially domestication) for domestic donkeys in the Horn of Africa (Kefena *et al.*, 2014).

Genetics of Disease Resistance

Genetics of trypanotolerance

The earliest major collaboration between ILRAD and ILCA was field characterization of trypanotolerant livestock – breeds reported to be able to survive and produce under trypanosomiasis challenge – in Africa. The African Trypanotolerant Livestock Network (ATLN) of NARS in West, Central and eastern Africa was an important tool for this work. Within the network, in-depth investigations were undertaken at many sites covering a range of trypanotolerant and trypanosusceptible livestock breeds under different levels of tsetse/trypanosomiasis risk and management. ILRAD scientists recognized the trypanotolerant attributes of certain breeds of *B. taurus* (humpless cattle), specifically the N'Dama. Despite evidence from the ATLN that N'Dama could be productive under trypanosome challenge without treatment, there remained reluctance among farmers in East Africa to adopt the N'Dama because of its small size and

low milk yield. This helped to draw attention to the trypanotolerance promise (based on early field results) of a particular Zebu cattle breed, the Orma Boran of East Africa. Farmer interviews at the time already suggested that introducing tolerance into larger breeds of cattle, including improved exotic (European) breeds, would be acceptable, and this held promise as a way to use trypanotolerance traits (see Chapters 2 and Chapter 3, this volume).

In a search of genetic markers for trypanotolerance, two polymorphic systems of bovine lymphocyte antigens were studied in 1988 by ILRAD in collaboration with ILCA. These systems were the MHC and a more limited polymorphic system of common leucocyte antigens, detected in cattle only. The first objective of the study was to survey the MHC and common leucocyte antigen phenotypes of populations of N'Dama cattle in Zaire and The Gambia and to compare these phenotypes with corresponding profiles of trypanosensitive Boran cattle in Kenya. The second objective was to look for associations between these MHC and common leucocyte antigen phenotypes, trypanotolerance and the productivity of N'Dama cattle. Significant correlations were found between the two classes of lymphocyte markers and the degree of resistance shown by trypanotolerant cattle exposed to trypanosomiasis by natural challenge. These results, which suggested the existence of genetically selectable markers for the trypanotolerant trait, were investigated further using larger numbers as well as family groups of cattle. The results indicated a central role for immunity in the manifestation of the trypanotolerant trait.

From 1987, N'Dama heifers produced at ILRAD from frozen N'Dama embryos brought in 1983 from The Gambia were regularly induced to superovulate using Folltropin, a follicle-stimulating hormone (Jordt and Lorenzini, 1990). By implanting the best of the N'Dama embryos in Boran foster mothers, ILRAD produced 24 N'Dama calves, which were used in studies of trypanotolerance and bovine genetics.

In the 1990s, ILRAD scientists undertook research to identify molecular mechanisms or markers for defining trypanotolerant cattle types – polymorphisms that differentiate breeds such as the N'Dama and Baoulé (both *B. taurus*)

from non-trypanotolerant African Zebu types. This work, among other things, examined variation in products of the MHC loci, biochemical variants of a variety of gene products, and both mitochondrial and nuclear DNA polymorphisms. Following an idea inspired by Morris Soller, of the Hebrew University of Jerusalem, to use molecular tools to map traits in cattle, ILRAD created a resource F_2 population segregating for trypanotolerance even before the technology was available for actual exploitation of such a resource population.

Among the early results were identification of informative polymorphisms, especially in the MHC, in the products of a small number of selected non-MHC loci, in nuclear satellite DNA and in a Y-chromosome sequence. This level of molecular and genetic characterization (Teale, 1993) provided what at the time was considered good differentiation of the major subspecies of cattle, providing a major transition from neutral to functional markers. The two marker types had previously been considered totally separate – 'fingerprinting' versus gene variants. It was anticipated that advances in molecular and computational technologies in the coming years would enable the examination and definition of genetic diversity beyond the subspecies level.

Informed by results of this early work, ILRAD and its collaborators (and other research groups that then entered this research area) focused on genome mapping to identify loci associated with QTLs, such as Taylor *et al.* (1998), who produced a genetic map of bovine chromosome 1, spanning more than 160 cM, with five laboratories contributing 31,962 informative meioses from 70 loci; Hanotte *et al.* (2003), who undertook F_2 mapping work, and Noyes *et al.* (2011), who identified candidate genes in pathways responding to *T. congolense* infection through genetic analysis and expression analysis of trypanosusceptible Kenyan Boran and trypanotolerant N'Dama cattle. Results of the F_2 mapping strongly supported a multi-locus model for the inheritance of trypanotolerance (Hanotte *et al.*, 2003). Trypanotolerance QTLs were found on 18 chromosomes, with an allele for resistance present at nine N'Dama QTLs and five Boran QTLs (Hanotte *et al.*, 2003). Multiple QTLs on several chromosomes were found to contribute to the three major tolerance indicators: anaemia,

body weight and parasitaemia. Overall, the proportion of the phenotypic variance of the trypanotolerance traits explained by these QTLs remains relatively low. Moreover, the estimated effects of QTLs that are detected in experiments of only moderate power tended to be overestimated. This suggested the presence of other QTLs affecting trypanotolerance that are segregating in the N'Dama, as well as other QTLs with effects too small to be detected. To determine whether these QTLs could be used in marker-assisted selection, relevant genes or markers tightly linked to these would need to be resolved. Thus, as was the case with endoparasite resistance in sheep (see 'Genetics of resistance to gastrointestinal parasites'), traits that distinguish N'Dama and Boran cattle trypanotolerance proved to be regulated by multiple, unlinked genes (Box 1.2).

In parallel, the use of mouse models inspired by Alan Teale and the advanced intercross work led by ILRI collaborator Ariel Darvasi (Hebrew University of Jerusalem) led to the mouse F_2 (Kemp *et al.*, 1997) and F_6 (Iraqi *et al.*, 2000) fine mapping of trypanosomiasis resistance loci in murine. ILRI researchers identified here three areas of the genome that contributed to the control of resistance to trypanosomiasis, a result that represented the first mapping of QTLs controlling resistance to a haemoparasitic disease of major economic importance (see Chapter 2, this volume). More recently, demonstration of trypanosomiasis resistance in transgenic mice laid a strong foundation for subsequent research on ILRI's 'Mzima cow' project and related goat and chicken transgenics and biodiversity work. It awakened the possibility of using existing immunity to engineer new therapies and transgenic livestock (Willyard, 2011) and inspired the concept of transgenic livestock in which the ILRI cattle/mouse genome mapping group linked up with human trypanosomiasis resistance research.

All of the above results, over time, generated various levels of scientific impacts by enabling the evaluation of performance under challenge rather than reliance on indicator traits, an approach with potential to improve efficiency in genetic modification with selection *in situ*. Indeed, one of the original polymorphisms in N'Dama cattle is currently being selected for at the ILRI research station at Kapiti, Kenya.

Box 1.2. Mapping trypanotolerant QTLs in African cattle.

To identify QTLs controlling resistance to trypanosomiasis in cattle, ILRI made an experimental cross between trypanotolerant African N'Dama (*B. taurus*) and trypanosusceptible improved Kenya Boran (Zebu) cattle (Hanotte *et al.*, 2003). Sixteen phenotypic traits were defined describing anaemia, body weight and parasitaemia. In total, 177 F_2 animals and their parents and grandparents were genotyped at 477 molecular marker loci covering all 29 cattle autosomes. Total genome coverage was 82%. Putative QTLs were mapped to 18 autosomes at a genome-wide false discovery rate of less than 0.20. The results were consistent with a single QTL on 17 chromosomes and two QTLs on BTA16 (*Bos taurus* chromosome 16). Individual QTL effects ranged from approximately 6% to 20% of the phenotypic variance of the trait. Excluding chromosomes with ambiguous or non-trypanotolerance effects, the allele for resistance to trypanosomiasis originated from the N'Dama parent at nine QTLs and from the Kenya Boran at five QTLs, and at four QTLs there was evidence of an overdominant mode of inheritance. These results suggested that selection for trypanotolerance within an F_2 cross between N'Dama and Boran cattle could produce a synthetic breed with higher trypanotolerance levels than the parental breeds.

Noyes *et al.* (2011) provided both the method and the pathway from QTL analysis to SNPs by combining analytics pipelines. Researchers analysed the transcriptomes of trypanotolerant N'Dama and susceptible Boran cattle after infection with *T. congolense*, followed by sequencing expressed sequenced tag libraries from these two breeds to identify polymorphisms that might underlie previously identified QTLs, and assessed QTL regions and candidate loci for evidence of selective sweeps. They identified a previously undescribed polymorphism in trypanotolerance QTLs that affected gene function *in vitro* and candidate genes by their expression profile and the pathways in which they participate (Box 1.3).

Box 1.3. Candidate genes involved in the response to *T. congolense* infection.

Scientists used three strategies to obtain short lists of candidate genes within QTLs that were previously shown to regulate the response to infection (Hanotte *et al.*, 2003). They analysed the transcriptomes of trypanotolerant N'Dama and susceptible Boran cattle after infection with *T. congolense*; they sequenced expressed sequenced tagged libraries from these two breeds to identify polymorphisms that might underlie previously identified QTLs and assessed QTL regions and candidate loci for evidence of selective sweeps (Noyes *et al.*, 2011). The scan of the expressed sequence tags identified a previously undescribed polymorphism in the *ARHGAP15* gene in the BTA2 trypanotolerance QTL. The polymorphism affects gene function *in vitro* and could contribute to observed differences in expression of the mitogen-activated protein kinases (MAPK) pathway *in vivo*. The expression data showed that Toll-like receptor (TLR) and MAPK pathways responded to infection and the former contained TLR adaptor molecule 1 (TICAM1) located within a QTL on BTA7. Genetic analyses showed that selective sweeps had occurred at the *TICAM1* and *ARHGAP15* loci in African taurine cattle, making them strong candidates for the genes underlying the QTL. Candidate QTL genes were identified in other QTLs by their expression profile and the pathways in which they participate.

Genetics of resistance to gastrointestinal parasites

Helminthiasis is of considerable significance in a wide range of agroclimatic zones in Africa and Asia, as well as in other developing regions of the world. This disease constitutes one of the world's most important constraints to small-ruminant production (ILCA, 1991; Over *et al.*, 1992). The widespread occurrence of infection of grazing animals with internal parasites, the associated loss of production, the costs of anthelmintics and the death of infected animals are some of the major concerns that drew ILRI's attention in the early 1990s. In addition, there were (and still are) environmental concerns influencing anthelmintic usage, including consumer demand for animal products and pastures free of chemical residues. The high cost of anthelmintics, their uncertain availability, the increasing frequency of development of drug resistance and the limited scope in many communal pastoral

systems for controlled grazing (Mwamachi *et al.*, 1995; Waller, 1997) further limit options for controlling this disease. In the 1990s, it was considered unlikely that new broad-spectrum anthelmintics and vaccines would be available and accessible to smallholders. Utilization of host genetic variation for resistance was considered a more viable and sustainable approach to the control of internal parasites.

ILRI conducted in-depth reviews (Baker *et al.*, 1992, 1994a,b; Baker, 1998) to develop strategies for this work. The best documented examples of sheep breeds showing resistance to endoparasites in Africa were the Red Maasai sheep of East Africa and the Djallonké sheep of West Africa (Preston and Allonby, 1978, 1979; Baker *et al.*, 2003, 1994b; Baker, 1995). Informed by this review, ILRI initiated an ambitious research programme on the characterization of African small ruminants for genetic resistance to endoparasites. Evidence of genetic variation in sheep and goats for resistance to, or tolerance of, gastrointestinal nematodes had first been documented 40–50 years earlier and comprehensively reviewed by Gray (1991) and Gray and Woolaston (1991). Although the reviews provided evidence for a genetic basis of resistance to endoparasites, both between and within breeds of certain sheep and goat populations, almost all published reports available at the time suffered from inappropriate experimental design, particularly in terms of small sample sizes (numbers of animals of each breed sampled) and lack of information on how the animals had been sampled. The evidence for genetic variations in resistance to endoparasites within breeds was, at this point, more convincing, with heritabilities averaging about 0.35.

With the objective of investigating and characterizing genetic resistance to endoparasites in indigenous African sheep and goat breeds, the programme (ILCA, 1991) studied Dorper and Red Maasai sheep and Galla and Small East African goats in coastal Kenya; and Menz and Horro sheep breeds in the highlands of Ethiopia. It was envisaged that a second phase of the programme would investigate – by examining groups of animals that were most resistant and most susceptible – the immunological and genetic mechanisms controlling resistance to endoparasites. This work was expected to lead to identification of immunological or genetic markers of resistance. By 1992, the initial studies in coastal Kenya that were started before the launch of the major continent-wide programme (Reynolds *et al.*, 1992) were already showing clear signs that the local Red Maasai sheep were more resistant to endoparasites than the introduced Dorper sheep breed.

Building on the Red Maasai and Dorper herds already established at the Diani Estate of Baobab Farm, located some 20 km south of Mombasa, ILRI scientists established several genetic groups to facilitate the planned experiments. In addition to pure lines of the two breeds, a double backcross population of Red Maasai and Dorper sheep was also created (with the ultimate goal of identifying QTLs controlling resistance to gastrointestinal nematode parasites, mainly *Haemonchus contortus*). Under the same programme, a goat flock was also established and used for a study from 1994 to 1996 to compare the resistance to naturally acquired infections of gastrointestinal nematodes (predominantly *H. contortus*) of the Galla and Small East African goats in the subhumid coastal region of Kenya.

Three possible approaches for breeding for resistance are: (i) breeding for resistance (reduced parasite numbers, as determined by faecal worm egg count); (ii) breeding for resilience (ability to produce under parasite challenge, as measured by packed cell volume); and (iii) breeding for the number of treatments required during parasite infection (Woolaston and Baker, 1996). The two traits used by the ILRI team in all the studies were faecal worm egg count and packed cell volume.

Resistance to gastrointestinal nematodes in Red Maasai sheep

Red Maasai sheep and three-quarter Red Maasai lambs were consistently more resistant (lower faecal egg count) and more resilient (higher packed cell volume) than the Dorper and three-quarter Dorper sheep. The difference between the backcrosses for both faecal egg count and packed cell volume was about half of the difference between the purebred Red Maasai and Dorper lambs, indicating additive gene action. Moreover, even in artificial challenge experiments where there were no significant genotype differences in faecal egg counts, the Red Maasai and the three-quarter Red Maasai lambs had

significantly fewer worms than the Dorper and three-quarter Dorper animals.

An experiment was conducted in two environments – coastal subhumid and semi-arid – to examine genotype–environment (G×E) interactions for both productivity and resistance to gastrointestinal nematodes (Baker *et al.*, 2004). Here, too, the Red Maasai were consistently more resistant and more resilient in both environments than the Dorper sheep, but there were significant G×E interactions for ewe reproductive performance, ewe and lamb mortality rates, and live weights. Overall, taking together live weights, reproductive performance and mortality, the Red Maasai breed was considerably more efficient than the Dorper sheep in the subhumid environment, while in the semi-arid environment, there was a negligible breed difference in productive efficiency.

In a simulation study examining opportunities for using the Red Maasai breed resource for cross-breeding versus pure breeding, König *et al.* (2017) concluded that cross-breeding with Dorper sheep was not recommended for harsh environmental conditions due to the large breed differences expected in such an environment, while the breed could be improved through within-breed selection (e.g. applying a nucleus breeding scheme),

Taken together, studies done on the Red Maasai by the ILRI team and partners have unequivocally demonstrated, on the basis of indicators that collectively provide a reasonably reliable picture of resistance – faecal egg count and packed cell volume – that the Red Maasai perform significantly better than Dorper sheep under gastrointestinal nematode challenge. Moreover, the associated lowered mortality rates in the breed lead to much faster flock growth and productivity. Heritability estimates for packed cell volume and faecal egg count (Baker *et al.*, 2003) point to the use of different traits for selection: within the Red Maasai breed, the focus should be on resilience (i.e. selection for high packed cell volume), while for the Dorper selection, it should be feasible for both improved resistance (low faecal egg count) and resilience (high packed cell volume).

Menz versus Horro sheep of Ethiopia

Inspired by the Red Maasai results in Kenya, similar studies were initiated in Ethiopia, where Menz and Horro sheep were compared on-station in a highlands environment (Rege *et al.*, 1996; Haile *et al.*, 2002; Rege *et al.*, 2002). The predominant gastrointestinal parasites at this location are *Longistrongylus* and *Trichostrongylus* spp. There was no difference in resistance to parasites between the Menz and Horro breeds as reflected by faecal egg counts. While packed cell volume is a useful indicator of resistance when *H. contortus* is the predominant gastrointestinal parasite, this was not the case in this highland site in Ethiopia. Thus, although the Menz lambs had a significantly higher packed cell volume than Horro lambs, this could not be related to their resistance to endoparasites and was instead attributed to an adaptation of this breed to higher altitude (their original habitat). The Menz lambs had significantly lower mortality than Horro lambs both pre- and post-weaning, which was also considered a reflection of their better adaptation to the high-altitude environment.

Small East African versus Galla goats

Results of experiments examining gastrointestinal nematode resistance in goats (Baker *et al.*, 1998a,b, 2001) showed that the Small East African kids were more resistant to gastrointestinal nematode parasites than Galla kids, with the former having significantly lower faecal egg counts in the post-weaning period (8–14-month-old kids) and lower mortality from birth to 14 months of age. However, there was no significant breed effect on packed cell volume, but Galla kids were significantly heavier at all measurement times between birth and 14 months. However, heritability estimates were generally low at 0.18 ± 0.08 (mean±se) for packed cell volume and 0.13 ± 0.07 for faecal egg counts.

ILRI studies inspire and provide benchmarks for national experiments

The sheep breeds used in the various ILRI studies have subsequently been widely used in other studies, and interpretations of results suggest that these early studies by ILRI served as benchmarks or references for similar research in Africa. For example, using Dorper sheep in their experiments, Matika *et al.* (2003) found Sabi sheep of Zimbabwe to be more resistant than the Dorper – the proportion of Dorper ewes needing

treatment with antihelmintics was significantly higher than that of Sabi ewes at all sampling dates, and this effect was particularly marked at 1 and 2 months post-lambing. Getachew *et al.* (2015) compared the Menz sheep breed with the Washera breed in the highlands of Ethiopia and found that Menz sheep were better able to maintain live weight during the parasite challenge, while Eguale *et al.* (2009) compared the Arsi sheep breed with both Menz and Horro on resistance to liver fluke infection and concluded that the Horro breed was more resistant than Menz and Arsi in that environment. Like the Red Maasai in eastern Africa, the Djallonké stands out in various studies in West Africa as the breed with the most compelling evidence of parasite resistance (e.g. Traoré *et al.*, 2012; Soudré *et al.*, 2018).

Following publication of the early ILRI results on goats, the West African Dwarf goat drew attention; studies demonstrated that, like its sheep counterpart the Djallonké, it was a promising candidate breed for genetic resistance to gastrointestinal nematodes (e.g. Chiejina *et al.*, 2010; Behnke *et al.*, 2011).

Link between resistance and productivity

In addition to evidence for between-breed differences in resistance to endoparasites, these studies also provided the first hard evidence of genetic variation within breeds of sheep and goats in Africa, i.e. significant heritability estimates strongly pointing to opportunities for within-breed improvement of this trait through selection. Specifically, the results confirmed that Red Maasai sheep and Small East African goats are more resistant to gastrointestinal nematode parasites (predominantly *H. contortus*) than Dorper sheep and Galla goats, respectively. The resistant Red Maasai sheep and Small East African goats were also two to three times more productive than the susceptible Dorper sheep and Galla goats in the subhumid coastal Kenya environment.

With the formation of ILRI in 1995, some new research initiatives were undertaken in South-east Asia, including work led by a small ILRI team based in the Philippines and involving ten countries. The objectives of the Australian Centre for International Agricultural Research (ACIAR)-supported project were: (i) to assess anthelmintic resistance in gastrointestinal nematode parasites (worms) of sheep and goats and to investigate methods of blocking their spread; (ii) to assess genetic variation in resistance to worms in indigenous and imported breeds of sheep and goats; and (iii) to disseminate information about control of worms in sheep and goats in the tropics. Interventions investigated included the strategic use of anthelmintics, the usefulness of ethnoveterinary therapies, biological control, improved nutrition, grazing management and housing, and utilizing local indigenous breeds with at least some resistance to worms. The results of this research are summarized in Sani *et al.* (2004). This work established that importation of purebred Merinos was not a good idea because of their susceptibility to worms, but that imported St Croix sheep showed resistance and adaptability to tropical conditions. In goats, the native goats in the Philippines and imported Boer goats were somewhat more resistant than imported Anglo-Nubian and Saanen goats. A key achievement of this work was the design and testing of integrated worm control programmes in a number of different countries and management systems in South-east Asia.

QTLs for resistance to endoparasites in small ruminants

The existence of within-breed variation strongly suggested that selection for nematode resistance in sheep (and goats) in breeding schemes would help to reduce the direct and indirect costs of parasitism to production. However, this is not widely practised because of the difficulty of measuring parasite resistance or correlated indirect selection criteria. It was considered, therefore, that identifying genes or linked markers with a significant association with the variance of indicator traits of internal nematode resistance in sheep would facilitate the inclusion of nematode resistance in breeding operations. New technologies were already becoming available that could be applied for breeding purposes if the genes or QTLs involved in parasite resistance or markers that are closely linked to these genes could be identified.

The hunt for QTLs (Silva *et al.*, 2011; Marshall *et al.*, 2013; Benavides *et al.*, 2015) did not point to a definitive region as an obvious candidate for selection. Several genomic regions featured in the search for markers for nematode resistance in sheep, and genomic regions that

have been identified as being significantly associated with indicator traits for nematode resistance vary widely among studies. This could be due to differences in experimental protocols and materials (studies differed in the sheep breeds and nematode species, the indicator traits for internal nematode resistance, and the challenge regimes), differences in the analytical approaches, population stratification, complexity of the physiological processes of nematode resistance or a combination of factors. Sayers and Sweeney (2005) reported similar results for the MHC genes, interferon-γ gene, IgE gene and microsatellites on chromosomes 1, 5 and 6. Crawford *et al.* (2006) reported a large number of suggestive QTLs (more than one per family per trait than would be expected by chance) and concluded that most of the genes controlling this trait are of relatively small effect. Marshall *et al.* (2009) suggested that where traits are controlled by multiple QTLs (such as age and/or immune status specificity in Merino sheep), a panel of QTLs is required to achieve significant genetic gains through marker-assisted selection.

Alba-Hurtado and Muñoz-Guzmán (2013) noted that genetically resistant sheep have non-specific mechanisms that block the initial colonization by *H. contortus* larvae, and that they also have an efficacious response of T-helper type 2 cells (e.g. increases in blood and tissue eosinophils, specific IgE class antibodies, mast cells, interleukin-5, interleukin-13 and tumour necrosis factor) that protect them against the infection. The use of a mouse model to help the genome-wide search for QTLs influencing immunological responses to infection with the gastrointestinal nematode (in this case the parasite *Heligmosomoides polygyrus*) did not help either (Iraqi *et al.*, 2003; Menge *et al.*, 2003; Behnke *et al.*, 2006). Here, too, many genomic regions with small effects were implicated.

Thus, although there are some genomic regions that have featured in multiple studies across breeds (e.g. the interferon-γ region on chromosome 3 has come up as influencing a significant proportion of the variance for nematode resistance traits by multiple authors; e.g. Coltman *et al.*, 2001; Paterson *et al.*, 2001; Beh *et al.*, 2002), there really is no compelling convergence on one or a few regions that explain the large variation in resistance. Currently, there is no evidence pointing to the possibility of establishing a breeding programme focusing on one or two genomic regions. Having realized that there was no major gene (or small number of genomic regions with large effects) involved in conferring resistance to gastrointestinal nematodes, and that there were instead many genes/genomic regions, each with small effects, a multi-trait selection programme was initiated at ILRI's Kapiti Ranch for both Red Maasai and the Dorper × Red Maasai crosses, under natural and continuous challenge (see section on 'Genetic improvement of livestock').

DAGRIS

Information on the extent of diversity, characteristics and use of indigenous farm AnGR in developing countries is the basis for their present as well as future sustainable utilization. Published data on this diversity were disparate, uncoordinated and largely inaccessible. In view of the lack of a systematic database on this information, ILCA initiated development of the DAGRIS in 1993 as a web-based electronic source of information on selected indigenous farm AnGR (Rege *et al.*, 2007). This was an important product of genetic characterization work over the years and into the future. The working objectives of DAGRIS were to: (i) compile and organize information on farm AnGR from all available sources; (ii) maintain the integrity and validity of the information; and (iii) disseminate the information in a readily accessible way to key stakeholders. Today, DAGRIS has information on breeds/strains of eight species, namely, buffalo (139 breeds/strains), cattle (189), chickens (126), dromedary camels (10), goats (83), pigs (166), sheep (179) and yak (30), with options to extend it further to cover geese, turkey and ducks. Its current geographical scope is Africa and selected Asian countries, with an envisaged future coverage of developing countries in Asia and Latin America and the Caribbean.

The database contains information on the origins, distribution, diversity, present use and status of indigenous farm AnGR from past and present research results, information that can be used to form the basis for designing breed improvement as well as conservation programmes. DAGRIS is available online (http://dagris.ilri.cgiar.org; accessed 28 January 2020) as well as

on CD-ROM, making it accessible even to those without internet connectivity. The utility of this resource is demonstrated by increasing trends in website visits and citation indices.

Biorepositories/biobank facilities

The Azizi Biorepository is the long-term storage system and associated informatics tools that comprise the biorepository at ILRI. The system supports and has supported a number of activities and projects, including 'Infectious Diseases of East African Livestock', 'Arbovirus Incidence and Diversity', 'People, Animals and their Zoonoses', 'Dynamic Drivers of Disease in Africa Consortium', 'African Bovine Trypanosomiasis', the ILRI livestock diversity collection and ILRI's unique collection of pathogen isolates. The core collection is approximately 450,000 samples in vapour-phase liquid nitrogen with uniquely robust, secure and well-monitored ultra-cold conditions for long-term storage. Samples and associated data collection are based on strict protocols and procedures to ensure that they meet the required and acceptable minimum standards. The repository provides a platform for researchers to mine samples and data that can be used in their research. This in turn means that expensively obtained samples can be used and re-used for additional purposes and that the metadata associated with each sample is continually enriched, thus enhancing efficiency. The repository approach also maximizes biological understanding as it facilitates different pieces of information about identical samples. In addition, samples and data in the repository are managed to ensure that they meet CGIAR requirements of open access. ILRI's Azizi Biorepository is the only one of its kind in sub-Saharan Africa for the products of long-term characterization work. It currently contains samples of a wide range of livestock species and breeds, wildlife, insects and disease-causing organisms. Samples are in various forms including blood, serum, milk, faecal material, DNA and RNA.

Economic valuation

In 1999, FAO and ILRI convened a workshop on 'Economic Valuation of Animal Genetic Resources' to provide expert guidance on valuing AnGR. In the face of strengthening laws for intellectual property protection of germplasm under the Convention on Biological Diversity, it was also becoming apparent that the past collegial system of free exchange of germplasm among researchers was going to break down fast, requiring that some mechanism (e.g. through mutually agreed terms) for genetic resources movement across borders would be needed, both for research and for commercial purposes. It was recognized that, because markets exist only for finished or nearly finished commercial genetic resources, the value of unimproved materials and the value added that were not 'valued by commercial interest' in the long process of breeding (including through efforts of indigenous communities) could not be measured directly. Yet this was going to be critical under the Convention on Biological Diversity regime, i.e. it was important that 'parties' (e.g. communities and countries) had a way of determining the values of the AnGR involved in an 'exchange', whether within countries or across borders. During the ILRI convening, Mendelsohn (1999) made at least three arguments for economic valuation of AnGR: (i) to inform breeding programmes; (ii) to guide choice of breeds in conservation programmes and (iii) to facilitate benefit sharing (in the context of the Convention on Biological Diversity). It was also considered that economic valuation would be instrumental in guiding resource allocation between biodiversity conservation and other socially valuable endeavours. Likewise, the results of valuation would be used in various types of genetic resource conservation, research and development, including in the design of economic incentives and institutional arrangements for farmers/genetic resource managers and breeders. For example, AnGR erosion could be understood in terms of the replacement of breeds and strains, not only by substitution but also through cross-breeding and the extinction of livestock populations.

Following the 1999 ILRI/FAO joint 'Economic Valuation of Animal Genetic Resources' workshop, ILRI initiated a programme on 'Economics of AnGR Conservation and Sustainable Use', focusing on valuation methodologies. The valuation dimensions covered included: risk of extinction as an important consideration for

allocating conservation resources (Reist-Marti *et al.*, 2003; Simianer *et al.*, 2003); farmer preferences (Jabbar and Diedhiou, 2003; Duguma *et al.*, 2011); trader preferences (Scarpa *et al.*, 2003a); effects of subsidies of local and imported germplasm (Drucker *et al.*, 2006); value and impact of cross-breeding (Karugia *et al.*, 2001; Ayalew *et al.*, 2003); valuation in the context of community-based management of AnGR (Drucker, 2003); specific genetic resources for specific environments (Scarpa *et al.*, 2003b; Omondi *et al.*, 2008); and influence on policy (Drucker, 2010). An important goal of the economic valuation of AnGR is the development of policies and strategies for conservation and sustainable utilization of these resources. Economic valuation tools were also seen as contributing to the development of policies and strategies for conservation and use by providing critical information for decision making in this domain. Of particular interest was the situation in developing countries, where, on the one hand, livestock make important contributions to human livelihoods and food security, while on the other, genetic erosion was placing at risk many breeds adapted to the low-input agriculture and extreme environments typical of these countries. For example, although their productivity in absolute terms is lower than commercial breeds under intensive production systems, indigenous AnGR are often the only option available for millions of farmers in the African agropastoral systems, where exotic improved breeds underperform (if they survive) in traditional management systems.

Tools for conservation decisions

Valuation studies undertaken by ILRI and partners have provided tools and methods for valuation that can be broadly applied. Choice experiments were found to be a promising tool for valuing phenotypic traits expressed by indigenous AnGR (Scarpa *et al.*, 2003a), while the Weitzman approach was found to be a potentially effective methodology for determining conservation strategies under highly varying circumstances and for many species (Reist-Marti *et al.*, 2003). Simianer *et al.* (2003) proposed a functional relationship between conservation funds spent in one population and the conservation effect in terms of reduced extinction probability. The results indicated that, in some cases, highest priority could be given to breeds for which the 'conservation potential' (i.e. the product of extinction probability and marginal diversity) is maximum, and that these are not necessarily the most endangered breeds.

Some of the results of this work have pointed to the fact that conservation goals can be generally modest (FAO, 2013), and in view of some of these findings, it has been estimated that the 'not at risk' status category (as applied in the FAO recommended framework) requires 2000 breeding females in species with high reproductive capacity and 6000 in species with low reproductive capacity. This suggests that the costs of conserving a priority portfolio of at-risk breeds may also be quite modest (Drucker, 2010). An assessment of public willingness to pay for conservation by Zander *et al.* (2013) and estimates of the support payments that would be required to achieve the stated conservation goals suggest that such conservation costs may well be both economically justifiable (benefits outweighing costs) and relatively low cost. Thus, conservation costs may be overestimated if based only on conventional economic opportunity cost estimates, especially considering findings by Krishna *et al.* (2013), which suggested that farmer willingness to participate in genetic resources conservation activities for the public good may be more closely related to the consumption values of the genetic resources in question than to their production opportunity costs (which generally do not take into account the existence of farmers' many non-market preferences and values).

ILRI's work in this area has received recognition. The first report on 'The State of the World's Animal Genetic Resources for Food and Agriculture' (first SoW-AnGR; FAO, 2007) included a section on methods for economic valuation with an overview of the various types of value (direct and indirect use values, option values, bequest values and existence values) and described potential methods and tools for assessing them, with explicit reference to work done by ILRI and examples of the use of these methods and tools and the findings obtained on the methods. The second SoW-AnGR (in 2015) focused on economics of use and conservation, reflecting and explicitly recognizing advances that

had been made on valuation methodologies during this period. It has been recognized, for example, that accounting for total economic value can determine, among other things, whether the benefits of intervention outweigh the costs, as well as appropriate intervention strategies, including for situations in which specific AnGR have little or no current market-development potential. Where conservation funds are limited, understanding the 'true' (i.e. total) economic value of different breeds and their contribution to the public good can be an important tool in priority setting and allocation of funds (Fadlaoui *et al.*, 2006). An understanding of the relative values of the different components of total economic value can also be used to provide insight into the viability of different use and conservation strategies, such as identification of the relevance of different types of economic value and associated ecosystems services to different stakeholder categories and their willingness to pay for the services provided by the maintenance of breeds (Zander *et al.*, 2013). Indirect use values, such as cultural and landscape maintenance values, are likely to be of more relevance to local communities, while option values are likely to be of relevance to a much broader range of stakeholders. To maximize societal welfare, strategies for conservation through active use need to be designed with a view to maintaining the ongoing provision of the public-good breed-related functions that people value most (Martin-Collado *et al.*, 2014).

Genetic Improvement of Livestock

Cross-breeding of indigenous livestock with exotic breeds has for a long time been considered a faster way of making genetic improvements and one that is simple because it does not require the same level of performance and pedigree recording as selection. However, inadequate nutrition and the presence of significant biotic and abiotic stresses, including poor management, have continued to limit the use of high-input exotic breeds of livestock and their crosses, and is largely why many farmers in Africa still keep the more resilient indigenous livestock breeds. There have been only a few success stories of within-breed improvements of indigenous breeds.

The productivity potential of native livestock breeds under various systems remains largely unexploited. This, plus the fact that cross-breeding is considered to produce faster results, has informed the widespread practice of upgrading indigenous breeds through cross-breeding using imported breeds, particularly for milk and meat production. East Africa (especially Kenya but also Ethiopia, Rwanda, Tanzania and Uganda to smaller extents) leads other sub-Saharan African regions such as West Africa in the use of cross-breeding, especially for generating 'grade' cows used in smallholder dairy systems. However, cross-breeding is also widely applied in beef systems in southern Africa and in sheep and goats as well as in chickens across the African continent. In addition to upgrading, systematic programmes aimed at creating new synthetic or composite breeds apply a combination of planned cross-breeding and selection. Kenya, like South Africa, has had programmes aimed at developing dairy goats – the Kenya dual-purpose goat and the Meru goat (Ojango *et al.*, 2010) – through systematic cross-breeding.

Other than its work on genetics of tolerance to trypanosomiasis, ILRAD's mandate did not include genetic improvement of livestock. For its part, despite a broader mandate on livestock production, ILCA's first-generation programmes in the 1970s and 1980s had a more diagnostic orientation – 'understanding African livestock systems'. However, aspects of breeding were introduced through work started by John Trail and colleagues on quantifying performance in smallholder and pastoral systems (e.g. Trail, 1981; Trail and Gregory, 1981, 1982; Trail *et al.*, 1982, 1984, 1985) and by NARS visiting scientists and collaborators (Kiwuwa *et al.*, 1983; Tawonezvi *et al.*, 1988a,b) recruited specifically for that purpose. The ILCA Strategy and Long-Term Plan from 1987 was more explicit in its attention to animal genetics and breeding. In this plan, the Cattle Milk and Meat Thrust included a sub-theme on 'evaluation of the genetic potential of cattle breeds and their crosses for milk and meat production', while that of Small Ruminant Meat and Milk included 'evaluation of small ruminant genetic resources to identify appropriate breeding strategies'. The Trypanotolerance Thrust committed to the collection and analysis of data on the productivity of trypanotolerant

breeds under various levels of trypanosomiasis risk, and definition of selection criteria for trypanotolerance (see Chapters 2 and 3, this volume), to devise optimum breeding programmes. Through these activities, mostly implemented in partnership with NARS, ILCA helped to analyse and publish data sets characterizing cattle and small-ruminant populations in Africa on the basis of performance traits, and ILRAD and ILCA led efforts in collaboration with NARS, ITC and CIRDES, among many partners, to document trypanotolerance traits in cattle and small ruminants. ILCA's breed comparisons were done principally by assisting NARS scientists to analyse on-farm and on-station data. In 1989 and 1990, ILCA recruited visiting scientists[1] and provided other support to sub-Saharan African countries in interpretation of breeding data (e.g. Mwenya, 1990).

Analysis of long-term breeding programmes

Much of this early work emphasized breed/genotype evaluations to provide information on how different indigenous African livestock breeds and their crosses performed under different management systems (e.g. Rege *et al.*, 1993a,b,c; Tawah *et al.*, 1993; Thorpe *et al.*, 1993; Moyo *et al.*, 1996; Kurtu *et al.*, 1999) or to assess the effectiveness of long-term national breeding programmes in terms of genetic progress made, for example, in cattle (e.g. Rege, 1991; Rege and Wakhungu, 1992; Tawah *et al.*, 1994) and sheep (Yapi *et al.*, 1994; Yapi-Gnaorè

et al., 1997a,b), the latter being through an Open Nucleus Breeding System (Box 1.4). ILRI also contributed to the evaluation of two composite breeds in Tanzania: the Mpwapwa cattle (Kasonta, 1992) and the blended goat (Das *et al.*, 1996).

Apart from informing breeding policies within sub-Saharan African countries, some of these studies also made methodological contributions as well as human capacity strengthening for the region. For example, the weight of calf weaned per 100 kg metabolic body weight of cow exposed to the bull was examined as a possible approach for adjusting for differences in maintenance requirements by different cow genotypes, thus providing a 'fair comparison' between small-bodied indigenous breeds and large-bodied exotic breeds and crosses (the belief that local breeds were small and not as good drove importations of exotic breeds); the effect of date of birth on growth performance in seasonally bred beef cows was examined as a means of determining the optimum breeding time in such systems (Rege and Moyo, 1993); and a method was proposed for estimating between-breed differences in cross-breeding parameters and their sampling variances in these systems (Rege *et al.*, 1993a). Recommendations based on in-depth analyses of the Sahiwal Stud of Kenya (Rege and Wakhungu, 1992) and the Kenya Dairy Cattle Improvement Program using long-term data provided evidence that informed changes in these breeding programmes, such as a decision to open the Sahiwal Stud herd (which until then had been a closed herd) to bring in new breeding stock to reduce inbreeding levels and to broaden

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Box 1. 4. Open Nucleus Breeding System for sheep improvement in West Africa.

A selection programme was set up in 1983 in Côte d'Ivoire to improve the growth and live weight of the indigenous Djallonké sheep using an Open Nucleus Breeding System (Yapi *et al.*, 1997a,b). Selection was based on male individual weights at 80, 180 and 365 days of age. Multiple sires were used in farmers' flocks. ILCA helped to analyse this programme in 1995/6. Individual animal models using an average numerator relationship was used to estimate breeding values from which genetic trends were derived. A total of 10,417 records of 80-day weights (WT80) of lambs born between 1984 and 1992 from 29 participating farmers, and 1978 and 849 records on 180-day weights (WT180) and 365-day weights (WT365), respectively, of lambs from the nucleus were analysed. Breeding values – as a measure of genetic trends – increased by 28, 11 and 14 g/year for WT80, WT180 and WT365, respectively. The results of the study indicated that genetic progress could be made in growth performance of indigenous sheep if reasonable levels of animal management as well as selection pressure are applied in the Open Nucleus Breeding System and suggested that community-based breeding schemes had potential for genetic improvement in small-ruminant populations in these systems.

the genetic base, and a reorganization of the Kenya National Dairy Breeding Plan and its management. In all cases, the collaboration with NARS scientists was in-built and used to provide training on aspects of design and analysis of livestock breeding programmes.

Towards the optimization of breeding programmes in Africa

ILCA scientists worked with NARS in the 1980s on breed comparison studies, which focused on cattle (both dairy and beef) and small ruminants. The finding by early researchers (e.g. Kiwuwa *et al.*, 1983) of similarity in performance of the 75% and 50% *B. taurus* crossed with African Zebu was among the first (based on a large data set covering 1968–1981) to signal that there was a 'limit to upgrading' and that this limit depended on the production system. Marshall *et al.* (2017) showed that exotic dairy cattle under good management do have higher milk yields than local × exotic crosses, but the additional cost of feed is such that local × exotic crosses are more profitable. A similar project implemented in West Africa – the Senegal Dairy Genetics project – resulted in strong recommendations on the best genotype in Senegal dairy systems, based on a trade-off perspective (Salmon *et al.*, 2018). These studies

plus evidence from genetic diversity research have induced a gradual recognition that 'upgrading towards exotic genotypes' across all systems is a mistake and that indigenous genetics should play an important role in breeding programmes.

The challenge to genetic improvement, however, goes well beyond the choice of breeds. Institutional and organizational challenges are as binding as genotype in many African countries (Kosgey, 2004; Kosgey and Okeyo, 2007; Rege *et al.* 2011). Consequently, even cross-breeding practice, considered to be easier than within-breed selection, has generally not been well-planned in Africa and outcomes have been inconsistent. Many cross-bred populations, including the dairy herds in Kenya and other East African countries where cross-breeding for dairy production is considered a success, tend to be a mix of genotypes (Aliloo *et al.*, 2018; Mrode *et al.*, 2018). The so-called 'grade' or cross-bred animals in smallholder systems in Kenya, for example, are composed of a wide range of genotypes, and in the absence of pedigree records, genotypes of individual cross-bred animals are generally unknown.

These challenges have informed ILRI's recent work in 'genetic improvement'. One problem has been determination of optimum genotypes for specific production systems. Figure 1.2 illustrates levels of milk production by different
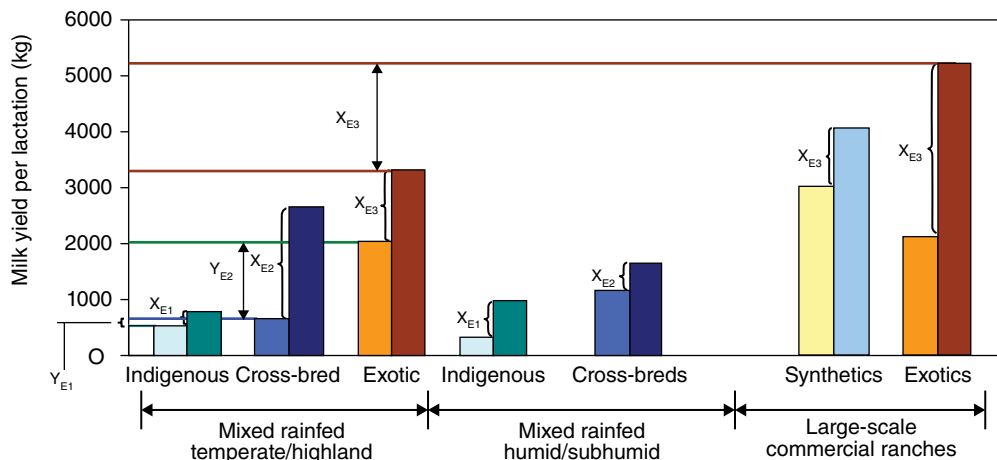
Fig. 1. 2. Milk production by genotype in dairy production systems of eastern Africa. Light-coloured bars, minimum production; dark-coloured bars, maximum production; x_i, differences in production due to 'animal husbandry practices'; y_i, differences in production due to 'genotype'. (From Mwacharo *et al.*, 2009.)

genotypes – indigenous, cross-breds, composite breeds and exotics – in dairy production systems in eastern Africa. The figure shows that cross-breeding certainly has a role to play and also illustrates the critical need for matching genotypes with production environments, especially considering that smallholder producers in these systems have little control over the many environmental and production factors/stresses that affect and constrain the productivity of their livestock. This was the compelling documentation of G×E presented in a way (yield gaps) that development partners can easily understand. Subsequent data from ILRI's own work (e.g. from the DGEA project) have not contradicted the general patterns in genotype comparisons but have shown diminishing returns to upgrading under smallholder systems (performance improvements beyond F_1 being rare in most situations).

Breeding programme design

There had been growing demand among NARS for ILRI engagement in: (i) non-ruminant livestock research, specifically chickens; and (ii) support for breeding programmes that went beyond analysis of existing information. In ILRI's long-term strategy to 2010 (ILRI, 2000), two decisions were made: (i) to expand the genetic characterization portfolio beyond cattle, sheep and goats to include, for the first time, an explicit commitment to 'contribute to the characterization of indigenous swine, poultry, camel, buffalo and yak populations in Africa and Asia'; and (ii) to engage more directly in 'developing breeding strategies to improve utilization of diversity of indigenous livestock to increase productivity in smallholder systems'. It is to be noted, however, that although there had not been a formal programme as such in this area up to this point, individual ILRI scientists were already contributing to breeding programme design, mostly through graduate student projects and fellowships (e.g. Kosgey, 2004; König *et al.*, 2017). Among the major activities initiated following the decision to engage in breeding programme design, four stand out: Two are in dairy – the DGEA and the African Dairy Genetic Gains (ADGG) projects – and two are in chickens – the Horro chicken improvement and the African Chicken Genetic Gains (ACGG) projects.

Appropriate germplasm for smallholder dairy farmers

The DGEA project was funded by the Bill & Melinda Gates Foundation. Determining the size of breed differences *in situ* (linking farmers' genotypes to productivity) was a core question of the DGEA project. The answer was expected to allow calculation of the net benefits of investment in germplasm delivery. Specifically, the DGEA project set out to answer two broad questions (Rege and Gibson, 2009): (i) what are the optimum breed combinations for smallholders in different production environments? and (ii) how can sustainable germplasm supply systems be developed?

Optimum breed combinations

High-density SNP technology was used to optimize choice among cross-bred dairy cattle in Kenya and Uganda, primarily for *in situ* assessment of the performance of existing genotypes (Ojango *et al.*, 2014). While SNP data accurately estimated breed composition, they only did so under very careful construction analyses and, as such, caution must be taken in applying their results in decision making.

Sustainable germplasm supply

The activities under sustainable germplasm supply involved the design, operation and support of an innovation platform, bringing together agents in the germplasm supply chain to smallholders. The innovation platform led to identification of business opportunities in dairy genotyping (specifically heifers and artificial insemination). Several local farmers and traders established businesses that identified sellers of heifers, found buyers, and built seller and buyer capacity in heifer management.

Supporting on-farm selective breeding by smallholders

The absence of breeding recording in developing countries has been a major limiting factor to systematic selective breeding in Africa (Kosgey and Okeyo, 2007; Zonabend *et al.*, 2013). Other limiting factors are poor breeding infrastructure and lack of good analytical tools (Gizaw *et al.*, 2014; Mrode *et al.*, 2018; FAO, 2016). It is now

well recognized that, unless recording is owned and run by industry (farmers themselves) with sufficient incentives to make them participate, it is unlikely that sustainable recording programmes can be achieved. This explains why the limited schemes remain restricted to the large commercial farming sector where owners recognize and are willing to pay for recording.

To address the recording challenge, ILRI, through the ADGG programme, in 2018/19 is supporting the establishment of farmer-driven ICT-based on-farm pedigree and performance recording in Ethiopia and Tanzania. The objectives of ADGG were to establish performance recording and sampling systems (FAO, 2016) to pilot farmer-feedback systems that help farmers improve their productivity, and to use the information and samples collected to develop systems for selecting cross-bred bulls and cows of superior genetic merit for artificial insemination and natural mating (König *et al.*, 2017). Informed by experiences of the DGEA project, the main thrust for this initiative is a digital platform for performance data capture/analytics that combines utilization of genomics to demonstrate and inform implementation of expanded genomic evaluation and better utilization of cross-bred cattle populations (see https://www.ilri.org/research/projects/african-dairy-genetic-gains). It is designed to collect and use on-farm performance information and basic genomic data to identify and provide superior cross-bred bulls for artificial insemination delivery and natural mating cows on smallholder farms. While at the time of writing the programme was still in the early stages, more than 82,000 smallholder herds and more than 190,000 animals were already being recorded on the platform in the two countries, with more than 5000 of these already genotyped and the results, together with the phenotypic records being used to generate genomic breeding value predictions (Brown *et al.*, 2016) in Tanzania and later in Ethiopia. Farmers on the platform received more than 6 million text messages in four languages to inform herd management decisions and benefitted from productivity gains.

Demonstrating potential for within-breed selection

In 2008, ILRI and Wageningen University started a pilot breeding project for Horro chickens in Ethiopia. What started as a 'proof of concept' has become a major success, the Horro chicken breed improvement programme in Ethiopia (Box 1.5), and has demonstrated that within-breed selection is possible in indigenous chickens. In November 2015, in recognition of these achievements, the prime minister of Ethiopia awarded the project the 6th National Science and Mathematics, Research and Innovation Award of Ethiopia.

The Horro chicken project, together with the community-based sheep and goat breeding program in Ethiopia (Box 1.6) and the Red Maasai and Dorper sheep breeding programme in Kenya (Box 1.7) are examples of success in establishing within-breed genetic improvement programmes. The improved Horro chicken was tested in the ACGG programme on-farm and on-station (Box 1.8). The aim was to compare the performance of this improved chicken in regions of Ethiopia with large differences in altitude, rainfall and temperature. The improved Horro chicken in the ACGG comparisons reached 714 g at about 16 weeks of age. Unimproved chickens could not reach the same live weight, even at 20 weeks of age and under improved management conditions. Moreover, the improved Horro chicken started egg laying at the age of 223 days compared with 256 days for unimproved indigenous chickens on-farm.

Towards adapted and productive chickens for African smallholders

Many past efforts to make smallholder chickens more productive in sub-Saharan Africa have not delivered optimal impact because they used high-producing commercial genotypes created for intensive temperate feeding systems. In collaboration with NARS in Ethiopia, Nigeria and Tanzania and involving several other partners, ILRI initiated a project (ACGG) in 2014 with the aim of identifying and delivering adapted chickens to support productivity growth and increased animal protein intake among rural people (Box 1.8). The key features of this project were: (i) a focus on delivery of farmer-preferred chicken genotypes; (ii) use of innovation platforms to identify chicken value chain challenges and to develop solutions in participatory processes involving key value chain actors;

Box 1.5. Horro chicken breed improvement programme in Ethiopia.

The Horro chicken breeding programme implemented by ILRI in collaboration with Wageningen University in Ethiopia started in 2008 as a PhD project of Nigussie Dana. The objective was to improve production of village chickens through participatory within-breed selection. The breeding objectives were identified using a participatory approach. The breeding programme aimed to develop a dual-purpose chicken through selective breeding. As a start, a survey was conducted to understand the production systems and the needs and constraints of smallholder chicken farmers in 225 households. The breeding goal traits identified were egg production (number), body weight, (decreased) age at first egg and survival. The base population was established from 3000 eggs purchased from various locations in the Horro region and these were placed at the Ethiopian Institute of Agricultural Research in Debre Zeit, Ethiopia. Twenty cockerels and 260 hens were successfully hatched and raised, and these formed the parental population. Selection was based on individual performance ('own performance' or 'mass selection') until the eighth generation. In each generation, approximately 600 males and 600 females were produced as selection candidates and recorded for body weight and egg production. Females were selected based on own performance for body weight and egg production. Males were selected based on their performance for body weight. Selection pressure was 10–20% in the males and 50–60% in the females.

   Evaluation of the breeding programme was conducted when the programme was in generation 8. Breeding values were estimated for both cumulative egg numbers at 45 weeks of age and body weight at 16 weeks of age to evaluate the trend of changes over the generations. The genetic trends showed that by generation 8, survival had improved from less than 50% in the base generation to almost 100% in generation 8. Body weight per bird at 16 weeks had increased substantially from 550 g to 1100 g. Egg production tripled from 64 eggs per hen per year in the base generation to 172 eggs per hen per year by generation 8. Every generation of pure-line Horro birds was kept and used as parents for the coming generations. The nucleus flock established was kept at the Debre Zeit Agricultural Research Centre. The genetic change achieved through selection was monitored by comparing the unselected animals with the selected ones. This breeding programme achieved a large and significant improvement above unselected village chickens. While the performance of this population was lower than that of commercial chicken lines (the difference decreasing with each generation of selection), the improvement was impressive. And when adaptability, taste and likeability were taken into account, the improved indigenous birds were clearly superior to commercial chickens.

Box 1.6. Community-based sheep and goat breeding programmes.

A community-based breeding programme, implemented by the International Centre for Agricultural Research in the Dry Areas (ICARDA), ILRI, Boku University and the Ethiopian NARS, was started in 2009 in Ethiopia (ICARDA, 2018; Haile *et al.*, 2019). The programme combined selective breeding of sheep and goats based on production parameters, such as body weight, lambing rate and survival. At the time of this assessment, 3200 households in 40 villages had benefitted with an average income increase of 20% in the programme sites of Bonga, Horro and Menz. Farmers had created 35 formal breeders' cooperatives to participate in the programme, and it had been replicated in more than 40 programmes that sprang up based on inspiration and learnings from the original site. Most of the participating households in Menz no longer needed assistance from government-run safety-net programmes that provided food; they were able to use their income from sheep sales to buy food. The breeding cooperatives were able to build capital from buying rams and bucks as well as from other investments. For example, the Bonga cooperative had a capital of around US$60,000. There was a high demand to breed rams and bucks from neighbouring communities and other governmental and non-governmental programmes. The government identified the community-based breeding programme as the strategy for genetic improvement of small ruminants in the Ethiopia Master Plan and Growth and Transformation Plan II, and the programme is being replicated in Iran, Malawi, South Africa, Sudan, Tanzania and Uganda.

(iii) developing sustainable public–private partnerships for improvement, multiplication and delivery of the identified genotypes and other value chain services; and (iv) placing women at the centre of the project to ensure its success, given that women are the primary owners, managers and traders in chickens and chicken products in these countries.

Box 1.7. Red Maasai and Dorper sheep breeding programmes.

Starting with a sheep flock established in 1997 as an experimental flock comprising purebred Red Maasai and Dorper sheep and their crosses, a breeding programme was introduced in 2003 aimed at improving the growth performance and resilience of the main breeds and their crosses under range conditions. Following droughts and loss of animals by pastoral livestock keepers in 2008–2010, the ILRI flock of 1100 sheep became a main source of breeding animals for communities living within the surrounding rangelands in Kenya and neighbouring countries. Informed by the finding that many genes, each with small effects, rather than one major gene were involved in conferring resistance in the Red Maasai breed to endoparasites, ILRI established a multi-trait selection programme for both Red Maasai and Dorper × Red Maasai crosses under natural and continuous challenge, with the next-generation sires and dams identified from among the young rams and ewes selected on the basis of survival, growth rate and lambing intervals under parasite challenge. The net effect was that the Red Maasai and their crosses with Dorper sheep had, over more than 12 years of selection, improved, with their 9-month weight having almost doubled, the age at first lambing and lambing intervals having slightly decreased, and lambing rates having improved. The most important outcome of this work was that ILRI's flock at its Kapiti Ranch remained one of the two major sources of improved Red Maasai rams in Kenya, with requests far above what could be supplied. Indeed, after the prolonged drought of 2008, ILRI provided many local farmers with replacements for Red Maasai sheep. With this experience, Kapiti rams were used to initiate further Red Maasai genetic improvement under community-based set-ups in Nyando, Kisumu County, and in Trans Mara, Bomet County, Kenya. Inspired by these developments, a Red Maasai breed society was registered in the Kenya Livestock Breeders organization and supported by a collaborative project of ILRI and the African Union–Interafrican Bureau for Animal Resources (AU-IBAR).

Box 1.8. Project to identify and deliver adapted chickens for productivity.

The vision of the ACGG project was to catalyse public–private partnerships for increasing smallholder chicken production and productivity growth as a pathway out of poverty in sub-Saharan Africa, with project sites in Ethiopia, Nigeria and Tanzania, countries with substantial poultry endowments and where the needs and opportunities for enhanced chicken productivity were considered among the greatest on the continent. The project was designed on the premise that having available and affordable brooded and pre-vaccinated chicks adapted to typical low-input systems in poor rural communities would greatly increase their chicken production and productivity and would reduce poverty, especially among poor women. Ten tropically adapted, low-input but productive chicken breeds from Africa and elsewhere were tested under on-farm conditions. Chicks were pre-vaccinated and brooded to 21 days old before distribution to households. The results showed that significant productivity gains could be made by testing and promoting chicken breeds that are more productive, tropically adapted and farmer preferred. The chicken strains that ACGG made available to farmers had significantly higher productivity in terms of both live body weight (an average of 200–300% higher than indigenous types) and egg production (100–200% higher) than the local chickens raised by more than 6000 farm households involved in the project.

With the testing nearly completed in the three project countries, the project in 2020 is focusing on developing the private-sector-led institutional arrangements for delivery mechanisms that will ensure that the preferred chicken strains identified are available to smallholders at competitive prices at the village level. For example, hatcheries partnering with ACGG started multiplication and delivery at scale to smallholder farmers. At the same time, the project has begun, as a next phase, to develop a roadmap for long-term genetic gains to ensure ongoing genetic improvement of the identified breeds/types. Beyond the project countries (Ethiopia, Nigeria and Tanzania), the germplasm, data and knowledge generated have the potential to benefit millions of poor rural and peri-urban households in other countries where backyard chicken production systems dominate.

Reproductive technologies for smallholders

In Africa, only Kenya and South Africa have had active research in semen sexing and *in vitro* fertilization. ILRI's work in its facilities in Kenya has adapted and tested potential applications of selected technologies to address smallholder challenges. For example, scientists from ILRI and the Department of Clinical Studies at the University of Nairobi succeeded in producing Kenya's first test-tube calf in 2009 using a technique called *in vitro* embryo production (IVEP), which makes it possible to rapidly multiply and breed genetically superior cattle within a short generation interval. IVEP eliminates the tedious steps of synchronizing donor cows and has the advantage of maximizing utilization of appropriate dam and sire genotypes by increasing the efficiency of multiplication in breeding, permitting determination of sex of the offspring and facilitating the pre-testing of actual fertility status of the sire. IVEP can produce up to 300 offspring per lifespan of a dam. ILRI and partners have also applied the IVEP technique in combination with sexed semen in what is called fixed-time artificial insemination. These protocols and the accompanying capacity were the basis of the programme for ILRI's cloned calf (Yu *et al.*, 2016).

Domestication of fixed-time artificial insemination (FTAI) protocols have enabled synchronization and have been used to extend artificial insemination to nine counties in Kenya that were previously considered unsuitable for high-yield dairying. This extension of FTAI has produced enough cross-bred heifers to support related businesses, such as private artificial insemination, and milk bulking and chilling services, in some of these counties. The Ethiopian application of FTAI has resulted in hundreds of thousands of new dairy cross-bred cows and is currently underpinning the country's dairy improvement plan.

Although the worldwide success rate of producing live cloned offspring from high-quality domestic livestock has improved in the past two decades since the successful cloning of Dolly the sheep in 1996, little has happened in Africa in this regard. ILRI scientists have undertaken research on cloning as a tool for supporting its animal health and broader research on genetics of adaptation, specifically as part of the efforts to explore the possibility of incorporating disease resistance traits of some of Africa's indigenous breeds into more productive breeds. Through these efforts, ILRI produced the first African livestock cloned by somatic cell nuclear transfer using primary embryonic fibroblasts. The only other successful cloning in Africa was Futhi (Zulu for 'replica'), a Holstein heifer born at the Artificial Insemination Centre at Brits, North West Province in South Africa, in April 2003, through a collaboration between scientists from South Africa and Denmark. Unlike Tumaini, Futhi was derived from a single cell taken from the ear of a donor cow, inserted into an ovum and later implanted into a recipient cow. Cloning of Tumaini was a proof of concept for a technology that could be used to develop improved farm animals, carrying traits of economic importance such as disease resistance (e.g. trypanotolerance).

Strengthening NARS Capacity in Livestock Genetics

Inadequate capacity is one of the major constraints to agricultural development in most of the developing world, especially in Africa and Asia. A recent study commissioned by FAO in 2017 found that the major constraints to application of most agricultural technologies in Africa relate to inadequate human capacities, facilities, financial investments and institutional capacities. In most countries, there remains a major lack of a critical mass of scientists in areas relevant for agricultural biotechnology, especially in the more advanced areas of modern biotechnology, such as molecular biology, genomics and bioinformatics.

In the livestock sector, working in partnership with national and other international partners, ILRI has contributed substantially in the research and application of medium- to high-level biotechnologies for genetic characterization and improvement of livestock. These have been implemented through four main streams: graduate training, group training, individual short-term training and internships, and coaching and mentorship achieved through collaborative projects. These are summarized below, with special reference to animal genetics and breeding.

Capacity development

ILRI has trained many MSc and PhD students in genetics and breeding, either through fellowships or in collaboration with NARS where ILRI-hosted fellows work. Since 2004, the facilities of the Biosciences eastern and central Africa–ILRI Hub (BecA-ILRI Hub), especially the Hub's genomics and bioinformatics platforms, were a major means of delivering high-quality training, including exposure to cutting-edge research facilities and approaches. As such, many of these fellows subsequently became research leaders in their own institutions, and some have retained intensive collaboration with ILRI and other institutions internationally, with these fellows using their relationships with ILRI to develop projects and to provide opportunities for next-generation graduate fellows. Indeed, many among the current generation of leading livestock geneticists in African and, to a smaller extent, Asian NARS have connections with ILRI, with a majority of these having spent time in ILRI's laboratories. ILRI has trained an estimated 200 BSc, over 69 MSc and more than 66 PhD graduates, as well as over 35 postdoctoral fellows in livestock genetics and breeding.

Group training

Through its research programmes on cattle and small ruminants, ILCA organized, starting in mid-1980 until its merger with ILRI in 1995, annual courses for 25–30 NARS scientists in the design and analysis of livestock breeding programmes. These early courses focused on analysis and interpretation of data from on-station and on-farm breeding programmes.

ILRI-SLU project

Starting in 1999, ILRI collaborated with the Swedish University of Agricultural Sciences (SLU) on a global project, 'Capacity Building for Sustainable Use of Animal Genetic Resources in Developing Countries', using a 'training the trainers' model (Fig. 1.3). This capacity-building project directly targeted NARS scientists in developing countries who are responsible for research and training in animal breeding and genetics. The objectives of the project were: (i) to strengthen the subject knowledge and skills of NARS scientists; (ii) to strengthen their communication skills, to catalyse curriculum development and delivery; (iii) to develop computer-based training resources, to stimulate contacts, collaborations and networks; and (iv) to strengthen the human base for work on AnGR in developing countries.

During the ILRI-SLU project period (1999–2010), 195 scientists from 46 countries in Africa and Asia were trained in animal breeding and genetics, including in design and implementation of breeding strategies, and in teaching and communication (Table 1.1) (Ojango *et al.*, 2011).

In addition, the ILRI-SLU project developed an electronic Animal Genetics Training Resource (AGTR; http://agtr.ilri.cgiar.org; accessed 28 January 2020), which is available online and on CD. The first version of this course was produced in 2003, a second one in 2006, and an updated and expanded one (version 3) in 2011 on a fully web-enabled platform, which allows direct online revisions of content. AGTR is a unique, 'one-stop', user-friendly, and interactive multimedia resource targeted at researchers and scientists teaching and supervising postgraduate students in animal breeding and genetics. It is a dynamic training resource designed to inform the design and implementation of breeding programmes and to provide information that empowers countries and institutions to undertake their own research applying the best available information and knowledge. The AGTR course covers established and rapidly developing areas, such as genetics-based technologies and their applications in livestock breeding programmes. AGTR is essentially a platform that extends the capacity strengthening work done by the ILRI-SLU project to reach more people over a long-lasting period.

One of the objectives of the project was to stimulate knowledge sharing and networks within regions. By linking NARS and university lecturers from different countries in the training courses, three virtual regional networks were subsequently established: (i) Afrib Breeders in Africa; (ii) IAGRA in South-east Asia; and (iii) the South Asia Genetics Group. These animal breeding and genetics virtual networks were created by the project participants as tools for sharing knowledge and information and for facilitating the development and review of collaborative proposals
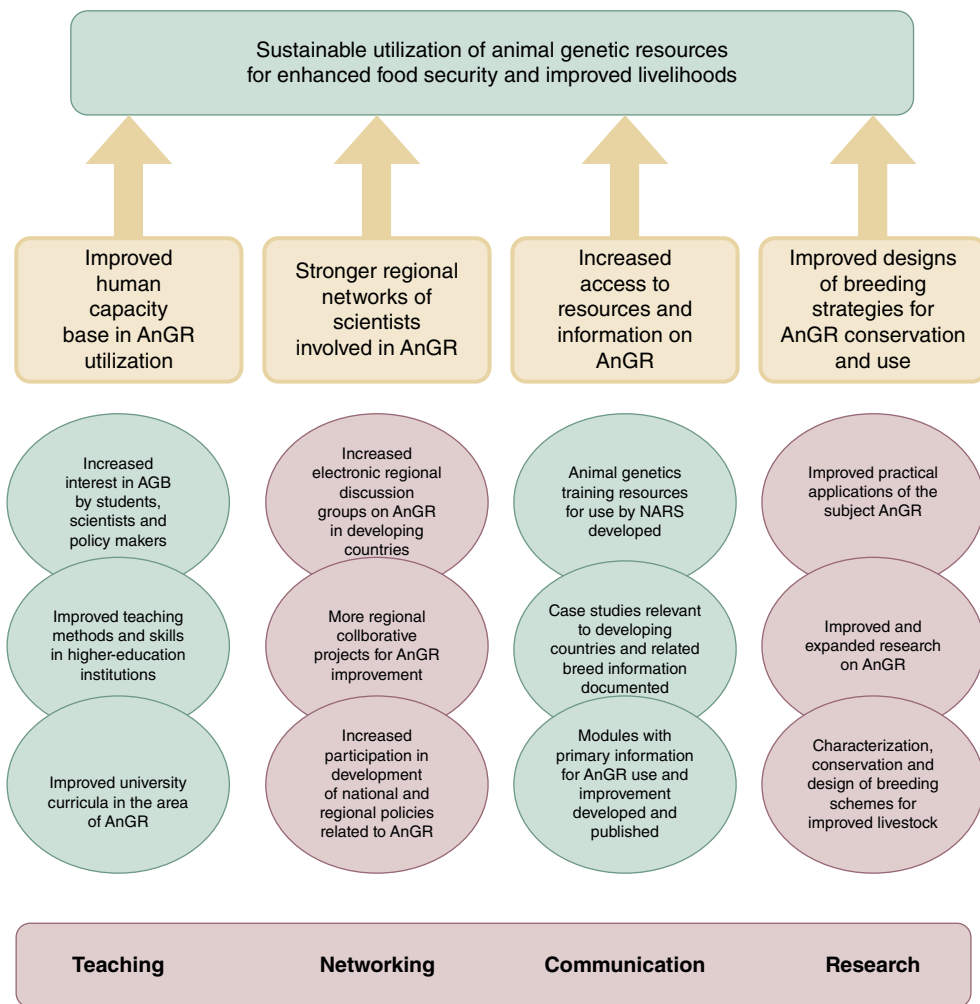
Fig. 1. 3. Outcomes of the ILRI-SLU capacity development project. (Data from ILRI archives.)

Table 1.1. ILRI-SLU training courses and trainees between 2000 and 2010. (Data from ILRI archives.)

Year	Region	Countries	Number of participants
2000	East and southern Africa	10	20
2001	West and Central Africa	10	18
2003	South-east Asia	9	18
2003	Sub-Saharan Africa	18	20
2005	South-east Asia	9	18
2006	South Asia	6	20
2006	Training request by ASARECA	9	19
2007	West and Central Africa	9	20
2008	East and Southern Africa	14	23
2009	South Asia	6	19

ASARECA, Association for Strengthening Agricultural Research in Eastern and Central Africa.

on the characterization, conservation and design of livestock breeding programmes. In this way, the project has helped to create 'communities of practice' in these regions.

ILRI has organized and delivered many short-term group training courses in genetics, genomics, bioinformatics and animal breeding, some in collaboration with the BecA-ILRI Hub platform team. For example, between 2008 and 2018, ILRI scientists provided 2-week trainings every year in a European master's degree programme in animal genetics and breeding that focused on practical applications in developing countries. The programme initially supported students from developing countries to study in Europe, after which they would return to implement their learnings in their home countries. The ILRI genetics team is a key resource for these training courses, providing topics for internships and MSc thesis co-supervision, and hosting students during their internships/MSc thesis projects. Other courses involving ILRI's genetics team include collaboration with Scotland's Rural College, which since 2014 has been running a 1-week annual training course for 21 African scientists from 14 different countries in quantitative genetics and genomic selection.

Through 'technical associates' and 'research fellows' mechanisms, ILRI's livestock genetics team has trained a large number of scientists from universities and national agricultural research institutions. Technical associates are technicians or scientific staff from NARS and other ILRI partner institutes who come to ILRI for up to 6 months for individual training at the request of their employers; this category is oriented towards persons already involved in research activities associated with ILRI. Research fellows are university and national agricultural research institution scientists undertaking work in research areas similar to those at ILRI. Designed to benefit the future research capability of the individuals and their home institutions, research fellows spend a maximum of 18 months at ILRI to undertake non-degree-related training in research methodologies, to discuss the design and planning of collaborative research, and to analyse and write up research results. While all areas of the livestock genetics programme have undertaken individual training through these mechanisms, the animal genetic characterization (phenotypic and molecular) team has hosted the largest numbers,

with operationalization of the BecA-ILRI Hub platform in the early-2000s being a major driver; large numbers of scientists from across Africa sought space to extract and analyse DNA samples and to get help with their data analyses. The major constraint to ILRI's hosting even larger numbers of technical associates and research fellows has been inadequate financial resources to support them.

ILRI's livestock genetics activities have been dependent on strong partnerships with NARS, both as providers/owners of samples and data and as direct collaborators in the research process, design, experimentation, analysis and reporting of research results. These collaborations have been critical for mutual learning, with ILRI scientists benefiting by deepening their own understanding of the relevant livestock production systems and institutional contexts of research in NARS. NARS scientists, on the other hand, have benefitted from exposure to advanced research facilities and methods that many of them have no access to in their home institutions. Very importantly, the exposure has allowed many of these scientists to engage in expanded and productive networks of scientists, both in their own regions (Africa and Asia) and internationally – especially with ILRI's many traditional advanced research institute partners. Through the direct coaching of these scientists in the research process and their exposure to, and mentorship by, the ILRI research community, as well as the expanded networks they can engage in, ILRI has created a large number of global leaders in livestock genetics for development in Africa and Asia.

Conclusions and the Future

The efforts of ILRI and its partners in breed surveys, phenotypic and molecular characterization, breed evaluation studies, genetics of disease resistance, genetic improvement strategies, development of associated tools and approaches, and the wider promotion and use of these tools have collectively contributed to a deeper understanding of African and Asian livestock populations. The associated capacity development efforts have helped to broaden the application of these results and tools both in space and in time. Taken together, these investments have led to:

(i) classification and characterization of indigenous livestock breeds of Africa and Asia, using phenotypic and molecular genetic information, facilitating a greater understanding of the underlying genetic diversity in these regions; (ii) databases on the geographical distribution and physical and performance characteristics of indigenous livestock; (iii) contribution to the reconstruction of genetic history and geography, with links to human migration and settlement; (iv) confirmation of the uniqueness of specific indigenous breeds and better quantification of their unexploited potential such as disease resistance; (v) development and testing of tools for genetic characterization and conservation; and (vi) targeted application of functional genomics. Recent and exciting findings include a study on the genome landscape of African livestock (Kim *et al.*, 2017) and the development of harmonized phenotypic and genetic characterization tools and protocols led by AU-IBAR for national and regional gene banks (www.au-ibar.org/angr/432-regional-inception-workshops-for-animal-genetic-resources; accessed 28 January 2020).

The future of ILRI's genetics research and development programmes will be influenced by four factors: (i) the CGIAR global livestock agenda; (ii) ILRI's long-term strategy; (iii) emerging and anticipated livestock challenges in coming years including new infections and disease variants spreading to new regions largely driven by climate change, challenges associated with smallholder intensification, and challenges imposed by the ever-decreasing farmland and limited forage resources, requiring more feed-efficient livestock; and (iv) partnership arrangements that will require constant re-examination of ILRI's comparative advantage.

ILRI currently has a rich resource base, collaborative arrangements and a wide-scale partnership model to push its livestock genetics agenda to higher levels and with greater impacts. These include the suites of techniques, protocols and approaches for genetic improvement of livestock as discussed in this chapter,

proven breeding technologies such as cloning and associated embryo transfer technologies, and other tools needed to navigate new areas of livestock improvement such as developing transgenic animals with resistance/tolerance attributes. These tools, together with global advancements in genetic technologies, including SNPs and gene drives as well as ICT platforms that can be used to facilitate the creation of integrated large-scale data systems, especially genomic data (and which can enhance the democratization of data to ensure unconstrained access by NARS), promise new possibilities for livestock improvement in the developing world.

In supporting the application of economic valuation methodologies, ILRI's work will focus on understanding and applying the economics of conservation and use in decision-making contexts such as choice of traits and breeds/genotypes, public willingness to pay for services (breeding and conservation) and incentive mechanisms for conservation. ILRI's work in this domain (e.g. Muigai *et al.*, 2009; Tarekegn *et al.*, 2016) has demonstrated the link between knowledge of genetic diversity and conservation and use programmes. In future, a more compelling link will need to be demonstrated, with practical examples across different species.

ILRI will need to explore partnerships with the private sector (the development of ICT-based platforms, such as that envisaged in the ADGG project, can provide proof of concept) while ensuring that the interests of smallholders are not compromised. Development of models for facilitating the testing and delivery of appropriate genotypes for smallholders and for ensuring ongoing genetic gains – such as what was piloted in the DGEA and envisaged in the ACGG projects – are examples. Indeed, ILRI has already shown increased involvement in on-farm breeding programmes and extension services in some countries in Africa and Asia, following enhanced partnership with NARS. It is envisaged that these endeavours will be pursued by an expanding network of global collaborators.

Note

[1]Sam Okantah, from Ghana; Wilson Mwenya, from Zambia; and Ed Rege, from Kenya.

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2 Control of Pathogenesis in African Animal Trypanosomiasis: A Search for Answers at ILRAD, ILCA and ILRI, 1975–2018

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Contents

Executive Summary

The problem

African animal trypanosomiasis (AAT, also known as 'animal African trypanosomiasis') is a serious disease of the tropics and subtropics, adversely affecting cattle production as animals suffer from loss of condition, emaciation and anaemia, resulting in reduced meat and milk production and draught power for agricultural production. Cattle mortality can reach 50–100% within months of exposure. The disease is caused by parasites that live in the host blood plasma, body tissue and interstitial fluids. Trypanosomes are transmitted to the host by a vector, the tsetse fly. The parasite replicates within the tsetse fly and is transmitted through saliva when the fly feeds on the animals. While this disease predominantly occurs in sub-Saharan Africa, it has also been found in South America, where one AAT agent (*Trypanosoma vivax*) has been established and tabanids (biting flies) act as the mechanical vector. The most rigorous calculation of the cost of AAT in sub-Saharan Africa dates from the late 1990s (Kristjanson *et al.*, 1999). Kristjanson estimated the annual cost to be US$1.3 billion, excluding losses from potential output in regions where trypanosomes prevent livestock production and excluding the costs of foregone power and manure output.

Animal trypanosomiasis can be managed by three strategies: (i) vector control/eradication; (ii) use of trypanocides; and (iii) use of trypanotolerant breeds of cattle (see Chapter 3, this volume). Vector control includes reducing the tsetse fly population with traps and insecticides, and in areas with a high population of trypanosome-infected tsetse, animals are prophylactically administered antiparasitic drugs. To date, there is no AAT vaccine available, as discussed below.

Scientific impacts

The International Livestock Research Institute (ILRI) and its two predecessors, the International Livestock Centre for Africa (ILCA) and the International Laboratory for Research on Animal Diseases (ILRAD), have made significant contributions to trypanosomiasis research since the early 1970s.

The first contribution was the establishment of protocols for cultivation *in vitro* of bloodstream stages of *Trypanosoma brucei* and subsequently *Trypanosoma congolense*. This advance facilitated downstream investigations of *T. brucei* and *T. congolense* cell division cycles, endocytic processes, interaction with antibodies against variable surface glycoproteins (VSGs) and other trypanosome antigens, interactions with trypanocidal drugs and mechanisms of development of drug resistance.

The second contribution was recognition that trypanosome strain complexity and surface coat antigenic variation precluded the development of an effective conventional vaccine targeting the immunodominant coat antigens. Subsequent identification of required macromolecular growth nutrients and uptake pathways also did not lead to an effective vaccine because, under steady-state conditions, anti-receptor antibodies did not kill the parasites or prevent acquisition of the nutrients.

Although the vaccine approach proved unsuccessful, studies in this area at ILRAD advanced our understanding of trypanosome biology.

The third contribution was a deepening understanding of bovine immunology per se (see Chapter 4, this volume) and as it pertains to responses against African trypanosomes and other pathogens.

A fourth contribution was an understanding of the biological and genetic basis of trypanotolerance. ILRAD, ILRI and their partners were able to characterize N'Dama cattle, a small multi-purpose indigenous breed that can survive without chemotherapy in some regions of sub-Saharan Africa where AAT kills susceptible breeds.

Field research in the area of trypanotolerance established the need for complementary technologies, such as spraying to kill the tsetse vector and trypanocidal drugs.

Analysis of trypanosomiasis in trypanotolerant N'Dama cattle and their crosses with trypanosomiasis-susceptible Boran cattle found that two major indicators of trypanotolerance, namely control of anaemia and parasitaemia, are unlinked. The work introduced an additional indicator of trypanotolerance, namely the ability to generate IgG1 antibodies against buried VSG epitopes and epitopes on many common trypanosome antigens, including congopain and heat-shock protein 70 (Hsp70)/binding immunoglobulin protein (BiP). Traits that distinguished between N'Dama and Boran cattle trypanotolerance in cattle proved to be regulated by multiple unlinked genes. Mapping of the trypanotolerance genes in cattle was an integral, and initially a leading, component of the bovine genome-mapping programme worldwide. The results of the study were consistent with a single quantitative trait locus (QTL) on each of 17 chromosomes, and two on BTA16 (*Bos taurus* chromosome 16), with individual QTL effects ranging from about 6% to 20% of the phenotypic variance of the trait, weighing against use of markers for these QTLs in breeding programmes to enrich for the trait. Archives of genomic and complementary DNA (cDNA) have been established from the bovine trypanotolerance studies carried out at ILRAD/ILRI and are available for deeper analysis as technology in this field undergoes further development to facilitate linking genes to disease-resistance traits. The genetic complexity of trypanotolerance

in cattle proved greater than that found in crosses between inbred strains of mice; here, three regions of host DNA were shown to be associated with trypanotolerance and a candidate resistance gene, *Pram1* (PML-RARA-regulated adaptor molecule 1), has been proposed for one of these regions.

A fifth contribution was the discovery of diagnostics and subsequent efforts to prevent and contain the development of trypanocidal drug resistance in the parasite.

ILRAD and subsequently ILRI developed computerized data management and analysis systems, geographic information systems and digital georeferenced databases to address the distribution and dynamics of AAT in the continent. Combined with measures of productivity during infection, such mapping tools have been used to evaluate trypanotolerance, to define the effect of trypanosomiasis control on land use and biodiversity, and to enhance decision making in livestock development programmes. ILRI's epidemiological research highlights include the development of a modelling technique to evaluate control options of AAT, such as: (i) chemotherapy, which remains the main parasite control option; (ii) trypanotolerant cattle, which is an important option if complementary chemoprophylaxis is adequate; and (iii) tsetse control methods, which are well established.

In terms of top-cited papers, ILRI has contributed to 36% of the global research outputs on animal African trypanosomiasis and 64% of the global research outputs on trypanosomiasis resistance, as shown in the Altmetric (www.altmetric.com/; accessed 5 February 2020) database.

Development impacts

Economic impacts

Estimates of economic losses to trypanosomiasis in sub-Saharan Africa have been made several times. Jahnke's pioneering work (1976) showed the potential output losses in East Africa. Several papers from ILCA/ILRAD (1988) showed positive economic returns to various forms of control, including spraying and trapping flies, trypanocides and use of trypanotolerant animals. Research has therefore had an economic impact outside the vaccine domain.

With respect to vaccine development, a 1990s *ex ante* assessment showed that a vaccine against trypanosomiasis in Africa would have generated a real *ex ante* rate of return of 33% (Kristjanson *et al.*, 1999). However, despite the known losses to trypanosomiasis and the potential economic gains to reducing those losses, it has not been possible to estimate indirect economic impacts arising from the main scientific impacts of trypanosomiasis research. In particular, *ex post* development impacts of vaccine research were zero because decades of investment in vaccine research failed to produce an effective vaccine.

Capacity building

ILRI has built capacity in both AAT control and farmer field training and information sharing in rational drug use. An estimated 258 scientists and students were trained through ILRAD, ILCA and ILRI on trypanosomiasis, of which 61 were specifically from the African Trypanotolerant Livestock Network (ATLN). The institution has supported 63 PhD students, 26 MSc students and four interns working on trypanosomiasis research.

Partnerships

Addressing AAT and the problems associated with trypanocide resistance has led to significant research collaborations, including: the Centre de Coopération Internationale en Recherche Agronomique pour le Développement/Département d'Elevage et de Médecine Vétérinaire (CIRAD/EMVT, France); the Centre International de Recherche-Développement sur l'Elevage en zone Subhumide, Direction Provinciale des Resources Animales (DPRA, Burkina Faso); the Food and Agriculture Organization of the United Nations (FAO, USA); Freie Universität Berlin (FU-Berlin, Berlin); the International Trypanotolerance Centre (ITC, Gambia); Justus Liebig University Giessen (Germany); the Laboratoire Central Vétérinaire (LCV, Mali); Oxford University (UK), Prince Leopold Institute of Tropical Medicine (now the Institute of Tropical Medicine, Belgium); the University of Edinburgh (UK); the University of Glasgow (UK); and University of Hannover (Germany). ILRI and its predecessors have contributed to the Programme Against African Trypanosomiasis (PAAT), which brings together agents working on this disease, ranging from rural communities to governments, research institutes and development agencies.

Introduction

In 1970, Wiley published *The African Trypanosomiases*, edited by H.W. Mulligan and W.H. Potts. Most of the contributors to the book, including A.R. (Ross) Gray, who served as Director General of ILRAD from 1982 to 1994, had gained expertise on African trypanosomes, their vectors, trypanosomiasis pathogenic processes and disease control strategies while working in Africa. As the first comprehensive work on these topics, the book was commissioned by the Trypanosomiasis Advisory Panel of the Ministry of Overseas Development of Great Britain and sponsored by the same ministry. The publication was in many respects a legacy to independent Africa from expatriate scientists who had worked to control the devastating spread of human African trypanosomiasis (HAT) and AAT during the colonial period, possibly as a result of changing ecological dynamics associated with colonial conquest and management (Ford, 1971; Scoones, 2014).

HAT and AAT are caused by tsetse-transmitted protozoan parasites that are endemic in the humid and semi-humid zones of sub-Saharan Africa. As a landmark book, Mulligan and Potts (1970) set the baseline for trypanosomiasis research programmes at ILRAD and ILCA and later at ILRI. *The African Trypanosomiases* set a standard against which progress in the field since 1970, both fundamental and practical, can be measured, because it documents the scientific investment made during the colonial period in West, Central and East Africa to control HAT, and to a lesser extent, AAT. Indeed, the decision to publish *The African Trypanosomiases* attests to the fragility of trypanosomiasis control strategies then in use, namely those based on tsetse control by environmental engineering, vector trapping and application of insecticides, and disease control by diagnosis and chemotherapy, all of which can break down in the face of infrastructure disturbance or parasite resistance to trypanocidal drugs.

The Consultative Group on International Agricultural Research (CGIAR) was formed, in

1971, shortly after the publication of *The African Trypanosomiases*. In support of its mandate, CGIAR established two livestock research institutes, IL-RAD, in Nairobi, Kenya, in 1973, and ILCA, in Addis Ababa, Ethiopia, in 1974. ILRAD was to 'serve as a world center for research on ways and means of conquering, as quickly as possible, major animal diseases which seriously limit livestock industries in Africa and many other parts of the world' and to 'concentrate initially on intensive research concerning the immunological and related aspects of controlling trypanosomiasis and theileriosis (mainly East Coast fever)' with the goal of decreasing the incidence and/or severity of disease. ILCA was to 'assist national efforts which aim to effect a change in the production and marketing systems of tropical Africa so as to increase the sustained yield and output of livestock products and improve the quality of life of the people of this region'.

The mandates of these institutes were partially merged in 1977 upon establishment of ATLN, which was based on the ILRAD campus in Nairobi. The network investigated the use of trypanotolerant cattle, primarily those of the N'Dama breed, as a resource for productive livestock farming in areas of sub-Saharan Africa where AAT is endemic; this was accomplished through analyses of animal health and production databases assembled from 13 countries in West, Central and East Africa (reviewed by d'Ieteren *et al.*, 1998). N'Dama are West African taurine cattle that have been farmed in Africa in tsetse-endemic areas for several thousand years (Hassan, 2000). These multi-use livestock animals have been used to establish commercial herds and are undergoing selection for production traits. However, N'Dama cattle are still not popular in East Africa, where cattle producers favour larger breeds, despite their susceptibility to AAT. Because of their trypanotolerant phenotype, comparative analyses of N'Damas and less trypanotolerant breeds with respect to immune responses, infection-induced pathology and the genetic basis of disease control became a focus of trypanosomiasis research at ILRAD and, with respect to identification of markers for selective breeding of trypanotolerant cattle, remain so today at ILRI, which was established in 1995 by merging ILRAD and ILCA.

In the 46 years since publication of *The African Trypanosomiases*, there have been fundamental advances in trypanosome biology, biochemistry, immunology and immunopathology, including new understanding of trypanosome virulence and host resistance mechanisms. Despite these advances, the scientific community is still some way from creating tools that would help farmers in sub-Saharan Africa to improve their livestock production in trypanosomiasis-endemic areas. Examples of such tools would include an inexpensive, sensitive and specific AAT diagnostic test to validate the need for, and efficacy of, chemotherapy; new inexpensive multi-target trypanocidal drugs; a vaccine to prevent AAT or accelerate its cure in trypanosomiasis-sensitive livestock; and fully trypanotolerant livestock with production traits more closely aligned to those of improved breeds than of the smaller multi-use N'Dama cattle. However, it is still reasonable to expect eventual success in developing at least some of these tools. ILRAD, ILCA and ILRI scientists have contributed to this work in the areas of AAT diagnostics, understanding mechanisms of AAT pathogenesis, defining the trypanotolerance phenotype, identifying QTLs that govern trypanotolerance and evaluating putative vaccine antigens. These contributions are discussed after the following review of the state of knowledge in 1970 regarding AAT, which outlines the problems tackled by ILRAD/ILCA/ILRI.

Scientific Challenges

AAT causative agents and tsetse, c.1970

African animal trypanosomiasis (AAT) in livestock is caused by infection with any of three species of African trypanosomes, namely, *T. brucei*, *T. congolense* and *T. vivax*. The pathogenic protozoans are transmitted to their mammal hosts in the saliva of tsetse flies (genus *Glossina*) in which the parasites undergo cyclic development and of which there are more than 30 species and subspecies, with eight playing a major role in trypanosome transmission (Cecchi *et al.*, 2015). African trypanosomes can also be transferred mechanically between hosts in blood held within the proboscis of biting flies other than tsetse, predominantly horse flies (family Tabanidae) and stable flies (family Muscidae). Mechanical

transmission of the parasites by biting flies causes spread of AAT within and across herds.

African trypanosomes live extracellularly in the blood of their mammal hosts, and in the case of *T. brucei* and *T. vivax*, also in tissues. They can be detected and distinguished from each other by microscopic examination of wet, thin or thick blood films, or dried, fixed and stained thin blood films. This simple diagnostic test is effective when the level of parasitaemia is high but can be problematic at other times. Fiennes (1970) reported, 'It was standard practice to examine 600 fields of thick smear preparations (of bovine blood) but in some cases trypanosomes were only detected after weeks or even months of daily searching.' In contrast, cryptic trypanosome infections could sometimes be revealed by inoculation of putatively infected blood into laboratory mice, although this was often unsuccessful because not all trypanosomes grow in mice. Thus, definitive diagnosis of AAT in the field was not always possible in the 1970s.

Tsetse distribution and effects on cattle, c.1970

Tsetse fly-infested areas of Africa extend from the southern edge of the Sahara Desert to Angola, Zimbabwe and Mozambique. Of the three trypanosome species that cause AAT, only *T. vivax* is found in the western hemisphere, in approximately ten countries in the Caribbean and South and Central America. AAT is endemic in livestock maintained in tsetse-infested areas of Africa. The disease is chronic and often fatal in cattle grazed in regions that are largely free of wildlife species, although it sometimes resolves without treatment. Cattle under chemotherapeutic support can achieve immunity provided they are exposed to restricted regional stocks of *T. brucei brucei*, *T. congolense* and *T. vivax*. In contrast, AAT is typically acute and fatal in regions where livestock come into contact with trypanosomes that are transmitted from the sylvatic (wildlife) reservoir by tsetse, possibly reflecting the intensity of challenge, trypanosome strain diversity, and the presence of strains of the parasites that are highly virulent (van den Bossche *et al.*, 2011; Motloang *et al.*, 2014).

As a result of acute AAT, cattle are excluded from much of the tsetse fly habitat, which has been estimated at various times since the founding of ILRAD to cover between 8.7 million and 10.3 million km^2 of the humid and semi-humid zones of sub-Saharan Africa. Ranching of cattle is possible on the fringes of the tsetse habitat where tsetse and trypanosome challenge are relatively low, but this requires support from trypanocidal drugs and insecticides. Chemotherapeutic support is also required for ranching of the relatively trypanotolerant taurine breeds of West Africa in trypanosomiasis-endemic areas, although not to the same extent as that required for trypanosomiasis-susceptible breeds. Use of chemotherapy and vector control to manage AAT is expensive and only partially effective. In those areas where challenge is low enough to permit ranching, calf mortality is still 6–10% higher than in regions where trypanosomiasis is not endemic, death in older animals is 2–8% higher, annual calving rates are 7% lower, milk yields are 2–26% lower and oxen are 38% less efficient (Shaw, 2009). AAT-associated production losses in Africa were recently estimated to exceed US$4 billion a year (AU-IBAR, 2018).

Antigenic variation and recurring parasitaemia, c.1970

Gray (1970) reviewed the state of knowledge of protective, but variable, antigens on African trypanosomes in Mulligan's *The African Trypanosomiases*. Briefly, it was shown in the 1960s that cell-free serum of infected animals, and wash buffer of trypanosomes enriched by differential centrifugation, contained trypanosome material, called exoantigen, that elicited trypanosome-agglutinating antibodies, indicating that target antigens were displayed on the surface of healthy trypanosomes. Antibodies are disease-fighting proteins that are secreted by plasma cells, which are terminally differentiated B-lymphocytes or B-cells. Antibodies against exoantigen were variant specific (i.e. reacted only with the exoantigen to which they were raised) and protected against that variant but not others.

Results from several scientists showed that a single trypanosome could give rise to many different antigenic types and Gray (1967, 1970) raised the possibility that 'the total number of antigens produced in one [trypanosome-infected]

host may be limited only by the time the animal lives'. However, despite the very large repertoire of variable surface antigens expressed by bloodstream-stage parasites, there was evidence, although far from convincing, that passage of a trypanosome strain through a tsetse fly resulted in expression of a basic antigenic type by the mammal-infective forms (metacyclic parasites), and when transmitted to new hosts these gave rise to a set of bloodstream-stage parasites with a restricted set of predominant antigenic types responsible for the first few waves of parasitaemia. These findings raised hopes that a composite vaccine based on a combination of the common and predominant exoantigens would be broadly protective. Despite this optimism, Gray also commented on the lack of knowledge of the structure of exoantigens, mechanisms of antigenic variation in mammals and tsetse, and the extent of variable surface antigen diversity, knowledge that would certainly be needed to evaluate possible use of basic and predominant antigens in a combinatorial vaccine.

AAT pathogenesis, c.1970

A good deal of information had been assembled on AAT pathogenesis before ILRAD was established. In Mulligan's *The African Trypanosomiases*, Fiennes (1970) reported that infections of cattle with *T. brucei*, *T. congolense* and *T. vivax* give a similar disease picture, suggesting 'that the fundamental processes of pathology in all forms of animal trypanosomiasis are possibly the same'. Fiennes reported that the cardinal signs of trypanosomiasis consist of fever that spikes on clearance of trypanosome parasitaemic waves but is later sustained, anaemia, cachexia/emaciation and hypoproteinaemia/hypervolaemia. The severity of these signs of disease was observed to vary depending on the age of the infected bovid, the virulence of the infecting parasites and the stage of infection. Fiennes also noted that other pathogens ellicit similar signs of disease in cattle, e.g. *Babesia bigemina*, which causes red-water fever; consequently, the clinical signs of AAT are not pathognomonic.

With respect to morbid anatomy, Fiennes reported that the spleen and lymph nodes of infected cattle became greatly enlarged in the early stages of AAT, but during the chronic stage of

disease, the spleen became small and atrophic, showing cell depletion. Furthermore, during the chronic stage of the disease, the red bone marrow of the shafts of the long bones disappeared. The infection-induced loss of erythropoiesis from the long bones may therefore affect the animal's capacity to replace red blood cells. Fiennes also reported that fatty tissues throughout the body, especially around the heart and kidneys, showed degeneration, the lungs showed marbling due to dilation of lymphatic vessels and became oedematous, the cardiac muscle also became flabby and oedematous, and exudates developed in the pleural and peritoneal cavities, all consistent with global inflammation. In addition, Fiennes reported that, as the infection progressed, parasitaemia often became cryptic, but aggregates of dead trypanosomes and areas of necrosis could be found in tissues in the case of *T. brucei*, and in capillaries often associated with small focal necroses in the case of *T. vivax* and *T. congolense*. There was also multiple organ and tissue degeneration in which kidneys became necrotic, the liver showed enlargement accompanied by central lobular necrosis in the parenchyma, and there was dilation of central veins and sinusoids and activation of phagocytic Kupffer cells. In addition, lymph nodes became fibrotic and their follicles and germinal centres were depleted of mature lymphocytes, showing that AAT-induced destruction of secondary lymphoid organs was not restricted to the spleen. Thyroid and adrenal glands were also severely affected in AAT, the former filling with colloid before disintegration and the latter becoming necrotic and fibrotic.

Anaemia is a consistent parameter of AAT and was used productively by scientists at ILRAD/ILCA/ILRI in comparative studies of AAT pathogenesis in infected N'Dama and Zebu cattle. In 1970, little was known about molecular mechanisms of anaemia in AAT, although analyses of cattle infected with *T. congolense* or *T. vivax* led Fiennes (1970) to propose four different courses of AAT in which anaemia featured differently: (i) hyperacute, which was characterized by severe haemolysis and early death; (ii) acute, which was characterized by hydraemia followed by dehydration, a haemolytic crisis and death (hydraemia is an increase in blood volume through water retention, resulting in a decrease in the specific gravity and protein concentration of blood plasma as well as a decrease in blood

packed cell volume (PCV) and red cell or haemo-globin content per unit volume); (iii) chronic, which was similar to acute but hydraemia persisted without dehydration and the haemolytic crisis was not fatal; and (iv) recovery, which was rare and typically occurred in AAT with little or no hydraemic phase. Mechanisms of hydraemia and dehydration were not defined, although Fiennes and colleagues implicated a haemolysin in trypanosome-induced anaemia showing that blood plasma from infected animals sometimes lysed red blood cells of healthy animals *in vitro* at 37°C. The identity of the putative trypanosome-derived haemolysin was not established, although it was shown to be inactivated by heating at 56°C for 30 min, consistent with involvement of a heat-labile complement factor.

Among the many pathological features of AAT, Fiennes drew attention to serum dilution and accompanying hypoproteinaemia as being mainly responsible for the progressive decline of animals during the chronic stages of trypanosome infections. Again, mechanisms of this pathology were not identified, although kidney failure leading to retention of sodium and water is a likely candidate. Fiennes cited the work of several investigators implicating kinins, which are inflammatory polypeptides, but it is unlikely that inflammation alone would cause hypervolaemia.

In summary, by the start of the 1970s, it was clear that AAT is a disease caused by three species of trypanosomes that undergo cyclic development in biting flies of the genus *Glossina* (tsetse) and are transmitted to mammalian hosts primarily in the saliva of these flies. Trypanosome isolates had been cryopreserved, shown to retain infectivity for mammals and shown in experimental systems to induce host responses, both pathological and protective, to the parasites. These early studies showed that the chronicity of infection was linked to possibly unlimited variation of trypanosome surface antigens/exoantigens and escape from immune elimination. It had also been shown that exoantigens of bloodstream-stage trypanosomes elicited protective antibody responses, but that protection was restricted to homologous parasites. The diversity of bloodstream-stage trypanosome exoantigens suggested that they could not be combined as a composite vaccine; however, there was some evidence, albeit weak, that infective trypanosomes present in tsetse saliva and the first populations of bloodstream parasites had only a few antigenically distinct exoantigens, which might therefore serve as vaccine antigens. Little or nothing was known about immune responses to parasite components other than the immunodominant exoantigens. In addition, little or nothing was known about trypanosome virulence factors or host susceptibility/resistance factors that affected the severity of the pathological processes elicited by AAT, or indeed the mechanisms of that pathology. All of these problems were solved, to various degrees, by the work of ILRAD.

Major additions to the field between 1970 and 1979 included isolation and partial characterization of the organelle that defined the order Kinetoplastida to which the genera *Trypanosoma* and *Leishmania* belong, namely the kinetoplast (Fairlamb *et al.*, 1978); localization of bloodstream-stage *T. brucei* glycolytic enzymes to a single microbody-like organelle called the glycosome (Opperdoes and Borst, 1977); isolation and partial characterization of the variant-specific surface antigen of *T. brucei* (Cross, 1975; Bridgen *et al.*, 1976), which was previously called exoantigen and is now called the variable surface glycoprotein (VSG); and cultivation of animal-infective bloodstream-stage *T. brucei in vitro* (Hirumi *et al.*, 1977). This last discovery was made at ILRAD.

During the 1970s, the pace of discovery in cell and molecular biology and immunology had greatly accelerated through advances in the manipulation of DNA and RNA, nucleotide and protein sequencing, antigen epitope targeting with monoclonal antibodies (mAbs), cell population analysis using fluorescence-activated flow cytometry and cell sorting, and data processing using personal computing, to name a few. Application of these technologies to the field of trypanosomiasis research at ILRAD/ILRI had major impacts on understanding the molecular biology of trypanosome antigenic variation and the host immune response to the parasites, as discussed below.

ILRAD's Initial AAT Mandate

The first researchers at ILRAD were challenged by the institute's mandate to 'conquer, as quickly as possible, major animal diseases [that] seriously limit livestock industries in Africa' and to make fundamental discoveries concerning the cell

and molecular biology of *T. brucei*, *T. congolense*, *T. vivax* and *Theileria parva*, and their interactions with mammal hosts.

The acquisition of knowledge of host and pathogen biology has potential application to the control of disease, but should it take precedence over more applied approaches? This question was posed by A.J.S. Davies and G.A.T. Targett in a lecture on 'Some perspectives in parasitic disease' presented at the Inauguration Symposium on Current Trends in Immunology and Genetics and Their Implications for Parasitic Diseases, a meeting held on the ILRAD campus in 1978 (Davies and Targett, 1978: p. 69). They wrote, 'Is there any way that ILRAD can create an environment in which serendipity can have its full force? What shall be the balance between fundamental and field-level investigations? In any instance, do we know enough about disease in general, and trypanosomiasis and East Coast fever in particular, to adopt any specific approaches?'

The ILRAD scientific community took a mixed view. It committed to fulfilling the mandate of the institute through the application of evidence-based research, while investigating the basic biology, biochemistry and molecular biology of African trypanosomes and their interaction with their hosts, with a view towards identifying vaccine and diagnostic antigens and increasing host resistance to AAT.

ILRAD, 1975–1979

Under the leadership of Jim Henson, who served as ILRAD Director General from 1974 to 1978, ILRAD built a modern tsetse laboratory and suites of modern open-plan laboratories, research support and administrative buildings, at Kabete in Kenya. Over the next few years, the institute was equipped with switchable power, backup generators, facilities for safely handling radioactive materials and storing radioactive waste, animal management facilities, and a flow cytometry core including highly trained staff who ran and maintained a Becton and Dickinson FACS II cell sorter. In short, in over 5 years, ILRI established standards of operation equivalent to those in reputable institutes worldwide.

By 1979, ILRAD had assembled an almost full complement of scientific support and administrative staff and, importantly, had established research focus groups with defined research goals. In addition, collaborations had been established among members of different disciplinary and focus groups, thus promoting interdisciplinary research.

In addition to assembling research teams at ILRAD, a number of questions had been identified by 1979 as important to the mission to develop AAT immunization and control strategies (Table 2.1).

Initial experimental questions on AAT vaccine development and control

By 1979, scientists had begun to answer the questions in Table 2.1.

- *T. brucei* undergoes antigenic variation *in vitro* in the absence of VSG-specific antibodies or other components of trypanosome-induced immune responses (Hirumi *et al.*, 1977; Doyle *et al.*, 1980). Thus, immune pressure was not required for antigenic variation.
- Purified messenger RNA (mRNA) encoding a *T. brucei* VSG induced synthesis of VSG in an *in vitro* translation system (Williams *et al.*, 1978) and was an early step towards characterizing the genetic basis of antigenic variation. Work at ILRAD later showed that expression of a single VSG gene could occur with or without duplicative transposition (Young *et al.*, 1983a), a process whereby a copy of a VSG gene was inserted into an active VSG gene expression site through recombination with repetitive sequence in the barren region on one side of the VSG.
- mAbs could distinguish between trypanosome VSGs (Pearson *et al.*, 1980). This technology opened the way to dissect and compare VSGs and other antigens of bloodstream-stage and metacyclic trypanosomes, of different trypanosome species and isolates.
- *T. brucei* and *T. congolense* VSGs have a common cross-reactive determinant (Barbet and McGuire, 1978). However, immunofluorescent staining of trypanosomes using sera with activity against the cross-reactive determinant showed that this determinant was not accessible on intact parasites.

Table 2.1. Experimental questions on AAT vaccine development and control.

Is the genetic information for all VSGs present in each trypanosome?

Do trypanosomes vary VSGs in response to immune pressure?

Do VSGs of bloodstream-stage trypanosomes have a common determinant or determinants that can induce a protective immune response?

Do mammal-infective, tsetse-derived (metacyclic) trypanosomes express a common VSG, and do the first bloodstream-stage trypanosomes derived from them express a limited set of predominant VSGs?

Are there conserved trypanosome antigens that can induce protective immunity against AAT or that can be used in the development of diagnostic reagents?

Do trypanotolerant animals mount protective immune responses against conserved components of VSGs and/or common trypanosome antigens?

Is trypanotolerance a genetically acquired trait, and if so, how many genes are responsible?

- Soluble *T. brucei* and *T. congolense* VSG activates complement *in vitro* (Musoke and Barbet, 1977), which raised the possibility that activation of complement by VSG released by trypanosomes might be the cause of inflammation in AAT.

- Two trypanosomiasis resistance models were established: (i) inbred strains of mice differ in their survival time after infection with *T. congolense*, which was independent of the haplotype of mouse major histocompatibility complex (MHC) expressed and which may be associated with the capacity to control parasitaemia (Morrison *et al.*, 1978); and (ii) N'Dama and Zebu cattle in The Gambia differed in their capacity to control experimental infections with *T. brucei* and *T. congolense* (Murray *et al.*, 1977b,c). These models were used, and are still being used, to identify the immunological, physiological and genetic basis for resistance to trypanosomiasis.

- *T. congolense* caused immune dysregulation in mice by inducing cells, called suppressor cells, that inhibit the responses of T lymphocytes *in vitro* (Pearson *et al.*, 1979), introducing a possible mechanism of immunosuppression in trypanosomiasis.

AAT Research at ILRAD, ILCA and ILRI, 1979–2017

This section traces the development of the research themes outlined in Table 2.1. It encompasses work on AAT at ILRAD, ILCA and ILRI up to 2015 and, where appropriate, references relevant work carried out at other institutions. This section addresses: (i) AAT vaccine antigens; (ii) AAT diagnostics; (iii) mechanisms of AAT pathogenesis; and

(iv) the genetic basis of trypanotolerance. The chapter is not a comprehensive review of all work relevant to AAT carried out at ILRAD, ILCA and ILRI. For example, development of expertise in bovine immunology and of tools to dissect bovine immune responses, which were critical to AAT research, is discussed elsewhere (see Chapter 4, this volume). Important work at ILRAD on the physical nature of *T. congolense* (Rovis *et al.*, 1978) and *T. vivax* (Gardiner *et al.*, 1987) VSGs, immunocapture of mRNAs encoding VSGs (Shapiro and Young, 1981) and resolution of the puzzling disparity between VSG expression with or without an expression-linked copy (Majiwa *et al.*, 1982; Young *et al.*, 1983a,b) are not discussed here. Similarly, research at ILRAD and ILRI on trypanosome biochemistry, metabolism and death pathways (Lonsdale-Eccles and Grab, 1987; Aboagye-Kwarteng *et al.*, 1991; Bienen *et al.*, 1991; Murphy and Welburn, 1997; Welburn and Murphy, 1998; Welburn *et al.*, 1999) and *in vitro* (Borowy *et al.*, 1985a, 1985b, 1985c; Borowy *et al.*, 1988; Dube *et al.*, 1983) and *in vivo* (Peregrine *et al.*, 1987, 1991; Sutherland *et al.*, 1991; Silayo *et al.*, 1992; Mamman *et al.*, 1993; Burudi *et al.*, 1994; Mamman and Peregrine, 1994; Mamman *et al.*, 1994; Peregrine and Mamman, 1994; Waitumbi *et al.*, 1994) assays of drug resistance in trypanosomes, which also fall outside the scope of the chapter, are not discussed.

The search for AAT vaccine antigens

Metacyclic and first-generation bloodstream-stage trypomastigote VSGs

T. brucei, *T. congolense* and *T. vivax* infect and undergo specific developmental programmes in

tsetse, ultimately maturing to mammal-infective stages at sites in the tsetse that allow deposition into mammal hosts in saliva. These mammal-infective trypanosomes are called metacyclic trypomastigotes and are diploid and non-dividing, which was shown for *T. brucei* by cell-cycle analysis in the first publication from ILRAD that used the flow cytometry core (Shapiro *et al.*, 1984), and was later shown by ILRAD scientists, in collaboration with others, for *T. congolense* and *T. vivax* metacyclics using culture-derived parasites and nuclear DNA microfluorimetry (Kooy *et al.*, 1989). Upon deposition into the mammal host, the metacyclic trypomastigotes differentiate to replicative bloodstream-stage trypomastigotes, thus establishing infection. Metacyclic and bloodstream-stage trypomastigotes have been selected through evolution to express a more-or-less contiguous layer of VSG on the outer leaflet of their plasma membrane. The VSG coat protects the parasites from antibody-independent lysis by plasma complement factors (Devine *et al.*, 1986), which are innate immune effector molecules that assemble to a lytic complex on some pathogens, including uncoated trypanosomes, but not on VSG-coated trypanosomes. As discussed earlier, bloodstream-stage trypanosomes generate diverse VSGs by antigenic variation. However, investigations prior to the establishment of ILRAD (reviewed by Gray, 1970) had suggested that metacyclic and the first bloodstream-stage parasites might express only a few common and predominant VSGs, which might therefore serve as vaccine antigens.

DIRECT ANALYSIS OF VSGS EXPRESSED ON METACYCLIC AND BLOODSTREAM-STAGE TRYPANOSOMES Two lines of investigation were initially pursued at ILRAD to seek possible vaccine antigens. The first was direct analysis of the VSGs expressed on metacyclic and bloodstream-stage trypanosomes. Analyses of expressed VSGs were performed using immune sera and mAbs, and were continued with a variety of molecular genetic approaches by colleagues in and outside of ILRAD. The studies conducted at ILRAD clearly showed heterogeneity of expressed *T. congolense* metacyclic VSGs (Nantulya *et al.*, 1983) and substantial heterogeneity of VSGs expressed by initial populations of bloodstream-stage *T. vivax* arising from metacyclic parasites (Gardiner *et al.*, 1986). Studies in Scotland showed that only a small subset of specific VSGs (fewer than 28, which is 1–2% of the total VSG repertoire) are expressed by the *T. brucei* metacyclic population (Turner and Barry, 1989). Similar data are unavailable for the metacyclic VSG repertoires of *T. congolense* and *T. vivax*, but recent genome analysis indicates VSG gene repertoire diversity in these species (Jackson *et al.*, 2012), and there is no reason to think that diversity of metacyclic VSGs expressed in a tsetse infected with a clone of either parasite will be more limited than that of tsetse similarly infected with *T. brucei*, particularly in light of the *in vivo* infection-and-treatment studies reported below. Although the repertoire of *T. brucei* VSGs expressed by metacyclic trypanosomes is smaller than that expressed on the bloodstream-stage parasites, it is still substantial, is unstable over time (Barry *et al.*, 1983) and, as discussed below, differs among different serodemes of *T. brucei*, *T. congolense* and *T. vivax*, thus showing that trypanosomes from different serodemes have different metacyclic VSG repertoires.

INDUCTION OF IMMUNITY BY THE INFECTION-AND-TREATMENT METHOD The second line of investigation involved induction of immunity by the infection-and-treatment method. Cattle, goats and mice were subjected to cyclic infection using *Glossina morsitans submorsitans* infected with *T. brucei*, *T. congolense* or *T. vivax*, cured by treatment with diminazene aceturate (Berenil; Hoechst AG, Frankfurt, Germany), and subsequently exposed to tsetse infected with homologous or heterologous trypanosomes (Nantulya *et al.*, 1980; Akol and Murray, 1983; Nantulya *et al.*, 1984; Akol and Murray, 1985; Nantulya *et al.*, 1986; Vos *et al.*, 1988; Taiwo *et al.*, 1990). These studies showed that trypanocidal treatment of an established infection resulted in protective immunity against homologous but not heterologous cyclic infection. Protection was associated with parasite control at the level of the tsetse bite (i.e. in the skin), because a chancre that results from an immune response induced by parasites at the bite site did not develop in the immune animals.

Immunity, at least in the case of infections with homologous strains of *T. brucei* and *T. congolense*, correlated with the presence of neutralizing serum antibodies specific for the VSGs of their metacyclic trypanosomes, whereas immunity in the case of infections with *T. vivax* resulted from accumulation of antibodies specific for

VSGs of homologous bloodstream-stage *T. vivax*. Disappointingly, from the perspective of immunoprotection, attempts to elicit protective immunity in individual animals against several serodemes of trypanosomes by simultaneous, or sequential, cyclic infection of hosts followed by trypanocidal treatment were unsuccessful (Dwinger *et al.*, 1987). This resulted from failure to establish mixed infections in the hosts, or from an inability of the infected and treated hosts to develop protective immune responses against the wider range of metacyclic and bloodstream-stage VSGs of the mixed populations.

One important observation made in sequential cyclic infections with bloodstream-stage trypanosomes was that the superimposed heterologous parasites did not establish an infection (Morrison *et al.*, 1982). Similarly, superimposed infections with metacyclic parasites did not elicit a chancre (Dwinger *et al.*, 1986), indicating that the heterologous parasites were killed in the skin or did not establish replicating bloodstream-stage parasites in the skin. This phenomenon was called 'interference'. Its maintenance required sustained infection, and it was not equally effective against all superinfecting trypanosomes (Dwinger *et al.*, 1989), all suggesting against interference as a manageable strategy of AAT control. Interference was hypothesized to result from elevated microbicidal responses by innate effector cells in the skin of infected cattle, but the mechanism was not studied at ILRAD. It is now well established that trypanosomes are killed by pro-inflammatory products of macrophages/monocytes, including reactive oxygen and nitrogen species, amphiphilic peptides/cathelicidins, and, in the case of some trypanosomes, the cytokine tumour necrosis factor (TNF). It is also established that interferon-γ (IFN-γ), which is produced by type 1 T-helper cells, greatly increases in trypanosome-infected animals and activates macrophages to produce these microbicidal products.

A NEW VACCINE APPROACH   It has recently been proposed that activation of the innate defence system of the skin should be a strategy for AAT vaccination (Tabel *et al.*, 2013). Thus, while immunization and infection-and-treatment regimens that induce immune responses against highly variable components of metacyclic VSGs are considered unlikely to have an impact on the control of AAT, it is possible that induction of type 1 T-helper cell responses against conserved components of these VSGs, such as the C-terminal-domain conserved peptides of *T. brucei* and against other conserved antigens that are accessible in trypanosomes present in the chancre and other tissue sites, might expedite the development of protective innate immune responses in these regions. This approach is currently under investigation (Black and Mansfield, 2016).

THE VSG CROSS-REACTIVE DETERMINANT   Rabbit antisera prepared at ILRAD against VSGs of antigenically distinct clones of *T. brucei* and *T. congolense* contained antibodies specific for epitopes that were unique to the immunizing VSG as well as antibodies specific for a cross-reacting determinant (CRD) common to all VSGs (Barbet and McGuire, 1978). The latter antibodies did not bind to intact trypanosomes. Thus, the CRD target epitope was masked, or cryptic, on membrane-bound VSGs, suggesting that antibodies against this epitope are unlikely to be host protective. Subsequent studies at ILRAD showed that the CRD was 'located within oligosaccharides linked to the VSG through *N*-glycosidic and other unidentified types of linkages' (Rovis and Dube, 1981) and that these were added to VSGs in the *trans*-Golgi region during export to the surface (Grab *et al.*, 1984) and were present at the C-terminal portion of the molecule and close to the trypanosome plasma membrane when attached to the parasites. Subsequent studies at Cambridge University, UK, showed that the CRD was exposed upon release of soluble VSG from the trypanosome membrane as a result of cleavage of the dimyristoyl glycosylphosphatidylinositol (GPI) lipid anchor, which attaches the VSG to the plasma membrane, by an endogenous phospholipase C (PLC)-like hydrolase (Cardoso de Almeida and Turner, 1983). Work at ILRAD showed that little or no soluble VSG is released by healthy bloodstream-stage trypanosomes (Black *et al.*, 1982), indicating that access of the PLC to the membrane-form VSG is tightly regulated. The possibility of disturbing this regulation to cause spontaneous release of VSG and exposure of naked trypanosomes to destructive complement components in host plasma spurred further research on the location and regulation of the VSG GPI-PLC.

Later work by Grab *et al.* (1987) at ILRAD showed that the VSG GPI-PLC was associated with flagellar membrane fractions of disrupted trypanosomes, and more recently it has been shown at Trinity College Dublin and Cambridge University to be present as a linear (patchy) array on the face of the flagellar membrane, between the paraflagellar rod and the cell body and close to the flagellar attachment zone (Hanrahan *et al.*, 2009; Sunter *et al.*, 2013). Despite exposure on the outer leaflet of the flagellar membrane (Sunter *et al.*, 2013), the GPI-PLC is not accessible on intact trypanosomes to specific antibodies and is unlikely to serve as a vaccine antigen. Nevertheless, VSG GPI-PLC may be the key to understanding the pathogenesis of AAT. It was shown that deletion of the gene encoding PLC from the trypanosome genome did not prevent the capacity of the parasite to infect and grow in tsetse or mammals but did substantially decrease trypanosome virulence (Webb *et al.*, 1994, 1997), implicating the PLC, or VSG GPI cleavage products, in dysregulation of immune control of the parasites. Thus, what began as a search for a conserved, possible vaccine, component of VSG at ILRAD was part of the path to the discovery of the only known trypanosome virulence factor, the VSG GPI-PLC.

Candidate vaccine antigens other than VSGs

In addition to characterizing VSGs of the AAT parasites (Rovis *et al.*, 1978; Gardiner *et al.*, 1987), scientists at ILRAD began the isolation and characterization of four antigen systems that might yield vaccine antigens: (i) conserved plasma membrane proteins (Rovis *et al.*, 1984); (ii) receptors for macromolecular nutrients (transferrin and serum low-density (LDL), intermediate-density (IDL) and high-density (HDL) lipoproteins) required by the parasites to grow (Black and Vandeweerd, 1989; Vandeweerd and Black, 1989; Grab *et al.*, 1993); (iii) trypanosome endosomal compartments (Webster, 1989; Webster and Fish, 1989; Grab *et al.*, 1992), including clathrin-coated endocytic vesicles (Shapiro and Webster, 1989; Shapiro, 1994), which would be expected to contain molecules involved in receptor-mediated endocytosis; and (iv) peptidases that might be released from living or dying trypanosomes and hence might contribute to pathogenesis

(Knowles *et al.*, 1987; Lonsdale-Eccles and Grab, 1987; Authie *et al.*, 1993a, 2001).

CONSERVED PLASMA MEMBRANE PROTEINS   The first immunization studies at ILRAD involved plasma membranes purified from bloodstream-stage *T. brucei* and also an 83-kDa protein that was present in lysates of *T. brucei*, *T. congolense* and *T. vivax*. Immunization of rabbits and goats with these materials elicited high-titre antibody responses but did not alter the course of the disease in the immunized animals following subsequent infection (Rovis *et al.*, 1984), suggesting that none of the target antigens was exposed at a high enough concentration on the surface of trypanosomes to support antibody-mediated killing, clearance or growth inhibition, and thus were not candidate vaccine antigens.

MACROMOLECULAR NUTRIENT RECEPTORS   Groups at ILRAD and elsewhere turned their attention to receptor-mediated endocytosis in trypanosomes, which might yield immunoprophylactic targets. Using axenic culture systems developed at ILRAD, Black and colleagues obtained definitive proof that the parasites required LDL, IDL or HDL to progress through their cell division cycle, and transferrin for sustained replication (Black and Vandeweerd, 1989; Morgan *et al.*, 1993, 1996). Studies by Coppens and colleagues in Belgium implicated an 86-kDa *T. brucei* protein in uptake of LDL, and suggested that uptake of lipoproteins and parasite growth could be inhibited by antibodies to this molecule (Coppens *et al.*, 1988). However, collaborative studies (unpublished data) between Coppens and Black carried out at ILRAD showed that the antibodies did not affect growth of culture-adapted bloodstream-stage trypanosomes, and further work on the putative LDL receptor did not yield a candidate vaccine. The trypanosome receptors for bovine serum LDL, IDL and HDL have not yet been identified.

Studies at ILRAD to identify the *T. brucei* components that bind transferrin revealed a 90-kDa holotransferrin-binding *T. brucei* protein (Grab *et al.*, 1993). This protein was isolated from parasites that had been grown in rats and when injected into rats induced production of specific antibody that inhibited growth of bloodstream-stage *T. brucei* in axenic cultures; further

vaccine tests were not carried out *in vivo*. Isolation of the *T. brucei* transferrin receptor (TbTfR) was subsequently achieved by Steverding *et al.* (1995) in Germany, who showed that it was a heterodimer of proteins encoded by VSG expression site-associated gene 6 (*ESAG6*) and *ESAG7* whose products had molecular masses of 50–60 kDa and 42 kDa, respectively, and thus were distinct from the material isolated at ILRAD. Interestingly, uptake of transferrin by *T. brucei* was poorly inhibited by TbTfR-specific IgG but strongly inhibited by fragments of these antibodies comprising their antigen-binding sites, which may have easier access than intact antibodies to the transferrin receptor that is embedded in VSGs of the trypanosome flagellar pocket. The investigators stated that attempts to protect mice from *T. brucei* AAT by immunization with the receptor were unsuccessful. Subsequent studies showed that: (i) the different VSG expression sites in *T. brucei* contain different copies of *ESAG6* and *ESAG7*; (ii) their products differ in binding affinity for different mammal transferrins; and (iii) culture of bloodstream-stage trypanosomes in medium containing transferrin to which their TbTfR had low affinity resulted in selection of parasites that had switched to a VSG gene expression site with *ESAG6* and *ESAG7* encoding a higher-affinity transferrin receptor for that transferrin (Gerrits *et al.*, 2002). Based on studies on the TbTfR to date, it seems unlikely that it will serve as a vaccine antigen. *T. congolense* also expresses *ESAG6* and *ESAG7*, but *T. vivax* lacks these genes (Jackson *et al.*, 2013). In addition, work at ILRAD showed that the *T. vivax* VSG is smaller than that of *T. brucei* and the surface coat is more diffuse (Gardiner, 1989); consequently, it would be of interest to determine how *T. vivax* acquires iron and whether this mechanism could be blocked by a specific antibody to the detriment of the parasite.

EXTRACTS OF TRYPANOSOME ENDOCYTIC VESICLES
An attempt was made at ILRAD to induce antibodies that interfere with endocytosis of essential molecules by trypanosomes. Rabbits were immunized with proteins isolated from purified *T. brucei* clathrin-coated vesicles hypothesized to be 'putative parasite receptors for adsorptive endocytosis'. The resulting antibodies recognized many parasite proteins, including epitopes on the parasite's endocytic surface, but did not stimulate *in vitro* lysis of the parasites, inhibit

their growth *in vitro* or improve control of infection in the immunized rabbits (Shapiro, 1994). Similar results were obtained with endosomal proteins, purified by tomato lectin affinity chromatography, reported below.

T. CONGOLENSE CYSTEINE PEPTIDASE (CONGOPAIN) A negative correlation was found at ILRAD between the titre of IgG1 antibodies specific for a *T. congolense* cysteine protease (CP), congopain, in post-infection bovine serum and the severity of AAT (Authie *et al.*, 1993a). To determine whether these antibodies have a protective role in AAT, cattle were induced to generate antibodies against the catalytic domains of two families of related *T. congolense* CPs, called CP1 and CP2, by immunization with recombinant truncated proteins that had been expressed in a baculovirus system and that lacked the trypanosome-specific C-terminal extension (Authie *et al.*, 2001). The immunized cattle were subsequently infected with *T. congolense* by the bites of eight infected tsetse flies. Cattle subjected to the same immunization regime with ovalbumin served as controls. Immunization with truncated CP1 or CP2 did not affect either the time to patency or the levels of parasitaemia throughout infection, or the rapid decline in blood PCV during the first 40 days after infection, but did accelerate weight gain and recovery of blood PCV and of residual leukocyte counts following the initial rapid decline in these parameters. Furthermore, cattle immunized with CP2 mounted rapid and higher-titre IgG antibody responses against a VSG (IL-C49) unrelated to that of the infecting parasites. This last result is difficult to interpret because the IL-C49 VSG-specific antibodies were not assayed for cross-reactivity with the VSG, or any other antigens, of the infecting parasites. Despite some difficulty in interpreting this study, it is quite clear that immunization with truncated CP2 alleviated some aspects of AAT pathology. This work was not continued at ILRAD, and there have been no reports (to mid-2018) on how the truncated CP2 vaccine accelerates recovery from AAT.

Other vaccine studies

The search for AAT vaccine antigens was not restricted to ILRAD. Other investigators reported inducing partial protection (reviewed by La Greca and Magez, 2011), achieved by immunizing with:

(i) trypanosome flagellar pocket fractions; (ii) DNA encoding an invariant surface glycoprotein; (iii) trypanosome cytoskeletal proteins; (iv) *Trypanosoma evansi* actin or tubulin; or (v) plasmid containing the catalytic and N-terminal domain of *trans*-sialidase. The primed animals were typically boosted with the priming antigen and infected shortly thereafter with a low number of trypanosomes (500–1000). This regime resulted in 40–60% of recipients showing sterile immunity (i.e. they did not become infected in contrast to the uniform infection achieved in control unimmunized animals). The opinion of the review authors was that these immunization regimes elicited short-lived innate immune responses that killed infecting organisms. This interpretation is consistent with data obtained in the author's laboratory in collaboration with Noel Murphy of ILRI and Derek Nolan of University College, Dublin, on the vaccine potential of *T. brucei* tomato lectin binding (TL) antigens (Nolan *et al.*, 1999), which encompass most if not all trypanosome endosomal proteins and macromolecular growth-factor receptors. Mice were immunized via the peritoneal cavity with TL antigens in the presence or absence of the antimitotic drug cyclophosphamide, which inhibits antibody production (Table 2.2). Irrespective of the generation of TL antigen-specific antibodies, 50–66% of the immunized mice resisted subsequent infection by the intraperitoneal route. Subsequent studies showed that the protective response was lost 3 weeks after the last immunization and could not be boosted using soluble TL antigens. It was concluded that infecting parasites were killed by a microbicidal innate immune response in the peritoneal cavity induced by the immunization regime.

Alternatives to an AAT vaccine

As research at ILRAD, and subsequently ILRI, on AAT vaccines waned, during the 1980s three AAT research themes emerged and were continued at ILRI. These themes are summarized in Table 2.3 together with pros and cons (with respect to ILRAD/ILCA/ILRI mandates) that were considered at the time. Perhaps it would have also been reasonable to take a drug-discovery approach (i.e. to interrogate axenic cultures of pathogenic trypanosomes developed at ILRAD with every compound made or extracted by humankind in search of new effective trypanocidal compounds). While this could have been done in collaboration with Big Pharma, which was equipped with robotic testing centres and vast libraries of testable compounds, ILRAD and ILRI did not have the resources to discover new drugs by brute force and that route was not followed. High-throughput *in vitro* drug-screening approaches for African trypanosomiasis have been taken up by other researchers in recent years resulting in more than 20 papers cited in PubMed on this topic during the decade 2008–2018.

Improved AAT Management through Use of Trypanotolerant Stock

ILRAD's interest in AAT diagnosis, treatment and management was linked to the decision to develop a field/epidemiology programme that would strengthen the institute within Africa and

Table 2.2. *T. brucei* TL antigens induce a protective innate immune response. (unpublished data, ILRAD).

TL antigen	Ovalbumin	Cyclophosphamide (200 mg/kg body weight)	Challenge	Animals protected (%)
+	−	−	+	66
+	−	+	+	50
−	+	−	+	0
−	+	+	+	0

Groups of mice (*n* = 6 per group) were primed by intraperitoneal injection of 20 µg of TL antigen (*T. brucei* clone ILtat 1.4; Nolan *et al.*, 1999) or with 20 µg of ovalbumin, emulsified in Freund's complete adjuvant, boosted after 1 month with the same amount of antigen emulsified in Freund's incomplete adjuvant, and challenged with exponentially growing trypanosomes (500 *T. brucei* strain GUTat 3.1) 8 days later. Tail-blood parasitaemia was assayed at 4, 8 and 12 days post-challenge, and mice in which parasites were not seen on any occasion were designated as protected. Antibodies specific for TL antigens reached a titre of 1:1600 in a TL-antigen enzyme-linked immunosorbent assay, but were not detected in mice that were given TL antigens plus cyclophosphamide, which kills dividing B-cells, and were not detected in the control ovalbumin-immunized mice. TL, tomato lectin.

Table 2.3. AAT research at ILRAD/ILRI in the post-trypanosomiasis vaccine era. (Constructed by author.)

Theme	Pros	Cons
Improve productivity of N'Dama cattle in large herds under natural tsetse/trypanosome challenge by diagnosis and chemotherapy	Helps producers Involves ILRAD with ILCA in workforce training and management of AAT in N'Dama Develops diagnostic tools to monitor AAT Identifies indicators of trypanotolerance expressed in a managed herd and generates data on the heritability of some of these indicators	Involves ILRAD in large-scale epidemiology studies that address the phenotype of trypanotolerance, not the mechanisms of trypanotolerance
Identify the cell and molecular basis of AAT pathogenesis by comparative analyses of innate and acquired immune responses of trypanotolerant and susceptible hosts	Adds to our understanding of the bovine immune system under AAT stress and adds reagents to the bovine immunology tool chest May identify molecular triggers of pathology in AAT and thus contribute to the elucidation of the genetic basis of trypanotolerance and its exploitation	AAT pathogenesis might be multifactorial and of unfathomable biological complexity
Identify genes linked to trypanotolerance through comparative analysis of post-infection phenotypes and genome linkage maps of F_2 progeny of N'Dama × Boran crosses	Involves ILRAD in the global effort to map the bovine genome May identify host genes that control anaemia, parasitaemia and mortality in AAT and expedite marker-assisted selection to enrich trypanotolerance	Trypanotolerance may be a polygenic trait with small contributions from each of many unlinked genes, precluding mapping

that would address mechanisms of disease resistance in the taurine breeds of cattle in West and Central Africa, namely the N'Dama and West African Shorthorn. These taurine cattle, particularly N'Dama, were reputed to be trypanotolerant, i.e. to have the capacity to survive and be productive in tsetse-infested areas without treatment (Camille-Isidore, 1906; Murray *et al.*, 1982). Trypanotolerance is thought to have arisen within the taurine breeds of West Africa during several thousand years of selection in tsetse-infested areas. The degree of trypanotolerance varies within the breed and may therefore be open to improvement through selective breeding. It may also be possible to introduce the trait into other cattle breeds by marker-assisted selection, creating a domestic bovid ideally suited to African agriculture.

African Trypanotolerant Livestock Network

The African Trypanotolerant Livestock Network (ATLN) was established in 1977 by John Trail (ILCA) and Max Murray (ILRAD) to identify indicators of trypanotolerance in N'Dama cattle under natural tsetse/trypanosome challenge and to improve management of N'Dama cattle under such challenge. ATLN was an unusually collaborative effort involving the United Nations Environment Programme (UNEP), FAO, the ITC and the Centre International de Recherche-Développement sur l'Elevage en zone Subhumide (CIRDES), as well as national entities of Côte d'Ivoire, Ethiopia, Gabon, Kenya, Nigeria, The Gambia, Togo and what was then Zaire (now the Democratic Republic of the Congo).

Importation of N'Damas to ILRAD for on-site study, which had been (reasonably) discouraged by the then-Director General of ILRI, Jim Henson, and by the Kenya Veterinary Service for fear of accidental disease spread, was eventually realized in 1984 when frozen N'Dama embryos were imported and implanted in surrogate Boran mothers, through the expertise of Ivan Morrison, Geoff Mahan and Torbin Jordt (Jordt *et al.*, 1986a,b). In 1984, 10 N'Dama calves were born at ILRAD. These animals and their progeny

were used extensively in studies of mechanisms of resistance to AAT and in linkage genome-mapping studies reported later in the text.

ATLN had aimed to 'improve livestock production in tsetse-infested areas of Africa by achieving a better understanding of genetic [-ally acquired] resistance, environmental factors that affect susceptibility and the efficacy of present control measures, and by ensuring better application of existing knowledge and recent research findings' (ILRAD, 1985). In 1985, the network was coordinating investigations at sites in nine countries of West and Central Africa. Five of these study sites were well established, (Gabon, Ivory Coast, Nigeria, Togo, Zaire), two were under development (Senegal, The Gambia) and two were under consideration (Benin, Congo).

ILRAD was to provide supervision of animal health, infection status, and tsetse evaluation, while ILCA was responsible for animal production, nutrition and data processing. Data collection was rigorous. 'Field operations involved the simultaneous collection of data on infection, health and productivity. Staff at all sites recorded data on simple pre-printed forms for transmission to Nairobi every month. These were checked for completeness, verified and entered into a computer file in Nairobi. Major analyses that were carried out on field data in Addis Ababa involved the computation of productivity indices based on reproductive performance, viability, calf growth, and cow weight, as well as the assessment of possible factors affecting animal performance at different sites (ILRAD, 1985). Data analysis programmes used for these studies had been developed and tested using detailed records of matching animal health, animal productivity and trypanocidal drug treatments kept for many years at two large ranches in East Africa, namely Kilifi Plantations, Kenya, and Mkwaja Ranch, Tanzania, with which ILRAD had a long-term involvement.

The dark-ground buffy coat (DGBC) phase-contrast diagnostic technique

A dual anaemia/infection diagnostic test that was developed by Murray *et al.* (1977a) played an important role in ATLN field studies. This test was specific for blood-borne trypanosomes, and was sensitive, scalable for high-throughput testing, could be used in a proximal field laboratory, provided an estimate of parasitaemia (number of trypanosomes/ml of blood) and allowed identification of trypanosome species determined by morphology. The test also provided matched data on the blood PCV of the test animal. Briefly, blood was drawn by capillary action into a heparinized haematocrit tube, centrifuged in a haematocrit centrifuge and the blood PCV recorded as a percentage of total blood volume, as shown in Fig. 2.1. The tube was nicked with a diamond pen 1 mm beneath the buffy coat layer, which is composed of white blood cells and trypanosomes and subsequently snapped to remove the red cell layer. It is then nicked 1 cm above the buffy coat (i.e. in the blood plasma layer) and snapped and the white blood cell/trypanosome plug is then expelled on to a glass slide, covered with a 22 × 22 mm coverslip and the preparation scanned by microscopy for the presence and prevalence of trypanosomes, which can provide an estimate of parasitaemia. This technique was used by ILRAD to train legions of veterinary technicians throughout Africa. The relationship of parasite prevalence in the buffy coat and estimated parasitaemia was established by seeding samples of blood with known numbers of trypanosomes.

With respect to animal health data, although the AAT-associated decrease in PCV might arise as a result of red blood cell lysis or phagocytosis, or through haemodilution, as discussed by Fiennes (1970), the decline in PCV denotes a detrimental change in subject health and therefore informs on disease. With respect to infection status, one drawback of the DGBC technique is that it provides an estimate of trypanosomes circulating in the peripheral blood only, and hence may underestimate infections where trypanosomes adhere to blood vessels (*T. congolense*) or inhabit tissues (*T. brucei* and to a lesser extent *T. vivax*). Thus, the DGBC diagnostic technique was supplemented with antigen-detection tests as discussed below.

Antigen enzyme-linked immunosorbent assays, isoenzymes and polymerase chain reaction

Expertise in mAb production at ILRAD, and in molecular genetic techniques, including the polymerase chain reaction (PCR) and

(a)

(b)

Number of trypanosomes	Score	Estimated parasitaemia tryps/ml
Swarming > 100 per field	6+	$>5 \times 10^6$
> 10 per field	5+	$>5 \times 10^5$
1 − 10 per field	4+	$10^4 − 5 \times 10^4$
1 per 2 fields−1 per 10 fields	3+	$5 \times 10^3 − 5 \times 10^4$
1 − 10 per preparation	2+	$10^3 − 10^4$
1 per preparation	1+	$10^2 − 10^3$
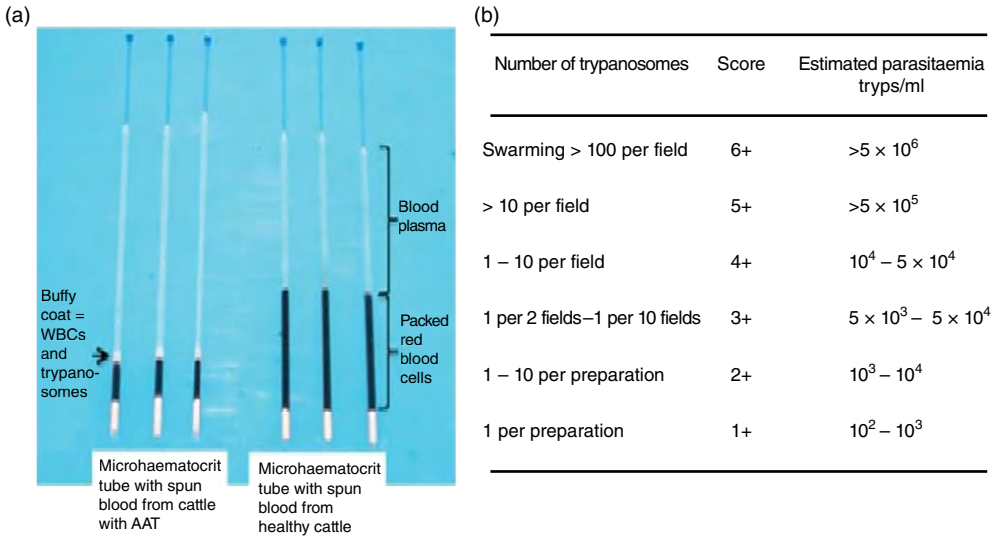
Fig. 2.1. Microhaematocrit and estimation of parasites in the buffy coat. (a) The percentage of blood packed cell volume (PCV) is calculated as: PCV = packed red blood cells/(packed red blood cells + plasma) × 100. WBCs, white blood cells. (b) The blood buffy coat layer + 1 cm column of plasma, collected by cutting the microhaematocrit tube shown in (a) 1 mm below and 1 cm above the buffy coat, is expelled on to a glass slide, dispersed beneath a 22 × 22 mm cover slip, observed under dark-ground illumination with a Phaco2 NPL25/050 objective and a 10× eyepiece. Observations as shown in column 1 are scored as shown in column 2, providing an estimate of trypanosomes/ml blood as shown in column 3. The test can be used with all species of pathogenic African trypanosomes. (unpublished data from ILRAD.)

orthogonal-field-alternation gel electrophoresis (OFAGE), made it possible to design additional diagnostic tests based, respectively, on trypanosome antigen capture from host blood or lysates of tsetse, and analysis of DNA extracted from the blood buffy coat, or from tsetse or purified trypanosomes. These tests provide an estimate of parasite material present in the sample and thus provide evidence of both an ongoing infection and the intensity of that infection. The mAbs used were generated at ILRAD against *in vitro*-propagated procyclic forms of *T. congolense*, *T. brucei* and *T. brucei rhodesiense* (the cause of East African HAT) and *T. vivax* (Nantulya *et al.*, 1987), and react with antigens in the corresponding bloodstream-stage trypomastigotes. PCR primers designed at ILRAD to amplify trypanosome species-specific nucleotide sequences (Kukla *et al.*, 1987; ole-MoiYoi, 1987; Dirie *et al.*, 1993a,b; Masake *et al.*, 1997) were also powerful tools for parasite analysis, allowing investigators to dissect trypanosome diversity more fully than could be achieved by morphological and mAb analysis. Similarly, OFAGE, which separates DNA of different lengths and hence resolves the numbers and lengths of chromosomes and minichromosomes in preparations from isolates and clones of trypanosomes, contributed to parasite characterization (Majiwa *et al.*, 1985; Masake *et al.*, 1988; Kihurani *et al.*, 2000), as did isoenzyme analysis, which detects polymorphisms that result in changes in activity, molecular weight and isoelectric point of a panel of enzymes detected by coupled coloured dye precipitation reactions after gel electrophoresis or isoelectric focusing (Gibson *et al.*, 1983; Knowles *et al.*, 1988; Fasogbon *et al.*, 1990). These studies, performed at ILRAD and in other institutions, contributed to the development of a molecular taxonomy of trypanosomes and a better understanding of patterns of their co-evolution (Hamilton *et al.*, 2007; Adams *et al.*, 2010).

The trypanosome antigen enzyme-linked immunosorbent assay (Ag-ELISA) is based on capture of trypanosome antigen from blood or another material using an antigen-specific mAb immobilized on a microtitre plate. Unbound material is removed by washing, and bound antigen is revealed by the addition of a second antibody specific for the captured antigen, tagged with an enzyme so that it gives a colour reaction. This

reaction is proportional in intensity to the amount of enzyme-tagged antibody bound and thus to the amount of captured antigen. This basic format was modified to facilitate tube capture and agglutination reactions for field analyses of infections.

Vinand Nantulya was the driving force for developing, validating and field testing trypanosome Ag-ELISA diagnostic tests at ILRAD. These included tests for HAT caused by *T. b. rhodesiense* (Nantulya, 1988, 1997; Komba *et al.*, 1992) and *T. b. gambiense* (Nantulya *et al.*, 1992a; Nantulya, 1997); for AAT caused by *T. brucei*, *T. congolense* or *T. vivax* in cattle, goats and horses (Nantulya *et al.*, 1992b; Nantulya and Lindqvist, 1989; Trail *et al.*, 1991b; Kihurani *et al.*, 1994; Masake *et al.*, 1995); and for surra caused by *T. evansi* in camels (Nantulya *et al.*, 1989; Waithanji *et al.*, 1993; Nantulya, 1994). Many of these tests were carried out in collaboration with scientists from institutes throughout Africa, including the University of Nairobi, Kenya; the Kenya Trypanosomiasis Research Institute, Kikuyu; the National Institute for Medical Research, Tabora, Tanzania; and the Noguchi Memorial Institute for Medical Research, Accra, Ghana; and with scientists from ATLN, discussed below.

As with the DGBC test, there are some operational limitations of the trypanosome Ag-ELISA. The trypanosome species-specific tests used the same capture and detecting antibody; hence, their sensitivity might be diminished by competition for the same antigenic epitopes. For these reasons, next-generation tests focused on generating capture and detection antibodies that recognize distinct epitopes on the same antigen. In addition, the capture antibodies are competing with endogenous host antibodies for the same antigens and quite possibly the same antigenic epitopes (the part of an antigen bound by an antibody), which will also diminish test sensitivity. Next-generation tests are being developed with nanobodies – recombinant antigen-combining sites of single heavy-chain camelid antibodies (Muyldermans *et al.*, 2009) – which, because of their antigen-combining site and size, bind antigenic epitopes distinct from those recognized by conventional antibodies and therefore do not compete with endogenous antibody for antigen capture.

Despite these concerns, the Ag-ELISA provides additional information to the DGBC diagnostic test and, when combined with parasitological data generated using the latter, allows infection classification as follows: (i) parasitaemic (DGBC positive); (ii) antigenaemic (Ag-ELISA positive); (iii) parasitaemic but not antigenaemic (DGBC positive but Ag-ELISA negative); or (iv) antigenaemic but not parasitaemic (Ag-ELISA positive but DGBC negative). These distinctions were of importance to field studies. For example, using a combination of the DGBC and Ag-ELISA tests on samples from N'Dama, Zebu and N'Dama × Zebu crosses subjected to sequential experimental *T. congolense* infections, colleagues at the ITC, in Banjul, The Gambia, found that during the course of the first parasitaemia wave, the overall percentage of positive cases detected by DGBC in blood was higher ($p<0.0001$) than that obtained by Ag-ELISA in tested samples of the three cattle populations. However, although the Ag-ELISA was less than 50% sensitive in detecting circulating antigens during the first 2 months of the primary infection, during the second infection, the overall number of infections detected by DGBC was lower in N'Dama ($p<0.005$) and the F_1 population ($p<0.001$) than that obtained using the Ag-ELISA (Mattioli and Faye, 1996). Similarly, Trail *et al.* (1991b), in ATLN, while studying infection of N'Dama cattle in Gabon, Central Africa, observed that of the animals detected as parasitaemic, 90% were also positive by Ag-ELISA; however, 40% of the animals with negative parasitological findings were found to be antigenaemic. Therefore, the tests should be used in combination wherever possible.

The trypanosome antigen-specific mAbs generated at ILRAD were also used to develop dot ELISAs for detecting trypanosome antigens in extracts of tsetse, i.e. for diagnosing infections of tsetse (Bosompem *et al.*, 1995a,b, 1996). The assay was performed by lysing tsetse or tsetse tissues in detergent (Triton X-100), adhering extract to a localized spot on a nitrocellulose membrane and treating with hydrogen peroxide to colour bleach the tsetse material, followed by membrane blocking with irrelevant protein to prevent non-specific sticking of the detection antibody to the membrane. An enzyme-tagged detection antibody was then added and an enzyme-linked colour reaction was carried out to detect the bound antibody. Thus, over time, ILRAD/ILCA/ILRI developed tools to map trypanosome infections of cattle and tsetse throughout Africa.

Combined with measures of productivity during infection, such mapping tools could be used to evaluate trypanotolerance and hence the possibility that N'Dama cattle were an African solution to an African problem.

Ranching with chemoprophylaxis and chemotherapy: the N'Dama advantage

In the absence of chemoprophylaxis and chemotherapy, the impact of AAT is proportional to tsetse challenge, with the killing of all trypanosomiasis-susceptible Boran cattle in areas of high challenge (Blaser *et al.*, 1979). In the absence of chemoprophylaxis/chemotherapy, AAT also has a substantial impact on trypanotolerant N'Dama cattle under natural tsetse/trypanosome challenge. In this respect, data from ATLN showed that productivity of N'Dama herds in The Gambia decreases by 11% in areas of low tsetse prevalence (determined by tsetse trapping), by 42% in areas of moderate tsetse prevalence and by 53% in areas of high tsetse prevalence, relative to that in areas without tsetse, based on analyses of the total weight of a 1-year-old calf and the live weight equivalent of milk produced by 100 kg of cow per year (Murray *et al.*, 1984). However, the presence of tsetse/trypanosome challenge does not necessarily preclude productive ranching of cattle, even that of trypanosomiasis-susceptible Boran cattle. Thus, ATLN analyses of 20,000 calving records for grade Boran beef cattle collected over 10 years at Mkwaja Ranch, located in a coastal region of Tanzania under high tsetse challenge, showed that these animals could be as productive as pure Boran cattle maintained under trypanosomiasis-free conditions in Kenya as long as they were supported by a chemoprophylactic regime based on the use of isometamidium chloride (Samorin; May and Baker Ltd, London) and occasional use of the therapeutic drug diminazene aceturate (Berenil; Hoechst). In fact, the animals required an average of 4.4 treatments with Samorin and 0.6 treatments with Berenil each cow-year to sustain their productivity (Trail *et al.*, 1985). In the absence of treatment, the level of tsetse challenge was such that cattle could not survive (Blaser *et al.*, 1979). Trypanosomiasis drug resistance did not pose a problem to this strategy at that time, although it has since been reported

for trypanosomes present in East and West Africa (Clausen *et al.*, 1992; d'Ieteren *et al.*, 1997).

Parameters of trypanosome infection and animal health under natural tsetse/ trypanosome challenge in N'Dama cattle

This section summarizes studies performed by the ILCA/ILRAD ATLN that established parameters of trypanotolerance under natural tsetse/trypanosome challenge, thus providing quality control for analysis of trypanotolerance in experimental infections in the ILRAD laboratory setting. In separate tests carried out in Gabon, Central Africa, between 1987 and 1989, a total of 436 1-year-old N'Dama cattle were maintained for periods of 12, 18 or 24 weeks under a medium natural tsetse/trypanosome challenge, and infection and health parameters measured. Infection prevalences were 25%, 31% and 9%, respectively, and anaemia, measured by the average packed red cell volume (PCV, measured as a percentage) over the test period, or by the lowest PCV reached, was found to be more closely associated with animal performance than when measured by average PCV when detected as parasitaemic (Trail *et al.*, 1990). The possibility that maintenance of PCV under tsetse/trypanosome challenge might serve as a measure of trypanotolerance was supported by studies of N'Dama cows maintained for 3.5 years under a high natural tsetse challenge in Zaire. Thus, a simultaneous evaluation of the effects of three possible criteria of trypanotolerance – namely, time detected as parasitaemic, parasitaemia score and PCV – showed that the latter had the major effect on reproductive performance, calf weaning weight and cow productivity (Trail *et al.*, 1991a). Additional studies of N'Dama cattle in Gabon under natural tsetse/trypanosome challenge showed that 'animals capable of maintaining PCV values, even when [trypanosome antigenaemic] on a high number of occasions, grew at the same rate as uninfected animals' whereas 'animals that could not maintain PCV values when infected had poorer growth' (Trail *et al.*, 1992), supporting the hypothesis that maintenance of PCV during AAT is an indicator of trypanotolerance and indicating variability in trypanotolerance within members of an N'Dama herd.

Trail *et al.* (1993) evaluated the impact of prophylactic and curative drug treatments on

the productivity of N'Dama cattle at the government ranch of the Office of Gabonais d'Amélioration de Production de Viande, in south-eastern Gabon. In one study, curative drug treatments were given to 13.7% of cows over the calendar year and to 40% of calves from birth to weaning. The mean number of curative treatments was 0.16 per cow per year and 0.52 per calf from birth to weaning (where 1 signifies that curative treatments administered are the same as the number of animals in the study, although not necessarily that all animals receive one curative treatment). Treatments were on the following basis: cattle that were parasitaemic and had PCV values of less than 25% were routinely given a curative treatment with Berenil, as were animals with PCV values below 20%, whether they were parasitaemic or not (antigenaemia was not measured). The kinetics and levels of recovery of PCV were similar in both groups of animals, indicating that, even though parasites were not detected in blood, animals with low PCVs in this study were nevertheless infected with trypanosomes.

Both calf and cow average PCVs were linked to calf weaning weight, 'there being a 0.91 kg increase for each 1% increase in calf average PCV, and a 0.95 kg increase in weaning weight for each 1% increase in cow average PCV' (Trail et al., 1993). Similar studies by Trail et al. (1991a) in Zaire where the prevalence of cow and calf infection was similar to those in the Gabon study showed that a high average calf PCV increased weaning weight by 9.9 kg (7.7% of total weaning weight) and a high average cow PCV value increased calf weaning weight by 8.8 kg (6.1%). Hence, maintenance of N'Dama PCV through curative drug treatment is an important production strategy. Half of the cattle in the Gabon study (Trail et al., 1993) received a prophylactic treatment with Samorin at 6 and 18 months into the study to determine its impact on prevalence of infection. This treatment regime decreased the number of curative treatments required in cows from an average of 0.25 per cow-year in unprotected cows to 0.06 per cow-year in protected cows. Although there are no data on the relative tsetse/trypanosome challenge at the Gabon study site versus the Mkwaja Ranch in Tanzania cited earlier, it is noteworthy that grade Boran cattle on the Mkwaja Ranch required 4.4 prophylactic treatments and 0.6 curative treatments per cow-year (Trail et al.,

1985), which is much greater than the treatments required by N'Damas and is consistent with the lesser ability of the Borans to survive and be productive under natural tsetse/trypanosome challenge.

The above studies support the idea 'that the ability to control anaemia during infection as indicated by average PCV might be one reliable criterion of trypanotolerance with which to identify trypanotolerant animals' (Trail et al., 1993). However, it is not the sole criterion. Thus, Trail et al. (1994), working with data from 255 N'Dama under high natural tsetse challenge in Zaire over a 2-year period from weaning at 10 months of age, showed that the species of infecting trypanosome, length of time parasitaemic, intensity of parasitaemia and anaemic condition had approximately equal effects on the final performance trait of daily live weight gain, and thus information on all of these is essential for assessing an animal's overall trypanotolerance phenotype. As evident from the number of animals studied and the number of parameters measured, these were demanding and comprehensive studies.

The ATLN findings have been summarized in a book (ILCA/ILRAD, 1988) and in several review articles (Trail et al., 1989; Murray et al., 1990; d'Ieteren et al., 1998). Those findings jointly validate the trypanotolerant status of N'Dama and identify indicators of the trait under natural challenge. These studies show that trypanotolerant cattle can be productive with low-level chemoprophylactic/therapeutic intervention in areas of moderate to high tsetse/trypanosome challenge, thus establishing N'Dama as a gene pool for use in tsetse-infested sub-Saharan Africa. In the period of broad and systematic studies of trypanotolerance, done jointly by ILRAD and ILCA in the 1970s and continued by ILRI after 1994, the three institutions generated more than 175 papers on various aspects of trypanotolerance, averaging four papers annually (24 mean citations per paper) from 1975 to 2018. Notable achievements were Murray et al. (1982) on host susceptibility, which remains at the 99th percentile of citations in its field within Scopus; the ILCA/ILRAD (1988) book on the achievements of the ATLN; Trail et al. (1993, 1994) on productivity; Hanotte et al. (2003) on genetic mechanisms of trypanosomiasis; and the later review article of Naessens (2006) summarizing more than 30 years of research on the subject.

The cell and molecular biology of trypanotolerance in cattle

T. congolense *cyclic infection and homologous cyclic reinfection of N'Damas and Borans*

N'Dama cattle produced by embryo transplants that were raised at ILRAD until 13 months of age were subjected to four sequential cyclic infections (*Glossina morsitans centralis*) with *T. congolense* derived from four different serodemes (Paling *et al.*, 1991a). After each infection, the cattle were treated with a curative dose of Berenil and rested for 1 month before the next cyclic infection. Boran cattle, a trypanosomiasis-susceptible breed of *Bos indicus*, were similarly infected and these animals were treated with a curative dose of Berenil as required. Irrespective of the infecting *T. congolense* serodeme, there was no significant difference between Boran and N'Dama groups in the number of chancres that developed at tsetse bite sites or in the kinetics or magnitude of their development, indicating that there was no pre-programmed (innate) component in either host breed that prevented infection by killing parasites in the skin.

All cattle became parasitaemic with similar kinetics irrespective of breed or trypanosome serodeme used for cyclic infection, indicating that there was no pre-programmed response in either breed that prevented migration of the parasites from the skin to the bloodstream, which occurs via the lymph (Akol and Murray, 1986). With three of the four test serodemes, levels of parasitaemia and the kinetics of parasitaemic wave remission were similar in N'Dama and Boran cattle for 30 days or so after infection; with the other serodeme, they were similar for the first 15 days after infection. These data showed that host protective immune responses were initially similar in the infected N'Damas and Borans. Thereafter, breed-related differences in parameters of infection became evident, replicating, in the case of N'Dama cattle, indicators of trypanotolerance observed with natural tsetse/trypanosome challenge, as discussed above. Thus, irrespective of the infecting serodeme, most infected Boran cattle, but no N'Dama cattle, rapidly developed life-threatening anaemia (PCV of 15% or less) by around 40 days after infection and were treated with a curative dose of Berenil.

In addition, all N'Dama cattle suppressed the level of parasitaemia in an incremental manner until it became cryptic (less than 10^2 trypanosomes/ml of blood), whereas those few infected Borans that did not require curative Berenil treatment were still presenting high levels of parasitaemia until all animals were treated with a curative dose of Berenil to terminate infection.

In a follow-up study, cattle that had been sequentially exposed to four cyclic heterologous infections were cured after the last infection, rested for 3 months and subjected to homologous cyclic reinfection with the first infecting serodeme, which was approximately 2 years after their first exposure to this *T. congolense* serodeme (Paling *et al.*, 1991b). Although five of the eight Borans and all eight N'Damas had neutralizing anti-metacyclic VSG antibodies present in their serum, determined by incubating the parasites in serum and their injection into mice, these antibodies did not prevent infection of the cattle and presumably were present in serum at much higher concentrations than in the skin. As with primary infections, neither the kinetics nor the size of the chancres that developed at tsetse bite sites following homologous reinfection differed significantly between N'Damas and Borans. However, infected N'Damas subsequently developed a single parasitaemic wave, which was two orders of magnitude lower than that developed on primary cyclic infection, and rapidly suppressed parasitaemia to a cryptic level, whereas the reinfected Borans developed multiple waves of parasitaemia, albeit of lesser magnitude, than those developed on primary cyclic infection, and these decreased in amplitude as infection progressed, thus tending towards cryptic infection. It is unclear whether these cattle, and in particular the N'Damas, had serum antibodies against bloodstream-stage *T. congolense* serodeme-1 VSGs that suppressed parasitaemia on homologous cyclic reinfection or had a recall adaptive response against these VSGs or both. It is clear that Borans had a lesser advantage in this respect. Importantly, N'Dama cattle that were reinfected by homologous cyclic infection did not show signs of anaemia, whereas similarly reinfected Borans had an acute drop in PCV, although less acute than Borans on the primary cyclic infection, and 50% of these animals required curative Berenil treatment by 50–70 days post-infection to avoid death.

Following curative treatment, the N'Dama and Boran cattle were again subjected to homologous cyclic reinfection, this time with tsetse transmitting *T. congolense* serodeme 2 (Williams *et al.*, 1991). The results were similar to those seen in the first homologous cyclic infection and, together with those for sequential cyclic infections, are summarized in Table 2.4.

Thus, cyclic *T. congolense* infections carried out at ILRAD showed that N'Dama cattle have a greater capacity to sustain blood PCV levels during infection than similarly infected Borans, in which PCVs dropped from a mean of 33% to 16% over a period of about 40 days after infection. Given that the lifespan of a bovine red blood cell is about 160 days, a drop in PCV of 50% over 40 days most likely reflects a substantial destruction of red blood cells. Thus, if the drop in PCV resulted solely from a shutdown of erythropoiesis and no other process, PCVs would have dropped by only 25% during the 40-day period, resulting in a PCV of more than 24% at 40 days after infection. Furthermore, a shutdown of erythropoiesis does not occur in *T. congolense*-infected Borans; it was shown at ILRAD that *T. congolense*-infected N'Damas and Borans have an erythropoietic response characterized by peaks above pre-infection levels of early and late erythroid progenitor cells (burst-forming units–erythroid and colony-forming units–erythroid, respectively) in the bone marrow of the fourth, fifth and sixth sternebrae (Andrianarivo *et al.*,

1995, 1996), and presumably in red bone marrow elsewhere in the animals, which agrees with conclusions from other investigators (Dargie *et al.*, 1979).

AAT-induced anaemia

Erythrophagocytosis by monocytes, macrophages and neutrophils has been demonstrated in cattle infected with African trypanosomes (reviewed by Murray and Dexter, 1988). While quantitative comparisons of this process were not made in infected N'Damas and Borans at ILRAD, colleagues at the University of Ibadan, Nigeria, who include ILRAD alumni Victor Taiwo and Victor Anosa, showed, using an *in vitro* assay, that erythrocyte phagocytosis and lysis by splenic plastic adherent cells (predominantly macrophages) from *T. congolense*-infected Borans was greater than that of splenic macrophages from similarly infected N'Damas and correlated dynamically with the degree of anaemia developed by these animals (Taiwo and Anosa, 2000). In addition, researchers at ILRAD showed that acute anaemia in *T. vivax*-infected cattle correlated with the production of TNF (Stijlemans *et al.*, 2016), a cytokine that increases the phagocytic activity of bovine neutrophils, by blood monocytes (Rainard *et al.*, 2000). In support of a role for erythrophagocytosis in AAT-induced anaemia, studies using a mouse model of *T. brucei* AAT showed that the acute drop in

Table 2.4. Characteristics of experimental cyclic *T. congolense* infections in N'Dama and Boran cattle. (Data from Paling *et al.*, 1991a,b; Williams *et al.*, 1991.)

Infection	N'Damas	Borans
Primary cyclic infection (four serodemes)	Drop in PCV but not life-threatening Parasitaemic waves decrease in amplitude incrementally over time to a cryptic level (<10² *T. congolense*/ml of blood), which is reached by 100–130 days post-infection Fast recovery of PCV as parasitaemia is suppressed	Acute drop in PCV: 75–100% of animals require curative treatment by about 40 days post-infection Repeating waves of parasitaemia do not decrease in amplitude over time Slow recovery of PCV in those animals that did not need curative treatment
Homologous cyclic reinfection	No change in PCV Rapidly suppress parasitaemia to a cryptic level with occasional low-amplitude spikes of parasitaemia	Drop in PCV, although less so than in primary cyclic infection: 50% of animals require curative treatment by 50–70 days post-infection Repeating waves of parasitaemia that decrease in amplitude over time in those animals that do not require curative treatment

PCV after infection results from phagocytosis of erythrocytes by activated liver monocytic cells and neutrophils and by splenic macrophages (Stijlemans *et al.*, 2015) and is induced by IFN-γ produced by natural killer (NK) cells, NK T-cells and CD8^{+} T-cells. Furthermore, the drop in PCV is prevented by the deletion of these cells and of the gene encoding the receptor for IFN-γ (Cnops *et al.*, 2015).

Dargie *et al.* (1979) noted a positive correlation between the severity of anaemia in cattle infected with *T. congolense* and the level and duration of parasitaemia. While this may be the case within a breed, it is not the case between breeds. Thus, work at ILRAD showed that *T. congolense*-infected Boran cattle developed anaemia more rapidly than similarly infected N'Dama cattle at ILRAD, despite initially similar levels of parasitaemia (Paling *et al.*, 1991a). It is possible that the number of *T. congolense* in the entire vascular system, rather than that of peripheral blood only, will correlate with the level of anaemia. In this regard, earlier work at ILRAD showed that *T. congolense* were not uniformly distributed in the host vasculature and that many more parasites were present in the microcirculation than were free in the cardiac blood, and some adhered to vessel walls (Banks, 1978). In addition, Trail *et al.* (1993) showed in their studies on N'Dama cattle in Gabon that some animals judged to be aparasitaemic by the DGBC technique developed low PCVs that were restored by a curative dose of the trypanocidal drug Berenil.

Whether or not differences in parasite load and distribution have an impact on AAT-induced anaemia in N'Damas and Borans, it is certainly not the only factor to do so; there is a clear impact of the genotype of the haematopoietic system. In a remarkable set of studies carried out at ILRAD, Naessens *et al.* (2003a) analysed levels of anaemia and parasitaemia in infected Borans and N'Damas exposed to cyclic infection with the *T. congolense* serodeme 1 ('IL 1180'). The cattle were either intact or modified experimentally to have a chimeric haematopoietic system, which in the case of N'Damas was 70–94% of Boran origin, depending on the individual, and in the case of Borans was from 30 to less than 5% of N'Dama origin, depending on the individual, based on analysis of a polymorphic T-cell marker, CD5, using mAbs that distinguish

between cells of *Bos taurus* and *B. indicus* origin. The development and severity of anaemia was significantly less in intact N'Damas than in Borans, chimeric Borans and chimeric N'Damas, all of which developed a similar degree of anaemia. Strikingly, levels of parasitaemia were lower in the N'Damas, whether intact or chimeric, than in the Borans, whether intact or chimeric. These results show that control of anaemia, which in the chimeric N'Damas was similar to that of infected Borans and is thus determined by the genotype of the haematopoietic tissue, is quite separate from control of peripheral blood parasitaemia, which in the chimeric N'Damas resembled that of Borans and is thus determined by non-haematopoietic elements although most likely acting on immune responses mediated by progeny of haematopoietic stem cells.

The haematopoietic chimeras were created by implanting an N'Dama and a Boran embryo at the late-morula stage into the same surrogate Boran mother, which results in anastomoses of chorioallantoic vessels in the placenta of the twin foetuses in early fetal life and haematopoietic chimerism in which the Boran component dominates. Haematopoietic stem cells give rise to erythroid, myeloid and lymphoid lineages, and hence, while it is clear that susceptibility to AAT-induced anaemia is a property of the Boran haematopoietic system and not other aspects of host physiology, it is unclear which component(s) of the haematopoietic system predispose(s) to this pathology.

Production of erythrocytes from precursor cells in the bone marrow is stimulated by erythropoietin, which is produced by kidney fibroblasts. Work at ILRAD showed that, while the transcript for erythropoietin was similarly increased in the kidneys of *T. congolense*-infected N'Damas and Borans at 35 days after infection, there was higher expression of the transcript encoding the erythropoietin receptor (epoR) in the bone marrow of the infected N'Damas than in the Borans (Suliman *et al.*, 1999). Assuming a direct association between expressed gene and protein, this finding suggests that haematopoietic progenitor cells in the bone marrow of the N'Damas would be more responsive to ambient erythropoietin than those of Borans, consistent with their resistance to AAT-induced anaemia. However, unexpectedly, this did not result in a stronger reticulocyte response, which is an

indicator of erythropoiesis, in the N'Damas. Rather, the reticulocyte response of the infected Borans during the early stages of infection was greater than that of the N'Damas (Andrianarivo *et al.*, 1996), despite the more profound anaemia that developed in the Borans. It is perhaps noteworthy that the epoR transcript analyses were performed with whole bone marrow from infected N'Damas and Borans and not from purified erythroid progenitor cells (Suliman *et al.*, 1999); hence, it is unclear which cell types in the former have the increased epoR transcript. This may be important because erythropoietin is now known to have pleiotropic effects on the immune system, where it inhibits macrophage functions (Nairz *et al.*, 2012), among other processes. Consequently, higher expression levels of epoR in bone marrow macrophages of infected N'Damas compared with infected Borans at an equal concentration of erythropoietin might result in a lower level of activation and thus a lower level of *in situ* phagocytosis of reticulocytes and erythroid progenitor cells consistent with haematopoietic-tissue intrinsic regulation of anaemia. Along similar lines, a significantly greater increase in transcript for the macrophage-activating cytokine IFN-γ, and the pyrogens interleukin (IL)-1α and IL-1β, was found in the bone marrows of infected Borans compared with those of the N'Damas (Suliman *et al.*, 1999), consistent with a greater potential for macrophage activation in the Borans. It is not known whether an N'Dama background would affect these properties of the Boran haematopoietic tissue; hence, we can only speculate that it would not, thus accounting for the inability of N'Damas bearing the Boran haematopoietic system to control anaemia.

A second haematopoietic-system intrinsic mechanism that could lead to greater destruction of red blood cells in animals with the Boran haematopoietic system affects expression on red blood cells of important surface antigens, including blood group antigens. Red blood cells of N'Damas have been shown to have significantly higher levels of sialic acids on their surface than red blood cells of Borans (Shugaba *et al.*, 1994), and hence are less affected by trypanosome *trans*-sialidases (Buratai *et al.*, 2006), which cleave sialyl groups from surface glycoproteins and glycolipids and directly promote phagocytosis of the red blood cells (Nok and Balogun, 2003; Guegan *et al.*, 2013). In addition, it has been

shown that AAT sometimes causes production of antibodies that react with antigens on healthy red blood cells, or against antigens exposed by infection-related processes, or bound as immune complexes with trypanosome VSG (Kobayashi *et al.*, 1976; Assoku and Gardiner, 1989; Rifkin and Landsberger, 1990), and thus promotes phagocytosis of the antibody-coated red blood cells. However, while this occurs in both N'Damas and Borans infected with a haemorrhagic *T. vivax*, as shown at ILRAD (Assoku and Gardiner, 1989; Williams *et al.*, 1992), there is no evidence that is the case in the *T. congolense*-infected intact and chimeric N'Damas and Borans. Indeed, Naessens and colleagues considered it unlikely that an adaptive immune response is responsible for anaemia in the *T. congolense*-infected cattle, because disruption of immune responses in N'Damas and Borans by complete deletion of CD4^{+} T-cells, CD8^{+} T-cells and γδ T-cells from the blood and peripheral organs using specific mAbs (Naessens *et al.*, 2003b; Sileghem and Naessens, 1995; Naessens, 2006) did not affect their distinct levels of anaemia, although the anti-CD4 treatment severely decreased host antibody responses (data not published, but summarized in Naessens *et al.*, 2002).

The pro-inflammatory cytokine TNF-α also has a role in the induction of anaemia, at least with some species/strains of African trypanosomes. Thus, studies in mice have shown that levels of anaemia were similar in *T. congolense*-infected TNF-α knock-out mice and similarly infected wild-type mice, suggesting that anaemia in this infection is TNF-α-independent. In contrast, the anaemia induced by *T. b. rhodesiense* (Naessens *et al.*, 2005) and *T. b. brucei* (Magez *et al.*, 1999) infection was significantly lower in TNF-α knock-out compared with intact mice, suggesting that the infected intact mice have a TNF-α-dependent mechanism that exacerbates anaemia. The highly virulent haemorrhagic East African strain of *T. vivax* may also induce this TNF-α-dependent mechanism of anaemia in infected cattle, including N'Damas, whereas *T. congolense* does not (Williams *et al.*, 1992; Sileghem *et al.*, 1994). Furthermore, N'Dama cattle proved not to be tolerant against an infection with the haemorrhagic *T. vivax*, suffering as much as or more so than susceptible cattle. Thus, N'Dama cattle may have evolved a trait that protects against TNF-α-independent

anaemia, but that is less, or not, effective against TNF-α-dependent anaemia.

AAT-induced lymphopenia and possible role of haemophagocytic syndrome in AAT

Studies at ILRAD on peripheral blood leukocyte dynamics in N'Damas, Borans, chimeric N'Damas and chimeric Borans following cyclic infection with *T. congolense* showed the same pattern as that of anaemia. Thus, while all groups of cattle had an initially similar acute decrease in numbers of total white blood cells, lymphocytes and neutrophils in the peripheral blood during development of the first parasitaemic wave (Ellis *et al.*, 1987; Williams *et al.*, 1991; Naessens *et al.*, 2003a), these values recovered quickly in intact N'Damas but not in intact Borans, chimeric Borans or chimeric N'Damas (Naessens *et al.*, 2003a). There was also a trend in gain of body weight to suggest that it, too, followed the pattern of anaemia and leukopenia in the infected intact and chimeric cattle, but these results were less clear cut than anaemia and leukopenia. Nevertheless, the correlation between anaemia, leukopenia and decrease in weight gain in intact and chimeric *T. congolense*-infected Borans, chimeric Borans and chimeric N'Damas is consistent with the possibility that these pathological processes are co-regulated, leading Naessens to consider them as a pathogenic syndrome and to seek other disease states in which these indicators of pathology are similarly linked. The result was recognition that AAT and haemophagocytic syndrome (HPS) share many clinical and pathological features (Naessens, 2006). HPS is 'a severe and often fatal syndrome resulting from potent and uncontrolled activation and proliferation of T lymphocytes, leading to excessive macrophage activation and multiple deleterious effects. It is associated with defects in cytotoxic granule-dependent cytotoxic activity of lymphocytes … thus highlighting the determinant role of this function in driving the immune system to a state of equilibrium following infection' (reviewed by Menasche *et al.*, 2005). While little is known about cytotoxic effector cells in AAT in cattle, the author's laboratory has recently shown that NK cells are globally activated in a murine model of AAT, deleting splenic B2 B-cells (Frenkel *et al.*, 2016) and CD8^{+} T-cells (D. Frenkel and S.J. Black unpublished data, 2019) in the spleen, and as yet unresolved target cells in the liver and lymph nodes. Perhaps this strangely aberrant behaviour of the NK cells is a futile attempt to dampen excessive immune system activation, an excessive application of the very response that is defective and inactive in HPS. Analysis of NK and other cytotoxic cell activation in AAT is warranted, as this might inform on the severe depletion of spleen and lymph node cells in late-stage infection, described by Fiennes (1970).

Antibody responses of trypanosome-infected N'Dama and Boran cattle

Studies by the ATLN clearly showed that a curative dose of Berenil restored PCV, body weight and productivity in cattle with AAT, thus showing that AAT-induced pathology is utterly dependent on the continued presence of trypanosomes in affected hosts. The goal of ILRAD scientists was to determine which aspects of the host immune response to trypanosomes promotes self-cure and recovery versus sustained infection and severe pathology by comparing immune responses that arise in similarly infected N'Dama and Boran cattle. Because African trypanosomes are extracellular parasites that are killed by VSG-specific antibody-dependent processes, researchers addressed antibody responses. Two antigenic variants of *T. congolense* were cloned from the first peak of parasitaemia arising in cattle that received the first cyclic infection (Paling *et al.*, 1991a). These clones were shown by VSG analysis to be present in first-wave parasitaemias of both N'Damas and Borans. Analysis of clone-specific antibodies in host serum was performed up to 35 days after infection, which corresponds to a major dip in parasitaemia in both host breeds (Paling *et al.*, 1991a). The studies showed that the clone-specific antibodies comprised both IgM and IgG classes and were similarly increased in both breeds of cattle, reflecting the similar patterns of parasitaemia in both breeds up to 35 days after infection. Both classes of antibody were shown to bind to VSG on intact trypanosomes and mediate their attachment to phagocytes (predominantly neutrophils and monocytes) from N'Damas and Borans *in vitro*, with attachment to adherent cells from N'Damas exceeding that of adherent cells from Borans, and with IgG1 being the most efficient antibody at facilitating this attachment (Kamanga-Sollo

et al., 1991). Clearance of antibody-coated African trypanosomes from the bloodstream in mouse models of AAT is mediated by phagocytic cells in the liver, spleen and other organs (Macaskill *et al.*, 1980; Black *et al.*, 1985); consequently, the superior capacity of phagocytes from N'Damas compared with Borans to bind antibody-coated trypanosomes *in vitro* might be expected to be associated with more efficient clearance of the parasites from infected N'Damas than from Borans *in vivo* and thus lower levels of parasitaemia in the former at equivalent levels of specific antibodies. Because this was not observed up to 35 days after infection of the cattle (Paling *et al.*, 1991a), it is possible that a disparity in binding of antibody-coated parasites to phagocytes from N'Damas and Borans does not arise in infected animals, perhaps as a result of activation of phagocytes, which is known to increase expression of IgG1 receptors on bovine monocytes (McGuire *et al.*, 1979).

In a related study of the same serum samples, an analysis was performed to determine the fine specificity of serum antibodies that recognize *T. congolense* clone ILNat 3.1 VSG (Williams *et al.*, 1996), a variant that arises in the first parasitaemic wave of infected N'Damas and Borans. This analysis is of interest because VSG is tightly packed on the surface of intact trypanosomes; as a result, only antibodies specific for antigenic epitopes present on the N-terminal domain of VSGs (exposed VSG epitopes) can bind to intact trypanosomes. An antigenic epitope is that small portion of the antigen that is bound by a specific antibody; a single antigen can have several different antigenic epitopes. Antibodies against other epitopes on the same VSG molecule (buried VSG epitopes) cannot bind to coated parasites but can bind once the VSG is released from the parasites, for example as a result of cleavage with the VSG GPI-PLC. Binding of antibody to soluble VSG and its clearance by phagocytes might be important because this material had been shown by investigators at ILRAD to activate bovine complement (Musoke and Barbet, 1977), which can elicit a cascade of pro-inflammatory components and thus might contribute to systemic inflammation. This investigation also showed that infected N'Damas and Borans made IgM and IgG1 antibodies against exposed VSG epitopes on infecting parasites, and in addition showed that IgG2 antibodies were made

(Williams *et al.*, 1996), which had not been assayed in the previous study. The kinetics and magnitude of *T. congolense* ILNat 3.1 VSG exposed-epitope-specific IgM, IgG2 and IgG1 responses by N'Damas and Borans were close to identical, as determined by fluorescent antibody-binding assays on intact parasites, consistent with similar control of the first-wave parasitaemia. However, this was not the case for antibodies specific for buried VSG epitopes, against which Borans made IgM antibodies and little IgG1, while N'Damas made IgG1 antibodies and little IgM. Analyses of splenic antibody-secreting cells from these animals showed a similar disparity in IgM:IgG ratios of plasma cells in infected N'Damas and Borans secreting antibodies that bind to soluble VSG (Taylor *et al.*, 1996b). Unfortunately, we know very little about how antibody responses against VSG on intact trypanosomes versus that of soluble VSG are regulated (Black *et al.*, 2010). However, it is possible that antibody responses against exposed VSG epitopes on parasite-attached VSG, versus those against epitopes on VSG that are buried on intact trypanosomes but accessible on soluble VSG, are made by different sets of B-cells that are differently regulated. Indeed, as a result of work at ILRAD, we know that a substantial portion of the antibody response to VSG is made up of low-affinity antibodies that react both with VSG and with a variety of cross-reacting proteins, including β-galactosidase and autoantigens (Naessens and Williams, 1992; Williams *et al.*, 1996). These antibodies are predominantly produced by a subset of B-lymphocytes that express the differentiation antigen CD5 (Williams *et al.*, 1991) and, at least with respect to antibodies that react both with ILNat 3.1 VSG and β-galactosidase, are a feature of the response of infected Borans but not of N'Damas (Williams *et al.*, 1996).

The concentration of IgM and IgG2 antibodies specific for VSG epitopes of *T. congolense* ILNat 3.1, and of IgM antibodies specific for buried VSG epitopes present in the blood plasma of Borans and N'Damas declined to baseline by 40 days after infection. In contrast, IgG1 antibodies in the blood plasma of the infected N'Damas and Borans that was specific for both exposed and buried VSG epitopes of ILNat 3.1 VSG remained at close to peak concentrations 40 days after infection in both breeds of cattle. Data were not obtained for later time points. At

appropriate concentrations, antibodies specific for exposed VSG epitopes neutralize trypanosomes expressing that VSG and therefore prevent recurrence of trypanosomes expressing that or a cross-reacting VSG. In this regard, the accumulation of trypanocidal/trypanostatic antibodies specific for exposed epitopes of multiple VSG types in the serum of infected Cape buffalo (*Syncerus caffer*) correlates with, and may be responsible for, maintenance of cryptic parasitaemia in this extremely trypanosomiasis-resistant bovid (Guirnalda *et al.*, 2007). It would therefore be interesting to learn how long the ILNat 3.1-specific IgG1 remained in the plasma of the infected N'Damas and Borans and whether similarly long-lived IgG1 antibody responses arise against later VSGs in both breeds of cattle. This would inform the relative effectiveness of host protective antibody responses over time in the trypanosomiasis-susceptible and trypanotolerant breeds.

Infected N'Damas were also found to differ from Borans by producing IgG1 antibodies against a greater number of proteins than are common to different trypanosome serodemes (Shapiro and Murray, 1982; Authie *et al.*, 1993b), including the 33-kDa congopain (Authie *et al.*, 1993a), which was discussed earlier with respect to its possible contribution to AAT pathogenesis and as a possible target for an anti-AAT vaccine. As with the response against buried VSG epitopes considered above, the more diverse antibody response against trypanosome-common antigens and the lesser production of antibodies against irrelevant antigens in infected N'Damas compared with Borans (Williams *et al.*, 1996) suggests functional differences in their immune responses. The possibility that this reflects differences in infection-induced T-cell-dependent B-cell responses in the infected cattle is considered next.

AAT-induced T-cell responses and immunosuppression

Infection with *T. congolense* and *T. vivax* compromises primary and recall vaccine responses in Boran cattle (Rurangirwa *et al.*, 1978, 1979, 1980, 1983; Whitelaw *et al.*, 1979; Ilemobade *et al.*, 1982; Sharpe *et al.*, 1982). This manifests as a substantial decrease in production of vaccine-specific IgM and IgG antibodies in the infected compared with the uninfected vaccinated ani-

mals (Ilemobade *et al.*, 1982). While AAT can dramatically affect primary and recall antibody responses to vaccines in cattle, it may not have an equally profound effect on recall antibody responses to early-arising VSGs, evidenced by occasionally recurring spikes of antibody against these VSGs during sustained infection in some infected Borans (Nantulya *et al.*, 1979; Musoke *et al.*, 1981; Vos and Gardiner, 1990). Similarly, processes that compromise antibody responses to vaccine antigens do not appear to prevent the immune responses that control newly arising trypanosome antigenic variants, reflected in repeating peaks of parasitaemia, each of which is cleared by antibodies specific for exposed VSG epitopes. These observations suggest that immune responses against exposed VSG epitopes differ in some important respect from primary and secondary immune responses against conventional antigens. Responses to conventional antigens are dependent on cognate interactions between B-cells, which produce the antibodies, and CD4^{+} T-cells, which provide critical stimuli (by cell contact and by secretion of helper cytokines) that direct B-cell proliferation and differentiation to antibody-secreting cells. To determine whether T-cells are required for antibody responses to exposed and buried VSG epitopes, Naessens deleted CD4^{+} T-cells from N'Dama and Boran calves with CD4-specific mAbs prior to their cyclic infection with *T. congolense* (unpublished data, summarized in Naessens, 2006). The antibody responses 'were found to be markedly reduced and delayed in the depleted animals. … This was the case for IgG and IgM antibodies to surface-exposed and internal trypanosome epitopes, as well as for natural IgM antibodies that react with non-trypanosome antigens.' Thus, help from CD4^{+} T-cells was required for these responses.

T-cells provide help for B-cell responses to two types of antigens, called T-cell-dependent (TD) and T-cell-independent type 2 (TI-2). TD antigens are soluble proteins without multiple repeating (identical) epitopes on each molecule. TI-2 antigens are usually polysaccharides that lack direct mitogenic activity and have multiple repeating epitopes. The B-cell response to TD antigens requires a direct interaction between: (i) B-cells that have endocytosed the antigen, processed it in an endosome and placed peptides derived from the antigen on their surface in complex with MHC class II (MHC-II); and

(ii) T-cells with receptors specific for the MHC-II antigen peptide complex. This response develops in germinal centres of lymphoid follicles and generates B- and T-memory cells, as well as antibody-producing plasma cells and memory plasma cells. The memory cells mount rapid immune responses upon re-encountering the same antigen. The plasma cells secrete lots of antibody specific for the antigen that simulated the B-cell, and the long-lived memory plasma cells migrate to niches in the bone marrow and continue to secrete this specific antibody, often for years. In contrast, the B-cell response to TI-2 antigens occurs in the absence of MHC-II-restricted T-cell help, although it can be facilitated by cytokines produced by activated T-cells (Mond *et al.*, 1995), does not require a germinal centre, and yields short-lived antibody-secreting plasma cells but not memory cells or memory plasma cells. Responses against TI-2 antigens, because they do not require complex interactions of T- and B-cells, arise faster than those against TD antigens and play an important role in protecting against pathogens (Vos *et al.*, 2000).

Trypanosome-common antigens such as congopain and Hsp70/BiP are most likely TD antigens, and soluble VSG has formally been shown to be a TD antigen in cattle, stimulating T-cells that require antigen-presenting cells (McKeever *et al.*, 1994). VSG epitopes exposed on the surface of intact trypanosomes could jointly be considered as TI-2 antigens. Thus, although each independent VSG molecule lacks repeating antigenic epitopes, the assembly of VSGs on the parasite surface is an array of repeating, antigenically identical epitopes. Therefore, the development of IgG antibody responses against congopain, Hsp70/BiP and buried VSG epitopes in *T. congolense*-infected N'Damas but not Borans, discussed above, suggests that the capacity to mount immune responses against TD antigens is, or becomes, compromised in Borans during infection but not, or to a lesser extent, in N'Damas. In support of this, Flynn and Sileghem (1991) at ILRAD showed that *T. congolense*-infected Borans were unable to generate T-cell responses to soluble VSG of an infecting trypanosome (cloned from the first parasitaemic wave) and developed only short-lived responses to other trypanosome antigens, whereas *T. congolense*-infected N'Damas generated long-lived T-cell responses to both VSG of an infecting tryp-

anosome and common trypanosome antigens, although these decreased somewhat with time after infection, and despite repeated curative treatments and reinfections, retained memory T-cells against these antigens for years after infection.

Infections with AAT parasites in mice are known to induce unresponsiveness of lymph-node T-cells to mitogens *in vitro*, which results from inhibition of secretion of the T-cell growth factor IL-2 and its receptor on T-cells, is mediated by nitric oxide and prostaglandin production by macrophages, which is stimulated by trypanosome components, IFN-γ and TNF-α (Sileghem *et al.*, 1991; Darji *et al.*, 1992; Schleifer and Mansfield, 1993; Sternberg and Mabbott, 1996; Gomez-Rodriguez *et al.*, 2009). Work at ILRAD showed that suppressive monocytes/ macrophages that inhibited T-cell proliferation in response to a mitogen (concanavalin A) *in vitro* arose in the peripheral blood, lymph nodes and spleen of *T. congolense*-infected cattle (Flynn and Sileghem, 1991) and simultaneously suppressed production of IL-2 and IL-2 receptor expression (Sileghem and Flynn, 1992b) by the T-cells but did not suppress their production of IFN-γ (Sileghem and Flynn, 1992a). Unlike the mouse AAT-induced suppressor cells, those in cattle were not inhibited by indomethacin, which prevents production of prostaglandins (Flynn and Sileghem, 1991), and did not produce nitric oxide in response to IFN-γ (Taylor *et al.*, 1996a), possibly because of a potent IL-10 response (Taylor *et al.*, 1998; O'Gorman *et al.*, 2006). The mechanism through which macrophages from the infected cattle inhibit T-cell proliferative responses *in vitro* was not resolved nor was a relationship explored between this *in vitro* T-cell suppressive response and the impaired responses of infected Borans and to a lesser extent N'Damas to TD antigen *in vivo*.

A loss in confidence that immunological differences between infected N'Damas and Borans could be resolved in any way that would improve productivity of either breed under natural tsetse/trypanosome challenge was perhaps a factor in the decision by ILRI to withdraw from this area of investigation and to diversify into studies of other pathogens. Nevertheless, it is noteworthy that this programme showed that two major indicators of trypanotolerance – control of anaemia and parasitaemia – are unlinked, and

introduced an additional indicator of trypa-notolerance, namely the ability to generate IgG1 antibodies against buried VSG epitopes and epi-topes on many common trypanosome antigens, including congopain and Hsp70/BiP. One pos-sibly practical finding from the programme was that infected N'Damas retain responsiveness to TD antigens throughout infection, whereas Borans do not. This suggests that N'Damas, more so than Borans, would benefit from priming with putative anti-AAT vaccine antigens such as con-gopain (Lalmanach *et al.*, 2002) and conserved peptides of VSGs (Black and Mansfield, 2016). A second possibly practical outcome is that the magnitude and diversity of IgG1 responses against trypanosome-common antigens and VSG buried epitopes should be used together with data on anaemia and body weight gain in infection-based screening for trypanotolerance.

The genetic basis of trypanotolerance

Selection for trypanotolerance has occurred in certain breeds of *B. taurus* (humpless) and *B. in-dicus* (humped) cattle (Dolan, 1987), such as the N'Dama, a small humpless long-horn from West Africa, and the Orma Boran, the smallest breed of the humped short-horned Zebu cattle from East Africa. Obviously, trypanotolerance is a de-sirable trait in cattle to be ranched in tsetse-in-fested areas, which includes most of sub-Saharan Africa. Despite data from ATLN showing that N'Dama cattle can be productive under low tsetse/trypanosome challenge without any treat-ment and can be productive under medium tset-se/trypanosome challenge when managed by diagnosis-based application of prophylactic and curative drugs, there is reluctance among pro-ducers in East Africa to adopt this breed because it is small, feisty and has a low milk yield. Produ-cers would prefer the trypanotolerant phenotype to be introduced by introgressive hybridization into larger breeds of cattle, including improved European breeds, which would be straightfor-ward if disease resistance was due to the pres-ence of one or a few genes only, but considerably less so if a large number of loci are controlling the trait. Selection of breeds with high expres-sion of trypanotolerance within a herd could be based on their high expression of indicators of

trypanotolerance following natural or experi-mental infection (Dolan, 1987) or, in the absence of infection, using markers with high fidelity to the trypanotolerance trait, such as polymorphic loci that affect or are responsible for trypanotol-erance, if such were available.

An ILRAD/ILRI Trypanotolerance Gene Mapping Programme was established in the hope of identifying markers of trypanotolerance for marker-assisted selection and also of providing insights into biological processes that control parasitaemia, anaemia and the efficacy of immune responses. Figure 2.2 (Ullmann *et al.*, 2005) outlines the approach taken and explains the mapping process, assuming that a single gene controls the trait; the legend additionally considers traits governed by expression of many genes in combination or multiple unlinked genes.

QTLs and murine trypanotolerance

ILRAD started a Bovine Trypanotolerance Map-ping Programme in 1990. Its leaders, A.J. Teale and S.J. Kemp, found that while the principle behind the mapping strategy is simple, the practice is extremely demanding (Kemp and Teale, 1998). Mapping required: (i) multiple ovulation families of full-sibling F_2 N'Dama × Boran; (ii) challenge of about 200 F_2 animals with *T. congolense* under carefully defined conditions of challenge and monitoring of responses; (iii) development of a genomic map of high marker density (with in-put from the global scientific community); and (iv) genotyping of the three generations of cattle (Kemp and Teale, 1998)

Clearly, this was a major undertaking, par-ticularly given the absence, at the time of initiation, of a high-marker-density bovine genome map, the age of cows at first calving (about 3 years) and calving intervals (time between birth of a calf and the birth of a second calf from the same mother – about 12–14 months). Given these constraints, it would take several years to gener-ate the F_2s. Mapping studies were also conducted in crosses of inbred mouse strains that had been shown at ILRAD to differ in susceptibility to in-fections with *T. congolense* following needle chal-lenge (Morrison *et al.*, 1978). Survival of inbred mice after infection with *T. congolense* might not be analogous to trypanotolerance in N'Dama cattle but nevertheless provided a robust pheno-type for mapping. Thus, infected C57BL/6 mice
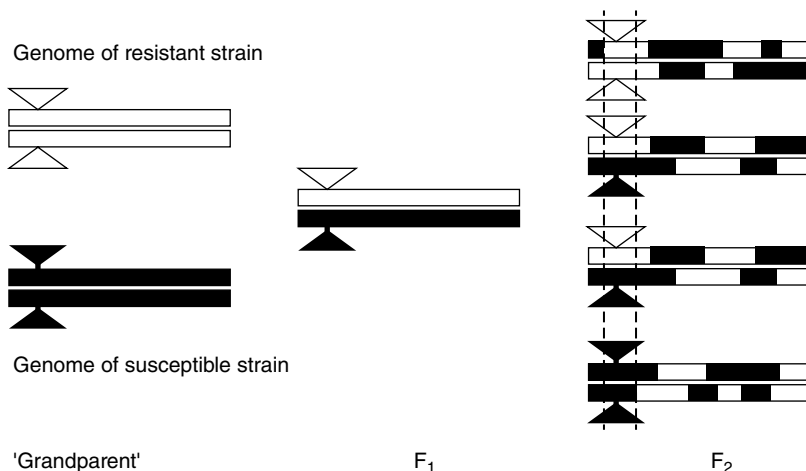
Fig. 2.2. Linkage mapping to identify genes responsible for trypanotolerance in N'Dama cattle. A single gene is used as an example. N'Damas are homozygous for a resistant allele (open triangle) and Borans for a susceptible allele (filled triangle). Their F_1 offspring obtain the resistant allele from the N'Dama parent and a susceptible allele from the Boran parent. When the F_1s are crossed, the F_2 generation contains animals with all possible combinations of alleles of the trypanotolerance gene. When infected with trypanosomes, individuals are expected to differ in expression of indicators of trypanotolerance. A correlation of indicators of trypanotolerance with areas of the grandparents' genomes in each animal allows mapping of areas of the grandparents' genome responsible for the trypanotolerance trait. The principle is the same for creating a linkage map for a trait that is controlled by many genes if these are arranged as clusters. Traits that are controlled by multiple unlinked genes that are dispersed throughout the genome are not good candidates for linkage mapping. (Constructed by author.)

survived for 110.2 days after infection and similarly infected BALB/c mice survived for 49.5 days, while few infected A/J mice survived longer than 20 days after infection. Inbred strains of mice have several advantages over cattle with respect to mapping studies. In each inbred strain, all genes are homozygous, a genome map had been developed using microsatellite markers (Dietrich *et al.*, 1996), the age of mice at first pupping is about 11 weeks, the mice have several offspring from each mating and there is a short interval between births. It is therefore unsurprising that mapping studies progressed somewhat faster in crosses between inbred strains of mice than in N'Dama × Boran crosses.

Loci (sites of genes) controlling the duration of survival of mice after needle challenge with *T. congolense* were mapped using C57BL/6, BALB/c and A/J grandparents and F_2 generations of the C57BL/6 × A/J F_1 and the C57BL/6 × BALB/c F_1 crosses. Survival and marker data were subjected to parametric linkage analysis, whereby the probability that a gene important for

a disease is linked to a genetic marker is determined by a statistical method, which yields a LOD score (logarithm of the odds to the base 10). This assesses the probability that a pedigree where the disease and the marker are co-segregating is due to the existence of linkage or to chance. For example, an LOD score of 3 means the odds are 1000:1 in favour of genetic linkage. Regions on mouse chromosomes 5 (maximum LOD score 4.6) and 17 (maximum LOD score 11), within large genomic intervals of 20–40 cM (1 cM contains on average 50 genes), were found to be important in determining resistance in both crosses, while a region on chromosome 1 (maximum LOD score 5.7) showed evidence of involvement in only the cross of C57BL/6 × BALB/c (Kemp *et al.*, 1997). The impact of these loci on survival times after infection was of large effect, accounting for most of the genetic variation in both F_2 populations. The three loci on chromosomes 17, 5 and 1 were designated, respectively, *Tir1*, *Tir2* and *Tir3* (for trypanosome infection response). *Tir1* represents the major trypanotolerance QTL in

mouse with an additive effect of 31 days on survival time. Following these initial QTL mapping results, an advanced intercross line approach was taken, which involves random and sequential intercrossing of F_2s, infection to assess phenotype and linkage mapping. Using F_6 crosses, *Tir1* was mapped to a 95% confidence interval of 1.3 cM, *Tir2* was mapped to a 12 cM region and *Tir3* resolved into three QTLs (*Tir3a*, 10 cM; *Tir3b*, 1.8 cM, and *Tir3c*, 8 cM) (Iraqi *et al.*, 2000), necessitating higher resolution mapping for positional cloning of genes underlying the QTL. An attempt to do this using F_{12} generations fixed for the susceptibility or resistance alleles at *Tir1* mapped *Tir2* to less than 1 cM but was less successful in narrowing the positions of *Tir3a*, *Tir3b* and *Tir3c* (Nganga *et al.*, 2010). An issue arising from F_{12} generation mapping was that the map positions of *Tir2* and *Tir3a*, *Tir3b* and *Tir3c* were different from the F_6 mapping study. Further mapping of congenic mice carrying the C57BL/6 *Tir1*, *Tir2* and *Tir3* resistance alleles on the A/J background partially resolved this disparity, supporting the F_6 location of *Tir2* and the F_{12} location of *Tir3a*. These studies, conducted by an international research team including ILRI scientists, showed that survival after infection was increased in *Tir1* and *Tir2* but not *Tir3* congenics (mice that are genetically identical except for the loci of interest) and that survival was negatively correlated with parasitaemia (i.e. mice with lower parasitaemia survived longer) but positively correlated with alanine aminotransferase levels in serum, suggesting that inflammatory responses in the liver were beneficial (Rathkolb *et al.*, 2009). Using a wide variety of techniques to identify candidate genes for murine tolerance to infections with *T. congolense*, it was postulated that *Pram1* (an adaptor protein used in T-cell receptor signalling) was the most plausible candidate QTL gene in *Tir1* and that Cd244 (NK cell receptor 2B4) was a strong candidate QTL gene at the *Tir3c* locus (Goodhead *et al.*, 2010). Thus, contrary to concerns that trypanotolerance in mice might be regulated by multiple unlinked genes, this proved not to be the case, at least with respect to events that control early mortality in *T. congolense*-infected mice. There have been no further publications in this area, so a contribution of a *Pram1* polymorphism to infection-induced early mortality remains to be confirmed.

QTLs and bovine trypanotolerance

Twenty-three groups of N'Dama × Boran F_2 animals, each containing between three and 13 calves, together with parental groups of N'Damas and Borans, were challenged with *T. congolense*-infected tsetse flies. Infections were followed for 150 days with respect to 16 phenotypic traits (Hanotte *et al.*, 2003). Twenty-eight of the F_2 offspring needed curative treatment (minimum day 14, maximum day 146), and the last value taken for these animals for all traits studied was taken as the value of the traits for the remainder of the challenge period. The traits measured informed infection-induced decreases in PCV, recovery of PCV, infection-induced loss in body weight, recovery of body weight, levels of parasitaemia between days 11 and 150 post-infection and the number of times an individual is parasitaemic by the DGBC technique, and thus jointly informed QTLs for parasitaemia, body weight and anaemia.

The animals were genotyped at 477 molecular marker loci covering all 29 cattle autosomes (i.e. any chromosome that is not a sex chromosome), covering 82% of the bovine genome. Putative QTLs were mapped to 18 autosomes. The results were consistent with a single QTL on each of 17 chromosomes, and two on BTA16. Individual QTL effects ranged from about 6% to 20% of the phenotypic variance of the trait. Alleles for resistance to trypanosomiasis originated from the N'Dama parent at nine QTLs and from the Kenyan Boran at five QTLs, and at four QTLs there was evidence of an overdominant mode of inheritance, when the heterozygote lies outside the phenotypic ranges of the parents (Hanotte *et al.*, 2003).

Noyes *et al.* (2011) tried to obtain short lists of candidate genes by focusing on polymorphisms within the bovine trypanotolerance QTL by transcriptome analysis of gene expression in the liver, spleen and precrural lymph node of N'Damas and Borans after infection with *T. congolense*. In this work, they assessed QTL regions and candidate loci for evidence of selective sweeps (the reduction or elimination of variation among the nucleotides in neighbouring DNA of a mutation as the result of the recent fixation of a beneficial allele due to strong positive natural selection). The gene expression data showed that Toll-like receptors and mitogen-activated protein kinase pathways responded to infection, and the former

contained *TICAM1* (TIR domain-containing adapter molecule 1), which is within a trypanotolerance QTL on BTA7. Genetic analysis showed that selective sweeps had occurred at the *TICAM1* and *ARHGAP15* (Rho GTPase-activating protein 15) loci in the N'Damas, making these strong candidates for genes underlying the QTL. *TICAM1* (also known as TRIF; TIR domain-containing adapter protein inducing IFN-β) is an adapter for a few Toll-like receptor signalling cascades, while *ARHGAP15* regulates signal transduction in the immune system. These proteins are involved in inflammatory and other immune responses. Field studies using 192 cattle produced from (N'Dama × Kenya Boran) × Kenya Boran subjected to natural challenge, and using a scoring system expanded to take into account avoidance of infection and genotyping using 35 microsatellite markers spanning five bovine chromosomes that were found in the above studies to contain trypanotolerance QTLs, showed that trypanotolerance was expressed in proportion to N'Dama origin marker alleles (Orenge *et al.*, 2011) and additionally showed the importance of sex and local environment conditions in determining the response to challenge (Orenge *et al.*, 2012). Given that trypanotolerance QTLs are present on 18 chromosomes, with an allele for resistance present at nine N'Dama QTLs and five Boran QTLs, the relevant genes, or markers tightly linked to these, would need to be resolved before the QTLs can be used in marker-assisted selection. Thus, traits that distinguish between N'Dama and Boran cattle trypanotolerance in cattle proved to be regulated by multiple unlinked genes. There have been no further publications on identifying candidate genes for trypanotolerance in bovids.

Mapping of trypanotolerance genes has been an enormous undertaking and, as with so many aspects of trypanosomiasis research, it has not been rewarded with leaps in understanding. Nevertheless, as a result of these studies we are now fully aware of the genetic complexity of the trait in cattle and its distinct and lesser complexity in mice, at least with respect to survival after infection. Indeed, given that a candidate gene for *Tir1* has been proposed, it would certainly be worthwhile to determine how expression of this gene, *Pram1*, affects infection-induced mortality and changes in immune parameters that accompany this (Morrison *et al.*, 1978). With respect to de-

termining the genetic basis for trypanotolerance in cattle, archives of genomic and cDNA have been established from the studies reported above and are available for deeper analysis as technology in this field undergoes further development to facilitate linking genes to disease-resistance traits.

Conclusions

From 1975 to 2015, scientists at ILRAD/ILCA/ILRI tried, with sustained focus and ingenuity, to identify trypanosome vaccine antigens and key aspects of trypanosomiasis pathogenesis that could be targeted immunologically or genetically to increase the productivity of cattle under tsetse/trypanosome challenge. Their research efforts, although logical, incremental and painstaking, did not achieve this goal.

Infection and treatment, a process commonly used to induce protective immunity to other pathogens, was shown to have limited success with African trypanosomes because of their huge antigenic diversity. Subsequent investigations of host-derived macromolecular nutrients that drive/sustain trypanosome cell-cycle progression were successful but did not have practical value because targeting their conserved receptors with lytic or blocking antibodies was ineffective. Although work at ILRAD identified low-, intermediate- and high-density serum lipoproteins and transferrin as required trypanosome growth factors, antisera against receptors for these molecules had little or no impact on trypanosome infectivity or growth in mammalian hosts. Despite the lack of translational impact of these investigations, the feeder layer-dependent and axenic culture systems, macronutrient bioassays and trypanosome cell-cycle analysis methodology developed at ILRAD for the above studies were forerunners of the high-throughput drug screens, genetic manipulation, and cell-cycle and differentiation pathway analyses that comprise much of the current basic research on the African trypanosomes.

Investigations at ILRAD/ILCA/ILRI to elucidate mechanisms of trypanotolerance using Cape buffalo and N'Dama and Boran cattle models were also scientifically rewarding but of little translational value. These studies showed that superior control of trypanosomiasis in Cape buffalo and, to a

lesser extent, in N'Dama cattle, was associated with the ability to suppress trypanosome parasitaemia and to sustain PCV, body weight and immune competence throughout infection, the latter evidenced by production of IgG antibodies specific for VSGs of newly arising trypanosome variable antigen types and other trypanosome antigens. However, the physiological mechanisms underlying this productive response, and its absence in trypanosomiasis-susceptible hosts, were not identified. Furthermore, analysis of the genetic basis of trypanotolerance in cattle showed this to involve 18 QTLs, all of which make relatively minor (10% or less) contributions to the trait and therefore are of little value for selective breeding to improve trypanotolerance of Borans and other livestock. While disappointing with respect to AAT control, studies of AAT pathogenesis at ILRAD/ILRI did identify the definitive question for immunological research on AAT, namely, how do trypanosomes eliminate TD antibody responses in trypanosomiasis-susceptible mammals? In addition, the work at ILRI on the genetic basis of trypanotolerance contributed a high-density single-nucleotide polymorphism (SNP) map of the bovine genome that has intrinsic value for analysis of QTLs that control other traits, including susceptibility to other diseases.

S.J. Black and colleagues continue to seek a key initiator pathway of trypanosomiasis pathogenesis and have recently shown (Frenkel *et al.*, 2016) that *T. brucei*, as well as *T. congolense* (S.J. Black and D. Frenkel, unpublished data, 2019), infection co-opts host NK cells to delete splenic B2 cells and thus prevent sustained TD antibody responses against VSG and other trypanosome antigens. Strikingly, when NK cell killing is prevented, trypanosome-infected mice suppress parasitaemia, do not develop anaemia or wasting, and do not succumb to infection-induced early mortality. Thus, elucidation of the trypanosome component that activates NK cells might provide a novel target for AAT immunoprophylaxis or a probe to identify cattle that do not respond to it and hence may be trypanotolerant. Finally, other events might supersede the need to selectively control AAT. S.J. Kemp and colleagues at ILRI have initiated a multinational project in Africa to identify those rare cattle that remain healthy and productive under ambient disease and environmental stress. This will entail animal productivity reporting by legions of smallholder farmers in disease-endemic regions, SNP analyses of blood leukocytes from cattle with a high-productivity phenotype, selective breeding and validation.

The Future

ILRI and ILRAD alumni and their global partners continue to seek solutions to AAT. Jayne Raper and colleagues are exploring genetic engineering of cattle to express a trypanosome-lytic factor derived from primates that are resistant to trypanosome infection (MacMillan, 2016).

Acknowledgements

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3   Tsetse and Trypanosomiasis Control in West Africa, Uganda and Ethiopia: ILRI's Role in the Field

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Contents

Introduction

African animal trypanosomiasis (AAT) occurs where the tsetse fly vector exists in sub-Saharan Africa, between the latitudes 15°N and 29°S (Randolph *et al.*, 2003). It affects ruminants, camels, horses and pigs, and constrains cattle production over an area variously estimated to be between 8 and 10 million km[2] in Africa. Around 67 million cattle live in tsetse-infested areas out of a total of 253 million in Africa[1]. In some situations, around one in 20 of the cattle at risk die each year, and the productivity of the survivors in terms of draught power, milk production, growth and birth rate are lowered by

10–40% (Swallow, 2000). Estimated total losses due to trypanosomiasis range widely depending on the methods used, assumptions made and types of losses estimated (ILRAD, 1994; Budd, 1999; Kristjanson *et al.*, 1999; Swallow, 2000). The upper range of published estimates would make annual losses from trypanosomiasis equal to one-third of the estimated livestock gross domestic product in sub-Saharan Africa.

The disease is complex, involving three species of parasite, namely *Trypanosoma congolense*, *T. vivax* and *T. brucei*. *T. vivax* can also be transmitted mechanically by biting flies, and thus is also found in parts of Africa free or cleared of tsetse and in parts of Central and South America.

Two related parasites, *T. brucei* subsp. *gambiense* and *T. brucei rhodesiense*, cause human African trypanosomiasis (HAT), also known as sleeping sickness. While HAT is generally considered a disease of people, livestock and wildlife act as reservoirs for *T. b. rhodienense* and possibly for *T. b. gambiense*, complicating the control of HAT. Knowledge of the biology of tsetse and trypanosomiasis was greatly advanced by Mulligan and Potts (1970) and by Maudlin *et al.* (2004).

Trypanosomes have the ability to undergo antigenic variation (Cross, 1975), enabling host invasion and allowing them to establish persistent infections. In addition, each species comprises an unknown number of strains, all capable of elaborating a different repertoire of variable antigen types. Hence, no vaccine is currently available (the problem of antigenic variation and the history of vaccine development are discussed in Chapter 2, this volume).

The initial mission of the International Laboratory for Research on Animal Disease (ILRAD) was to tackle AAT and East Coast fever, two of the most serious intractable African livestock diseases. As a result, a large body of research on AAT was conducted over 30 years: genetics, breeding and immunology research are discussed in Chapters 1, 2 and 4 of this volume, respectively. This chapter reviews the earlier field work of ILRAD followed by that of International Livestock Research Institute (ILRI) after 1994 in East and West Africa, including the engagement of those institutions with regional and global initiatives.

Field Work on African Animal Trypanosomiasis

AAT has long been regarded as the single most important cattle disease in Africa, and between 1905 and 1960 it commanded the attention of five imperial powers, dedicated government services, and national, regional and international research institutions. It has been estimated that 25% of colonial research spending went to trypanosomiasis (Rogers and Randolph, 2002). However, the final decade of the last century saw practical control of trypanosomiasis. With the onset of the Great African Depression in the 1980s (Leonard and Straus, 2003), tsetse programmes, like other government services, became increasingly underfunded and dysfunctional, and donors were less willing to pay for large-scale, long-term control. Moreover, control efforts before the 1980s usually relied on ground and aerial spraying of insecticide, which was increasingly seen as expensive in economic and environmental terms. One study (Meyer *et al.*, 2016) argues that tsetse control operations covered barely 1.3% of the estimated infested area in sub-Saharan Africa.

As a result of this decline in the funding available for control, an upsurge of AAT cases occurred during the post-independence period. In some countries, this was exacerbated by the movement of people and livestock into formerly sparsely inhabited tsetse-infested areas. AAT incidence increased rapidly in the 1980s and 1990s, and cattle herds almost disappeared in some areas, such as the Ghibe Valley of Ethiopia and the Yale agropastoral zone of Burkina Faso. The 1980s also saw a major epidemic of HAT in Sudan and Uganda, which spread into Kenya. As a result of these upsurges in human and animal disease, there was renewed interest in the field control of AAT, several new initiatives were established involving ILRAD and the International Livestock Centre for Africa (ILCA).

Apart from efforts to understand and manage AAT, ILRI focused on three major areas: (i) the promotion of trypanotolerant cattle; (ii) community-based control of tsetse in Ethiopia and later Burkina Faso; and (iii) managing resistance to trypanocides. ILRI did not engage with the attempt to eradicate tsetse from Africa, which scientists believed was infeasible. The areas of ILRI activity are first briefly outlined, and the rest of the chapter focuses on the work done and the impacts achieved in different countries. Table 3.1 summarizes ILCA/ILRI research since about 1990 on field aspects of trypanosomiasis control.

Trypanotolerance

The challenges of tsetse control and the ongoing cost of trypanosomiasis control by veterinary drugs were recognized early in the history of ILRI. One option that gained attention early on was to exploit the genetic tolerance to trypanosomiasis infection found in several African cattle breeds, such as the taurine N'Dama and West African

Table 3.1. Research on tsetse and trypanosomiasis control in West Africa and East Africa since 1990 by ILRI and partners. (Data from ILCA and ILRI annual reports, various years.)

Institution	Location	Period	Objectives	Interventions	Tsetse reduction from baseline	Reduction of AAT prevalence	Difficulties	Sustainability
ILCA	Ghibe River Valley, Ethiopia	1990–1992	Vector control	ITC, ITT, TRY	74–81% depending on species	85%	Theft of traps, socio-political disturbances	Unsustained. Tsetse reinvasion, second phase from 1993 mixed results
ILCA	Ghibe River Valley, Ethiopia	1991–1993	Vector control	ITC, TRY	0–93% depending on species	60%	Slow decline in tsetse densities	Sustained in the short-term. Control was in place 5 years later. Full cost recovery from farmers
ILRI evaluation on CIRDES projects	Burkina Faso	1990–2000	Vector control	ITC, ITT	98.4%	80%	Farmers could not meet costs to continue control	Epidemics controlled; however, tsetse reinvasion and return of AAT after campaign
ILRI evaluation of ICIPE project	Kenya	2002–2006	Vector control	ITC	Not measured	22%	Low effectiveness	No business case for innovation
ILRI	Burkina Faso, Mali, Guinea	2002–2006	Integrated control	ITC, ITT, TRY, TTC	Significant	Significant	Communal action difficult; disabling policy	Only TRY proved sustainable

CIRDES, Centre International de Recherche-Développement sur l'Elevage en zone Subhumide; ICIPE, International Centre of Insect Physiology and Ecology; ITC, insecticide-treated cattle; ITT, insecticide-treated traps and targets; TRY, trypanocidal drugs; TTC, trypanotolerant cattle.

Shorthorn breeds of West and Central Africa. These breeds had evolved over millennia to acquire a significant degree of innate resistance to trypanosomiasis. Trypanotolerant cattle were therefore identified as a promising approach to livestock keeping in tsetse-infested areas (Murray *et al.*, 1982).

There is evidence that cross-breeding occurs between bos indicus and bos taurus in West and Central Africa and that this may enhance resistance to trypanosomiasis (Traoré *et al.*, 2017 for southern Mali). The African Trypanotolerant Livestock Network (ATLN) was established in 1977 as a joint venture between ILRAD and ILCA. ILRAD was to investigate animal health, infection status and vector behaviour, while ILCA was responsible for animal production, nutrition and data processing. This research fell into four areas: (i) the epidemiology of AAT; (ii) the criteria of trypanotolerance; (iii) the genetics of trypanotolerance; and (iv) the health and productivity benefits of interventions. Field sites were located in Côte d'Ivoire, Ethiopia, Gabon, Zaire, The Gambia and Senegal. Along with the Food and Agriculture Organization of the United Nations (FAO), ILCA surveyed the number and distribution of trypanotolerant cattle in 1977 and updated those figures in 1985.

Two ILCA/ILRAD monographs established the state of scientific knowledge at the outset of the ATLN (Trail *et al.*, 1979a,b). A long compendium (ILCA/ILRAD, 1988) summarized the work of the first decade of the ATLN, findings that were extended by Rowlands and Teale (1994) and Itty (1992). The work of the ATLN included the following:

- Establishment of a research network to improve livestock production by ensuring optimal application of existing knowledge and recent research.
- Understanding the vectorial potential of tsetse.
- Supporting multiplication of herds of trypanotolerant animals.
- Maintaining experimental cattle and small ruminant herds.
- Evaluating the performance of livestock under AAT risk.

Community-based tsetse control

Tsetse (*Glossina* spp.) are unusual flies. The females do not lay eggs but instead produce a single, large larva and have only up to 12 offspring in a typical lifetime. Their low reproductive rate makes them vulnerable to interventions that cause even small increases in mortality. Historically, area-wide and aerial spraying was successfully used to control tsetse. However, the flies reinvaded after control, and repeated campaigns proved expensive and raised environmental concerns.

A more targeted approach is the use of cloth traps or targets that are soaked with insecticide, with or without baits. In the early 1900s, sticky traps worn by plantation workers were successfully deployed on the Island of Principe to eradicate *Glossina palpalis*. In the mid-20th century, great advances were made in the design of traps and targets, making them highly effective at reducing tsetse. The live-bait technique involves treating cattle with appropriate insecticide formulations, usually by means of cattle dips, or as pour-on, spot-on or spray-on veterinary formulations. These are highly effective against tsetse and have the additional advantage of controlling other flies and cattle ticks. The availability of these simple, cheap and effective technologies led to interest in community-based approaches to tsetse control.

Trypanocide resistance

In the absence of a vaccine (Chapter 2, this volume), the principal control strategies are reducing or eliminating the tsetse vector, applying trypanocides and keeping trypanotolerant stock. Less than 1% of the infested area is under vector control and fewer than 20% of the cattle at risk are trypanotolerant, but around the majority of cattle at risk receive trypanocidal drugs making this the most popular control option and one that is both effective at scale and sustainable without continued external support. Current trypanocides have been in use for over 40 years and new drugs have not been developed because drug development is expensive. One older survey of drug research and development costs derived an estimate of 'nearly' US$900 million per new compound across a range of human drugs (DiMasi *et al.*, 2003). The market for trypanocides in smaller African markets is estimated to be US$20 million per year (Sones, 2001). Hence, it will probably be unprofitable for private firms to develop new trypanocides for the African market. Given this context, threats to the efficacy of

the older trypanocides undermine the most widely used strategy for control.

Drug resistance is the heritable loss of sensitivity of a microorganism to an antimicrobial to which it had been sensitive. Modern cattle trypanocides were introduced in the 1950s, and the first cases of resistance were reported in the next decade. The emergence of resistance further complicated the breakdown in testse control that had led to reinvasions of tsetse.

ILRAD scientists had a major role in this emerging research area. Much of this work was laboratory based, focused on understanding the mechanisms of resistance and developing tests and assays for resistance. In addition, drug-resistant strains isolated from the field were characterized at ILRAD. However, ILRAD and ILCA scientists were also involved in some of the early studies on field resistance and were among the first to assess resistance in Ethiopia, Uganda, Kenya, Guinea, Mali, Ghana and other countries.

ILRI scientists were also instrumental in developing field tests for trypanocide resistance. These involved testing cattle for the presence of trypanosomes, treating them with trypanocides and then examining blood at intervals over 98 days to see if the trypanosomes were still present despite treatment (an indication of resistance). These methods were widely applied by other researchers and subsequently refined by shortening the follow-up period to 28 days. This abbreviated methodology for evaluating the presence of resistance lowers the cost significantly so that it can be used more readily by national agencies as an initial protocol for screening (Mungube *et al.*, 2012). The abbreviated trypanocide resistance tool has subsequently been used by other researchers.

efficacy and subsequently cost–benefit of using prophylactic versus curative control. (Prophylactic drugs are given to prevent the animals from becoming sick; curative drugs are given to animals when they become sick.) Prophylactic treatment was more expensive but more profitable, mainly because lactation loss was avoided. When disease fell below a certain level, prophylaxis was less profitable (Itty *et al.*, 1988).

For example, ILRI research did contribute to the growing interest in using pour-ons for control of tsetse. A study in Kwale found incidence rates of trypanosomiasis in the biweekly-treated (28.2%) and monthly-treated (38.6%) animals were statistically lower than in the bimonthly (63.9%) and control (72.6%) groups (Muraguri *et al.*, 2003). Similarly, a study in a trypanosomiasis endemic area in Teso District, western Kenya, found that when the tsetse density was very low, control of trypanosomiasis in the Orma-Teso Zebu offspring in western Kenya required targeting of individual affected animals in the dry seasons (Gachohi *et al.*, 2009).

One of the most important studies in Kenya was a combined epidemiological and economic investigation into a promising novel technology: a synthetic tsetse repellent (Bett *et al.*, 2010). The evaluation involved 2000 cattle: 1000 head in a control group and another 1000 animals treated with tsetse-repellent dispensers suspended from neck collars. The effectiveness of the repellent was monitored for 16 months. The trial results showed that the treatment reduced trypanosomiasis infection rates by between 18% and 23% compared with the control levels, indicating that the repellent was not 'a viable alternative to existing control techniques' (Irungu *et al.*, 2007).

ILRI impacts on AAT in Kenya

Given that ILRAD's mandate focused on vaccine development, there was relatively little field epidemiology in Kenya. Moreover, East Coast fever was seen by most stakeholders as of higher priority in Kenya. Small studies addressed aspects of control resulting in useful recommendations, although it is not clear to what extent recommendations were taken up or what impact they had.

An early study, conducted between 1982 and 1986 in coastal Kenya, evaluated the

ILRI impacts in Ethiopia

In the 1970s and 1980s in Ethiopia, there were substantial movements of people and their livestock from the densely populated northern highlands to the scarcely populated, tsetse-infested south-western region. These livestock were vulnerable to AAT, and losses were originally high. Concern over the situation in Ghibe Valley, south-west Ethiopia, prompted ILCA to select it as the Ethiopia study site for the ATLN. This network comprised a set of 11 research sites located

in different trypanosomiasis-risk areas throughout tropical Africa in order to study the complex interactions that affect trypanotolerance, to provide baseline data for livestock development in tsetse-affected areas and to evaluate different methods for controlling trypanosomiasis (see Map 4, p. xx).

Studies on the prevalence of trypanosome infections in East African Zebu cattle and the tsetse challenge that such animals are exposed to started in January 1986. An average of 840 East African Zebu cattle (non-trypanotolerant) from around ten herds in the Ghibe Valley were monitored from January 1986 to April 1990. The studies provided information on the epidemiology and transmission dynamics of AAT, which were subsequently used in disease models and in planning control. Moreover, they resulted in the detection of drug resistance for the first time in Ethiopia (Rowlands *et al.*, 1993). Although sick animals were treated with trypanocides, the prevalence of AAT increased yearly, raising the suspicion of drug resistance, which was confirmed by laboratory analysis of trypanosome isolates collected in 1989.

It was decided to test an intervention based on tsetse control using cloth screens impregnated with insecticides. This approach had been first used in 1914, when tsetse was eradicated from the Island of Principe, in the Gulf of Guinea, by killing the flies using 'sticky traps' – wooden boards coated with sticky material strapped to the backs of plantation workers. Serious interest in the use of vector capture was revived in the 1970s with the development of more effective cloth traps and screens and the discovery that particular colours and odours attract tsetse flies. Much of the foundational research was conducted in Zimbabwe, with another focus in West Africa.

Both traps and targets (cloths or screens) were developed and successfully piloted in South, East and West Africa, but had not been used for the control of trypanosomiasis in cattle in situations where resistance to trypanocides occurs. The trial found that use of targets reduced vector populations and infections, even in the presence of drug resistance, but did not appear to be sustainable due to widespread thefts of targets (Leak *et al.*, 1996).

Another approach to tsetse control is to turn cattle into mobile targets. The animals are dipped or sprayed with insecticide or the compound is poured on them. This method was first tried with limited success in the 1940s using dichlorodiphenyltrichloroethane (DDT). However, development of pour-on formulations using pyrethroids, a safe and biodegradable insecticide, led to successful control of tsetse in trials in Zambia and elsewhere. In 1991, a control scheme was started in Ghibe Valley using insecticides poured directly on to cattle. This was considered to be more sustainable, as farmers directly benefited and the transaction costs in maintaining screens or traps were avoided. For the first 2 years, insecticides were given free of charge. The control was very effective and promoted widely by ILCA, and as a result, many families migrated into the area.

An economic assessment quantified the benefits (Omamo *et al.*, 2002). Following control, the apparent density of tsetse and biting flies in the region fell by 95%. This reduction in tsetse challenge led to a decrease in trypanosome prevalence in cattle of over 61%, despite a high level of resistance to trypanocides. The number of curative drug treatments per animal fell by 50%. Mean calf growth rate increased by 20%, while mean calf mortality and abortion decreased by 57%. Average cow body weight was boosted by 4%, the cow:calf ratio increased by 49% and adult male body weight increased by 8%. Between 1995 and 1997, expenditure on trypanocidal drugs fell by US$39,000, which more than offset the US$16,000 cost of the pour-on. The value of increased output of meat (40%) and milk (30%) implied a benefit:cost ratio of 11.6 over 2 years and of 9.3 over 10 years, with increases in annual household income between 10% and 34%.

After 2 years of free treatments, a more sustainable model was investigated with the imposition of a charge of US$0.6 per treatment. An economic study found that, while many farmers continued to pay for treatments, there was a reduction in demand (from 97% of farmers to around 60%) and that poorer farmers dropped out disproportionately (Swallow and Woudyalew, 1994). There were also efforts to hand management of the scheme over to the community. By 2000, ILRI was no longer able to continue supporting the scheme; it appears that the treatments stopped and the tsetse increased (Wilson, 2003). In a subsequent project from 2008 to 2011, ILRI helped to establish 13 trypanosomiasis cooperatives to link private

veterinary drug suppliers to the remote communities to ensure a supply of trypanocides to and to reduce dependence on the public supply system. This promising delivery approach has not been systematically evaluated.

An analysis of land-use change by ILRI in 2003 revealed huge increases in human and animal populations, as well as land cultivated in the Ghibe Valley (Wilson, 2003). This analysis concluded that the control of tsetse had a role in attracting migrants, but this was difficult to quantify because other climatic and demographic factors influenced population movements.

ILRI impacts in Uganda

Trypanosomiasis has long been a concern in Uganda. Both the Gambian and Rhodesian forms of HAT are found in Uganda, and one of the largest recorded human epidemics occurred in the early 19th century, when over 500,000 people are estimated to have died. After the political unrest of the 1980s, tsetse invaded new areas of Uganda, and various control campaigns were implemented (Okello-Onen et al., 1994; Okoth, 1999).

ILRI was a partner in one of the research projects, which aimed to better understand the infection dynamics and drug sensitivities of the trypanosome parasites prevalent in dairy systems in peri-urban Mukono District, Uganda, between 1995 and 1999. This demonstrated a low prevalence and a low pathogenicity of trypanosome infections in cattle. An economic study by ILRI found that, while trypanocides constituted up to 7.2% of health costs, they decreased profitability on farms only by 1%. The dairy farms were profitable, and the authors suggested trypanosomiasis was less important than previously thought, demonstrating the importance of economic analysis to justify interventions (Thornton and Odero, 1998).

As a result, the research consortium decided that the methodologies developed in the project should be applied to other areas of Africa where the disease was thought to have a significant detrimental effect on livestock production, particularly in areas where drug resistance was suspected to occur, and Burkina Faso was selected for the next phase.

ILRI contributed to research on the control of HAT in South-east Uganda from 2000 to 2003 (see Chapter 8, this volume). Surveys found that reporting was strongly biased to areas near health centres with good capacity, and models suggested that the major impact of sleeping sickness was deaths in people who were never treated or reported. A livestock survey helped identify hotspots. It linked cattle movement to the introduction of sleeping sickness to new areas and suggested that mass treatment of cattle might prevent the spread of sleeping sickness. The treatment of 30,000 cattle in Kamuli was highly effective at removing human-infective HAT parasites from the cattle reservoir and contributed to a significant decrease in human HAT cases (Fyfe et al., 2016). This work noted relatively little interest in trypanosomiasis as a stand-alone issue and concluded that community approaches would need external support.

In 2002, ILRI undertook research in Uganda to develop decision-support tools for improving trypanosomiasis control. This objective was to enable technicians working with tsetse and sleeping sickness in Uganda to learn techniques for conducting geographical information system (GIS) analysis to provide decision makers with information to facilitate targeting for control of the disease. The project successfully established GIS capacity within Uganda.

ILRI impacts in West Africa

Field work in West Africa initially started under ATLN. These conducted ground-breaking research into understanding the presence, prevalence and impacts of tsetse and HAT. For example, herds were monitored monthly for several years to understand production economics under the risk of trypanosomiasis. The ATLN work concluded, in seven papers in the Democratic Republic of the Congo (formerly Zaire), Togo, Ethiopia and The Gambia (summarized by Thornton and Odero, 1998, pp. 8–11), that trypanotolerant cattle were 'economically justifiable' in a variety of situations with respect to tsetse challenge, control methods and experience with trypanotolerance.

Following the Ugandan and ATLN work, ILRI collaborated and later led a research programme on trypanocide resistance in West Africa. The recommended control strategy was an integrated approach. This comprised vector

suppression in epidemiological hot spots, disease management at the herd level and strategic use of trypanocides, combined with keeping local tolerant breeds. The first activity, from 1998 to 1999, was to assess AAT prevalence, tsetse challenge and drug use. Resistance of trypanosomes to isometamidium and diminazene was also demonstrated by both *in vivo* and *in vitro* methods (McDermott *et al.*, 2003; Knoppe *et al.*, 2006).

This led to a more ambitious programme that sought to ensure the efficacy of trypanocides as a component of integrated control of trypanosomiasis in the cotton zone of West Africa. The first objective was to assess the presence and level of resistance across three countries (Burkina Faso, Mali and Guinea) in the cotton zone of West Africa. This entailed an enormous survey, eventually covering more than 30,000 cattle. The results showed a marked gradient in land cover, tsetse species, cattle breed, resistance and productivity, from more extensive, low-input, low-output, low-disease systems in east Guinea to more intensive, productive and high-disease systems in west Burkina Faso. The pattern of tsetse distribution, trypanosomiasis prevalence and trypanosomiasis risk varied predictably, with intensified agriculture apparently driving change from a situation of low disease and little resistance to one of high disease and high resistance. Tailored recommendations were made for optimal control across the region (Clausen *et al.*, 2010).

An epidemiological model describing the transmission dynamics of trypanosomiasis was developed and used to explain the trends identified in the spatial analysis for West Africa (Grace, 2006). The model suggested that a change in cattle breed is driving the emergence of resistance through the increase in drug use by farmers to maintain trypanosusceptible Zebu – the main driver is hence the change in preferred cattle breed rather than drug use. Moreover, the situation in West Africa appears to be on the accelerating portion of the sigmoidal resistance curve, implying that prevalence, morbidity and mortality, and resistance are likely to deteriorate considerably from the present levels (Grace, 2006). The optimistic conclusion from modelling is that vector control, even if only resulting in small increases in tsetse mortality, may rapidly reverse the trend of emerging resistance.

In the next stage, four 'best-bet' strategies were evaluated: (i) trypanotolerant cattle; (ii) community-based trypanosomiasis control; (iii) training farmers and paravets in integrated AAT control; and (iv) rational drug use information for farmers and service providers. Community-based control using insecticide-treated targets and insecticidal spraying decreased cattle mortality (71%), decreased abortion (66%), increased traction (95%) and decreased farmer expenditures on drugs (50%), while milk production increased by 10%. The intervention was deployed in a highly participative way, testing the hypothesis that previous attempts at community-based control had failed because they were top down and insufficiently participatory (Meyer *et al.*, 2016). (A review of previous vector-control projects in Burkina Faso showed that community-based control was in all cases effective and in no case continued after the project withdrew; Grace, 2003). However, while efforts were more sustainable than attained previously, most of the activities were eventually abandoned. Researchers concluded that community tsetse control does work but does not continue without external support because of high transaction costs of setting up and maintaining the community-level institutional innovations needed to sustain control efforts (Box 3.1). This substantiated earlier theoretical work that also argued that community-based control was not sustainable because of its 'prisoners dilemma' nature (McCarthy *et al.*, 2003).

As part of the capacity building, several appropriate technologies were developed, adapted and tested. Anaemia is an important sign of trypanosomiasis and one that farmers were poor at detecting. Researchers tested two field devices: a colour chart developed for diagnosing anaemia in sheep and a blood prick test designed for diagnosing anaemia in pregnant women. Both were effective, but the colour chart system was simpler and cheaper (Grace *et al.*, 2007). The project also calibrated a weight band for the cattle population in the cotton zone. This is a tape measure that converts girth into body weight and hence allows more appropriate dosing. Several decision-support tools to aid differential diagnosis were also tested with varying success.

Trypanotolerant cattle keeping was evaluated and it was found that, while farmers regard

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Box 3.1. Community-based trypanosomiasis control.

An ILRI initiative to improve control of AAT in Burkina Faso started with an evaluation of previous projects (Grace, 2003). Research projects are rarely revisited after initial implementation, and this threw light on the 'life after project' scenario by looking at eight completed projects in Burkina Faso, six of which had a major participatory component. The projects took place over 25 years and encompassed a wide range of farming systems, institutions, partners and social conditions. They incorporated community participation and used low-cost and effective strategies that resulted in the rapid and total resolution of trypanosomiasis problems in all project areas. Participation and long-term viability issues (including cost recovery) were incorporated from the onset, and benefits to farmers were major, obvious and acknowledged. Yet, despite these substantial successes, none of the communities has continued with the strategies; tsetse reinvasion has occurred in all cases, and after years of investment in participative trypanosomiasis control, farmers are once more 'on their own' and experiencing substantial losses from trypanosomiasis. The review identified some factors that blocked sustainability. While farmers learned technical skills for tsetse control, they did not learn management or business skills in implementing these. Although control was relatively cheap, the small financial requirements were a barrier. Farmers showed much more hypothetical willingness to pay than actual. None of the projects used delivery systems that were capable of delivering control after the withdrawal of the project. The systems used were either of known low sustainability (e.g. government, project or existing village groups) or new institutions whose sustainability and appropriateness for village conditions was unproven (e.g. private vets). Communities encountered unexpectedly high transaction costs in avoiding free riders.

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the productivity (and disease resistance) of trypanotolerant cattle quite highly, they also cite their undesirable features: unpredictable temperament, low working speed, short legs rendering them liable to damage the crop while weeding, slow growth and slow weight gain, smaller overall size, and low sale price and slower sale. The project confirmed other findings that trypanotolerant cattle were gradually being replaced as farmers switched to more productive breeds, and concluded that encouraging trypanotolerant cattle was not a viable strategy, at least while development, wealth and market integration were on an upwards trend.

The second intervention combined training on vector control, diagnosis and treatment of trypanosomiasis, and diagnosis and treatment of other common diseases, as well as use of traditional medicines and nutrition. Scientists found large and significant differences in knowledge and skill both in farmers (in Burkina Faso) and in paravets (in Guinea) before and after training, and between those trained and their peers who had not been trained (Grace *et al.*, 2008). Ten months after training, there was no significant decrease in the level of knowledge and skill. Moreover, there was a clear synergistic effect between training and vector control. For example, in the villages with intervention, the annual expenditure on trypanocides per farm household

was reduced substantially. In villages with paravets, the expenditure was reduced by 36%, while in villages with both vector control and paravets, expenditure was reduced by 58%. Integration of trypanosomiasis control strategies is often advised, both because each strategy has limitations and because perverse effects are possible (successful vector control in the absence of training and information on drug use, for example, has resulted in paradoxical increased use of trypanocides; Kamuanga, 2001a,b). Researchers concluded that the intervention was successful but the cost of training farmers and paravets was a barrier to widespread use. Moreover, in some situations, paravets are not allowed to operate.

The project was the first to explore rational drug use in a context of 'harm reduction' as an option for trypanosomiasis control. This was a concept borrowed from human health work with prostitutes and drug users. It assumes that if people are highly motivated to do things that are not recommended by authorities, punishing them will lead to worse outcomes and they should instead be supported to undertake the activities as safety as possible. Although official policy is that veterinary treatments should only be given by veterinarians or paraprofessionals under their direct supervision, the project had shown that most veterinary treatments were given by farmers and that it was neither feasible

nor economically viable for treatments to be given by veterinarians. In this context, the project set out to see whether farmers who were going to treat their animals anyway could be persuaded to treat them more rationally.

Much effort was spent in developing messages that could be understood by illiterate farmers. These addressed the problems identified as being most likely to lead to treatment failure, specifically misdiagnosis, underdosage and poor injection technique. The intervention was evaluated through a large cluster-randomized, double-blinded, controlled trial, which at the time was one of the most rigorous evaluations conducted by ILRI. It found that rational drug information improves farmer practice and reduces drug underdosage: the improvement in dosage was particularly encouraging, given the highly significant relationship between underdosage and treatment failure. In the medium term, there was a 35% increase in farmers giving the correct dosage and an 8% increase in the appropriate use of isometamidium as a prophylaxis in the test group versus the control. In addition, there were better clinical outcomes and fewer treatment complications with rational drug use information: improvements in clinical parameters were significant only for a decrease in animal temperature (indicating less fever). The simple hygiene information that was provided resulted in an important decrease in side effects. High levels of complications are associated with unhygienic administration. The researchers conclude this was an effective, cheap, sustainable and scalable option. The main challenge was the reluctance of national authorities to countenance farmers giving treatments.

The researchers saw the need for additional action to promote the uptake of successful strategies. Customized informational brochures and training materials were designed to support 'Rational drug use' (Fig. 3.1). Prototype materials, including a visually appealing, cartoon-style booklet with an engaging storyline were designed for targeting adult literacy programmes and primary-school children. A communication strategy for dissemination of rational drug use messages, including using radio messages, was also formulated. The project formulated recommendations for how drug companies could improve the quality of the information provided with their products that would promote 'Rational drug use'. While company representatives were in favour of the suggestions, they felt that the current low returns to investment in the trypanocide market did not merit the added cost of adopting the recommendations.

Fig. 3.1. An example of extension material to promote rational drug use.

A subsequent study assessed farmers' knowledge and management of trypanosomiasis. In the absence of a clear control group, propensity score matching was used (Liebenehm *et al.*, 2009). Using three different matching algorithms, significant and robust differences between matched participants and non-participants regarding cattle farmers' knowledge were identified. Hence, it can be concluded that the gain in farmers' knowledge is attributable directly to participation in the research intervention. The strongest effect of the research intervention is on the curative knowledge of AAT and subsequent adequate control decisions. Moreover, significant advancements in preventative strategies were also observed. Overall, the research project was effective in increasing farmers' knowledge of good practices and contributed significantly to improved livestock and farm productivity (Affognon *et al.*, 2009).

ILRI found widespread concern among farmers and market agents about a proliferation of fake and substandard trypanocide drugs. However, market studies using 'dummy customer' or 'secret shopper' methods found no evidence of counterfeit drugs, and the results of drug quality tests conducted in 2005 on samples of drugs taken from both formal (veterinary pharmacies) and informal (black markets) sources revealed no major difference in quality of the products.

Economic and policy analysis was undertaken in parallel with the epidemiological studies. Affognon (2007) investigated the short-term productivity effect of drugs in controlling AAT under increasing drug resistance. For the first time, a damage-control framework was applied to animal disease control in Africa. The results showed that the marginal value product (MVP) of isometamidium in all epidemiological conditions and the MVP of diminazene in conditions of high disease prevalence and high drug resistance revealed a suboptimal (underuse) of these two major trypanocide molecules, not taking into account the externality of resistance. This means that, even in the face of increasing drug resistance, trypanocidal drugs remain economically attractive. Moreover, at the current suboptimal level of isometamidium use for the epidemiological conditions, investing in more drug use would be more than compensated for by avoided production losses. For decades, the veterinary experts had promoted reduced use of

trypanocides in response to resistance and these economic findings suggest why the messages might not have high uptake.

AAT economic and environmental studies

A methodological innovation at ILRI was combining economic analysis with herd simulation models. Von Kaufmann *et al.* (1990) developed a bioeconomic herd model (called here the ATLN model) that was used to quantify the costs of AAT, to assess control strategies and to evaluate the benefits of trypanotolerant livestock (Itty, 1992; Itty and Swallow, 1994). Some estimates of these costs are as follows:

- The Gambia: 37% of the national herd in The Gambia were at risk annually from trypanosomiasis (ILRAD, 1993). The annual economic costs of trypanosomiasis were estimated to be less than 1 % of the annual value of the total cattle herd and nearly all of the costs of trypanosomiasis were attributed to production losses.
- Zimbabwe: due to extensive tsetse control campaigns, only 4% of Zimbabwe's cattle population were at risk in the late 1980s and early 1990s (ILRAD, 1993). The annual cost of trypanosomiasis control in Zimbabwe was largely attributable to tsetse control by spraying, not to production losses, which were small as a percentage of the value of the national cattle herd.
- Côte d'Ivoire: the annual cost of trypanosomiasis was estimated to be 90% from production losses and 10% from control costs.
- Cameroon: in Adamawa Province, tsetse control led to substantial reductions in mortality rather than to significant increases in cattle numbers. Changes in land use involved a shift to mixed farming among previously pure pastoralists.

Subsequent economic analyses estimated that AAT in West Africa (Burkina Faso, Mali and Ghana) was estimated to cause annual losses of US$450 million in the 1990s (Itty, 1992). The use of trypanocides in those three countries was thought to protect some 17 million head of cattle from the disease. However, the general use of trypanocides was inducing resistance to trypanocides

and though the older studies mentioned the cost of resistance they did not quantify it.

The economics of trypanosomiasis control using trypanotolerant cattle were investigated under the auspices of ATLN in Kenya, Ethiopia, The Gambia, the Democratic Republic of the Congo, Togo and Côte d'Ivoire (Itty, 1992). Itty and Swallow (1994) showed that tsetse control appeared appropriate in situations with higher disease risk and that imports of trypanotolerant stock (in the Democratic Republic of the Congo and Togo) were not necessarily profitable. Studies were undertaken to determine farmers' willingness to participate in vector-control programmes. These so-called 'contingent valuation surveys' have been conducted in Burkina Faso, Ethiopia and Kenya to assess willingness to contribute labour and money to vector control (Thornton and Odero, 1998, pp. 69–71, summarizing three studies). Contingent valuation methods suggested that farmers were willing to pay around US$0.5–1 per treatment. In several countries, this was compared with the revealed willingness to pay during campaigns: in general, the observed willingness to pay correlated with the estimates derived from contingent valuation studies but was less and, in at least one country, declined with time (Kamuanga *et al.*, 2000, 2001b).

The most recent work on the economic benefits of intervening against AAT is a study of Ethiopia, Kenya, Somalia, South Sudan, Sudan and Uganda. Using a map of cattle production systems, herd models for each system were developed for scenarios with or without AAT. The herd models were based on estimated parameters of cattle productivity (fertility, mortality, yields, sales) from which growth of cattle populations and income were estimated over a 20-year period. A spatial expansion model was adapted to estimate how cattle populations might migrate to new areas when maximum stocking rates are exceeded in older production areas. Last, differences in income between the with and without scenarios were mapped, giving a measure of the potential benefits that could be obtained from intervening against tsetse and trypanosomiasis (Shaw *et al.*, 2014). The estimated net present value of benefits to livestock keepers for the entire study area is nearly US$2.5 billion, at a discount rate of 10% over 20 years – is approximately US$3300/km² of tsetse-infested area – varying from from less than US$500/km² to more than US$10,000/km². The greatest potential benefits are to Ethiopia, because of its high livestock densities and the historical importance of animal traction, followed by regions of Kenya and Uganda (Shaw *et al.*, 2014).

A related study built on these findings to evaluate the cost:benefit ratios as profitability measures for various control methods (Shaw *et al.*, 2015). Trypanocide prophylaxis is the only profitable approach at low cattle density. Where cattle densities are higher, the use of insecticide-treated cattle is the most consistently profitable method, with benefit:cost ratios greater than 5. In areas of high potential for mixed farming using oxen in Western Ethiopia, the fertile areas north of Lake Victoria and the dairying areas of western and central Kenya, all control methods achieve benefit:cost ratios from 2 to over 15, and for elimination strategies, ratios from 5 to over 20. The costs of interventions against tsetse exceed benefits where cattle densities are less than 20/km².

McCarthy *et al.* (2003) developed a theoretical model to explain why farmers might use different methods of trypanosomiasis control. They argued that the public goods nature of traps and targets, combined with an underlying incentive structure that may resemble a prisoner's dilemma, explained the well-documented failure of community-based control with traps and targets, a failure that was most commonly attributed to a lack of community participation.

ILRI also developed guidelines on methods and tools for conducting impact assessments of tsetse/trypanosomiasis interventions on the environmental, social and economic systems and on approaches for the integrated impact assessment of the interventions (Maitima *et al.*, 2007)[2].

Other AAT research and impacts

ILRI examined possible changes in distribution of the three groups of tsetse in relation to changing climate, human population density and expected disease control activities (Reid *et al.*, 2000; Coleman *et al.*, 2001; Grace, 2014). The key findings of these studies were that climate change is indeed likely to change the distributional potential of tsetse but that anthropogenic

changes resulting directly from population expansion would be more important in determining actual changes in tsetse distributions. With respect to population density, it was estimated that human population growth after 2000 would reduce tsetse-infested areas from roughly 8 million km^2 to between 5 and 6.5 million km^2 in 2040 (Reid *et al.*, 2000, p. 231).

In the early 2000s ILRI developed a deterministic mathematical model for trypanosomiasis transmission. This was initially used to compare the effectiveness of different control strategies (McDermott and Coleman, 2001). The relative rankings of the effect of control strategies on reducing disease prevalence were vector control, vaccination and drug use, in that order. Epidemiological modelling was used in several other projects, mainly to inform design and research questions.

Conclusions and the Future

AAT has long been regarded as the single most important disease of the single most important livestock species in Africa. Early research at ILRI focused on developing a vaccine. As it became clear that this was no easy endeavour, and as AAT worsened or became more obvious in many African countries, ILRI stepped up to address our understanding and control of AAT in advance of a vaccine.

Work started in East Africa and then extended to West Africa. There was emphasis on understanding the disease and its impacts and on testing solutions. Over four decades of field research on AAT, an evolution is evident: researchers went from publishing in proceedings to publishing in high-impact-factor journals, from focusing on the efficacy of solutions to their uptake, and from forthright advocates of favoured strategies to more nuanced critiques of the challenges of AAT control.

ILRI participated in important networks, most notably ATLN, and did not participate in important failed attempts to control AAT. It investigated all three of the major strategies for controlling AAT and found two of them wanting, at least without continued external support.

Trypanotolerant cattle have many advantages in terms of disease resistance, but they are not preferred by farmers who are increasingly focused on productivity. However, trypanotolerant cattle populations have been declining for decades relative to Zebu crosses, which are preferred for their production characteristics. One study (Agyemang and Rege, 2004) found that the shares of trypanotolerant stock in all cattle in west and central Africa were falling in the late 1990s 2004).

Trypanotolerant stock are likely to persist, without the need for much external support, in areas where, because of poor market access and other constraints, low-input, low-output systems remain attractive. In other areas, trypanotolerant cattle will probably continue to be replaced by higher value and more productive Zebu crosses. Control of tsetse flies by insecticides has been much promoted and has generated many scientific innovations and successful pilots. However, the high cost and high level of coordination and management needed means it has never proven sustainable outside ranches and externally supported projects. The use of trypanocidal drugs, in contrast, is both sustainable and scalable. Farmers are willing to buy and use curative and, although to a considerably less extent, preventative drugs. Drugs are on the whole wisely used, but the lack of information on correct treatment certainly leads to some irrational use and hastens the development of resistance. ILRI research showed how providing simple information to farmers can slow this.

Looking to the future, AAT is likely to remain a priority constraint for African livestock. We now have approaches that are highly effective at reducing the impact of AAT, either singly or in combination. We also understand better the challenges of adoption of even economically attractive strategies and how the changing dynamics of AAT may lead to future opportunities for optimized control.

Acknowledgements

Notes

[1] William Wint, personal communication, April 2019.
[2] See Introduction, Box I.1 on 'Aspects of the Economic Burden of Trypanosomiasis' for mention of *ex-ante* modelling of a hypothetical trypanosomiasis vaccine.

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4 Impact Assessment of Immunology and Immunoparasitology Research at ILRAD and ILRI

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Contents

Executive Summary

The problem

African animal trypanosomiasis (AAT, also known as 'animal African trypanosomiasis') is a parasitic disease caused by flagellated protozoans belonging to the family Trypanosomatidae, genus *Trypanosoma*, section Salivaria. The parasites are transmitted by biting flies known as tsetse flies (family Glossinidae, genus *Glossina*), which inhabit much of tropical and subtropical Africa. The parasites live in the blood plasma, body tissue and fluids of their host. In tropical Africa, AAT constitutes a major obstacle to the development of animal production, causing major economic losses as the animals suffer from loss of condition, emaciation and anaemia, resulting in reduced meat and milk production and draught power. While the annual cost of the disease varies among agroecological zones, mortality in cattle can reach a rate of 50–100% within months of exposure and there are substantial losses from the exclusion of cattle from regions where the disease prevents cattle production and from the loss of animal draught power in areas where mixed farming is feasible.

Theileriosis, commonly known as East Coast fever (ECF), is another parasitic disease. Fatal to cattle, this disease is also caused by a protozoan parasite, *Theileria parva*. The disease occurs in 12 countries in eastern, central and southern Africa, where the tick vectors of this parasite are found. ECF causes major economic losses by affecting both dairy cattle and young Zebu cattle in pastoralist systems and ranches. It is among the most serious constraints to cattle productivity in the countries where it is found. Some of the direct losses due to ECF include cattle mortality, the stunting of calves and reduced milk production. Indirect losses include the lack of adoption of more productive breeds of cattle and the costs associated with ECF prevention and control. ECF affects households by reducing the milk supply,

depleting assets and reducing incomes, all of which are detrimental to household food and nutritional security. The classic form of ECF control has been to spray acaricides to kill the ticks. Beginning in the 1970s, and advancing over the years, an immunization procedure was developed against ECF, which involved inoculation with live *T. parva* sporozoite forms and simultaneous treatment with a dose of the antibiotic oxytetracycline. The development of a vaccine to protect cattle against ECF was one of the founding aims of the International Laboratory for Research on Animal Diseases (ILRAD), a forerunner of the International Livestock Research Institute (ILRI).

ILRI's contribution in the global context

This chapter assesses the research on bovine immunology and immunoparasitology conducted over 42 years, from 1973 to 2015, first at ILRAD (1973–1994) and subsequently at ILRI, which was formed by merging ILRAD and the International Livestock Centre for Africa (ILCA) in 1995. This assessment covers the approaches taken, the performance of research teams, the scientific truths uncovered, the cost-effectiveness of the research undertaken and the practical outcomes achieved, notably, the development of monoclonal antibodies (mAbs) and other tools to better define the bovine immune system. The chapter makes extensive use of citation data along with the personal reflections of scientists who participated in the research and surveys of opinion leaders in the field.

The specific scientific goals and achievements of ILRI and its predecessors were as follows:

- Making a substantive contribution to bovine immunology was realistic and has been substantially achieved.
- Measuring the diversity of strains of *Theileria parva*, *Trypanosoma brucei*, *Trypanosoma*

vivax and *Trypanosoma congolense* was realistic and has been substantially achieved.

- Identifying mechanisms of immunity that kill parasites or limit the growth of the above parasites was realistic and has been substantially achieved.
- Developing an effective subunit vaccine against any of the parasites was an ambitious goal and so far has not been achieved.

Impacts of ILRI research

ILRI and its predecessors led global research in trypanosomiasis (see Chapters 2 and 3, this volume) and in ECF (theileriosis) (see Chapters 5 and 6, this volume). A vital part of work on both diseases was in immunology and immunoparasitology.

Scientific impacts

The scientific impacts of the immunology and immunoparasitology work started at ILRAD and continued at ILRI have been substantial. These studies resulted in a substantive body of work, as shown by the well-cited 68 peer-reviewed publications (see Table 4.6).

- First, the immunology programme developed a comprehensive suite of mAbs that identified the major bovine T-cell subpopulations, immunoglobulin isotypes, phagocytic cell populations, several bovine lymphocyte antigens (BoLAs; also called major histocompatibility (MHC) antigens) and the circumsporozoite coat of *T. parva* sporozoites used in host-cell invasion.
- Second, the team developed and maintained *in vitro* clones of bovine CD4$^+$ and CD8$^+$ T-cells that facilitated analysis of mAb specificity, investigation of *T. parva* antigenic diversity and *T. parva* peptide–BoLA complexes that induce *T. parva* strain and host MHC-specific protective immunity.
- Third, the team used these tools to investigate, and to a large extent elucidate, host immune responses that control the frequency, magnitude and duration of African trypanosome and *T. parva* parasitaemic episodes in cattle and Cape buffalo, the latter of which are disease-resistant reservoir hosts of the parasites.

While the ILRAD/ILRI *T. parva* vaccine programme has not yet resulted in full disease control, contributing scientists have identified, cloned and expressed recombinant *T. parva* proteins that stimulate protective T-cells and antibody responses (Nene *et al.*, 1992, 1995; Graham *et al.*, 2006). They have further provided evidence that a subunit vaccine, perhaps comprising a sporozoite p67 subunit that elicits sporozoite-neutralizing antibodies together with schizont epitopes that stimulate appropriate CD4$^+$ helper T-cells and CD8$^+$ cytotoxic T-cells in cattle, is a realistic possibility. While research towards a *T. parva* vaccine at ILRAD/ILRI continues to progress, this was not the case with research to develop a vaccine effective against AAT, where high variation of protective parasite antigens blocked the vaccine research programme from the outset and led to its closure in 2001. Studies of mechanisms of trypanosomiasis susceptibility and tolerance at ILRAD/ILRI covered a wide field and left a legacy of infection-induced immune response data in cattle but did not identify candidate vaccine antigens or definitively identify resistance genes for introgression into the gene pool of desirable Boran livestock. Nevertheless, this work made notable contributions to our understanding of trypanosome biology and immunology.

Development impacts

Many of the aims of the *T. parva* immunology programme at ILRAD/ILRI were achieved, but development of an effective subunit *T. parva* vaccine remains a challenge. The immunology and immunoparasitology research at ILRAD and later ILRI had high scientific and technical impacts on a moderate budget. Outputs from this research were primarily publications and mAbs specific for bovine leukocytes and immunoglobulins, which are still being used in many laboratories throughout the world. Despite its academic/scientific successes, this immunology/immunoparasitology research did not affect the incidence or economic impact of theileriosis or trypanosomiasis in any substantial way. However, the authors remain optimistic that the fundamental research on bovine immunology and the immunoparasitology of theileriosis and trypanosomiasis carried out at ILRAD/ILRI will

ultimately have development outcomes. Development impacts of the ECF work eventually emerged through use of the infection-and-treatment method (ITM) (see Chapter 6, this volume).

Capacity building and partnerships

The immunology work at ILRAD and ILRI had major capacity development effects. First, it contributed to the achievements of scientists who went on to have distinguished careers in immunology and related fields. Second, it contributed to the development of scientific methods applied to immunology and other fields and to diseases other than ECF and trypanosomiasis, notably the identification of bovine leukocyte populations and subpopulations using mAbs, cloning and long-term propagation of bovine T-cells, and the use of cloned bovine T-cells to identify host-protective parasite antigens.

Introduction

ILRAD was established in 1973 with the mandate to conduct basic research to develop safe, effective and economical control measures for livestock diseases that seriously limit world food production.

Theileriosis and AAT (Randolph *et al.*, 2003) were chosen as target diseases because they severely constrain livestock production in sub-Saharan Africa. Prior research on their causative agents, which are, respectively, tick-transmitted apicomplexans of the *Theileria parva* species and tsetse-transmitted kinetoplastids, namely, *Trypanosoma brucei*, *T. congolense* and *T. vivax*, had shown that it was possible to immunize livestock so that they were protected against reinfection with the immunizing strain. However, this immunity broke down when animals were exposed to other stains of *T. parva* or trypanosomes. Thus, it was important to establish the nature of protective immunity against the parasites and the mechanisms leading to breakdown of immunity upon heterologous strain challenge as steps towards identifying and implementing immunologically based disease control strategies. It was envisaged that knowledge of the pathogens and of effective immune responses would lead to strategies for disease control, with fundamental research tailing off over time and improved control of these diseases eventually dominating the research efforts. While the authors have no doubt that this will eventually prove to be the case, it should be appreciated that investment in the immunological control of challenging diseases, especially those caused by complex, protozoan, parasites, is not for the impatient. Clear evidence of this is provided not only by ILRAD's long experience with its target diseases but also by the many other organizations, programmes and consortia conducting similar long-term disease research on such important disease problems as cancer, human immunodeficiency virus (HIV)/acquired immune deficiency syndrome (AIDS) and malaria.

Scientific impact measurements defined

The evaluation in this chapter looks at both 'outputs' (the quality and amount of research products produced) and 'outcomes' (the changes in behaviour or influence brought about due to the research) as measures for assessing the impacts of the research. Assessments of how the research altered hunger, nutrition and poverty – the ultimate aims of this research – is not attempted here. Although there is a strong push to measure impacts in development work in terms of how work changes a given situation for the better, it is often unclear how to measure such changes stemming from development programmes and interventions. One way to measure impact is to address the question, 'Would the same changes have occurred if this investment had not been made?', but this approach is hampered by the fact that a negative control for this question is commonly missing. (This is particularly true regarding achievements in the basic scientific research required to develop interventions such as vaccines.)

Another measure of research impact, and the one taken here, is to determine whether what was found and assumed to be 'true' at the time of publication of research results remained true over the following years and was taken up or built upon by other scientists. This evaluation aims to determine whether the right experimental directions were chosen and to measure the performance of ILRAD/ILRI immunology and

immunoparasitology research with respect both to the outputs (e.g. the scientific truths uncovered and new tools generated) and to the cost-effectiveness of that work. Regarding the latter, to assess the magnitude of investment needed to achieve those 'scientific truths', the only possible comparators are the kinds and levels of investments made for similar diseases having the same goals – of preventing infection or reducing pathology – as those made for ECF and AAT at ILRAD and more recently at ILRI. The performance indicators and formal surveys outlined below were used to measure the impacts on the field of veterinary – more specifically, bovine – immunology and the application of knowledge gained for controlling infectious diseases in ruminants.

Traditional bibliographic measurements

Traditional bibliographic measurements of the output of scientific research in the form of peer-reviewed manuscripts include measurements of both quality and quantity. While it is important that research papers are published in 'top-tier' scientific journals to be broadly read by the scientific community, it is equally important to have a body of work that includes papers in speciality journals and on social media.

This chapter thus presents data on: (i) quantities of manuscripts, including citation indices and the Web of Science index for each; and (ii) the number of papers of a collective body of manuscripts with ten or more citations, used to calculate an individual's i10 index (the number of papers with more than ten citations) to assess both the quantity and quality of the collection.

Influence measurements

Research influences are used here to show how research affects behaviour and discourse. Research that has influence has the 'capacity to produce an effect on the advancement of scientific knowledge' (Donaldson and Cooke, 2013). This includes how a researcher or research group influences other groups or directions of research. The 'change in behaviour' concept here includes whether ILRAD/ILRI influenced a given field of research or the approach taken by individual researchers regarding solving scientific problems at institutions other than ILRAD/

ILRI. To assess this behaviour change, the following were evaluated:

- The Hirsch index (*h*-index) of individual scientists (discussed later), which measures their productivity and influence on others over their careers up to 2015.
- Results of a survey to obtain personal reflections on the influence that working at ILRAD/ILRI had on post-ILRAD/ILRI career choices and research directions of scientists.
- A survey of opinion leaders in relevant fields on ILRAD/ILRI impacts.
- Examples of former ILRAD/ILRI scientists continuing to address infectious diseases that affect world food production.

Practical outcomes

Practical outcomes are defined here as commercialized or shared tools or methods and additional training of individuals who are productive in the field. Tools are physical entities such as mAbs but also methods and protocols developed such as bovine MHC typing and lymphocyte cloning. Commercialized products include mAbs, vaccines and diagnostic kits. An outcome of trainees means that such individuals stay in the field and are productive rather than simply a number listed under 'output' (i.e. trained but did not get a job in that field). To determine practical outcomes, the following were assessed by survey responses:

- Tools generated at ILRAD/ILRI and used by others outside of that environment; this includes an analysis of the diseases to which such tools were applied and the geographical distribution of that application.
- Former ILRAD/ILRI scientists who had trainees who remained in their scientific fields.
- Commercialization of scientific tools.

Historic Overview

An historic overview of the goals and achievements of the research was made from the scientific literature. (Note that Altmetric (www.altmetric.com/; accessed 5 February 2020),

which counts Twitter re-tweets, Facebook 'likes', comments in journals, electronic views and downloads, and posts on other social media, was not considered here due to the historic nature of many of the publications.) This includes descriptions of the bovine immune system and research landscape at the inception of ILRAD and how ILRAD/ILRI research helped that landscape develop and mature in parallel with other groups addressing fundamental immunological questions in a variety of host species or addressing diseases and pathogens closely related to those targeted by ILRAD/ILRI. The questions addressed in these narratives are:

- Was the right research direction taken to fulfil the mandate of ILRAD/ILRI?
- Was the team successful, i.e. was the research reflective and creative?
- Was there a substantive body of work that showed the step-by-step progression of knowledge in addition to key papers in top-tier journals?
- Were the results published in a timely manner?

State of knowledge of immune systems at ILRAD's founding

When ILRAD started, it was known from studies in mice and humans that lymphocytes could be divided into two major groups, B-cells and T-cells. The former were known to be precursors of antibody-producing cells and the latter to be comprised of at least three subpopulations, which express distinct functions, namely: (i) cytotoxic T-lymphocytes, now generally called CD8^{+} T-cells, which kill infected host cells; (ii) T-helper lymphocytes, now called CD4^{+} T-cells, which facilitate the development of antibody responses, delayed-type hypersensitivity, and phagocyte recruitment and activation; and (iii) suppressor T-lymphocytes, which decrease the magnitude of immune responses, now known as regulatory T-cells (Tregs). It was also known that antibody-producing B-lymphocytes had differentiated from B-cells that expressed membrane-bound, cell-surface, antigen-specific receptors composed of immunoglobulin heavy and light chains and that those of a single cell could bind only one or a restricted group of antigens.

As shown by seminal work from Hozumi and Tonegawa (1976), these antigen-specific receptors are encoded by multiple immunoglobulin gene segments that rearrange during B-cell development.

In addition, several functionally distinct classes of antibody had been identified and there was evidence from immunoglobulin heavy-chain allotype expression in mice that the genes encoding these proteins were arranged in a single genetic locus. Although the T-cell antigen-specific receptor had not been identified, it was known from the work of McDevitt *et al.* (1972) that genes encoded in the immune response region (I region) of the mouse MHC could control antibody responses. It was also known from Zinkernagel and Doherty (1974) that genes encoded in the H-2 region of the mouse MHC restrict the specificity of cytotoxic T-cells reactive with virus-infected cells. This led Zinkernagel and Doherty to propose that cytotoxic T-cells recognize MHC proteins that are changed by virus infection, a hypothesis that was later proven by receptor isolation and co-crystallization with ligand–MHC complex. It was also known that macrophages were required for inducing immune responses *in vitro* and that activated T-cells secrete materials that control other leukocytes, but these molecules, which were later to be called cytokines, had not been isolated.

Despite elegant work done on immune system function carried out first in chickens to delineate the Bursa as an organelle required for B-lymphocyte development (thus Bursa-derived or B-cell) and the thymus as an organelle required for T-lymphocyte development (thymus-derived or T-cell) (Cooper *et al.*, 1966), and later in ruminants to characterize cell components of the peripheral lymph (Smith *et al.*, 1970; Scollay *et al.*, 1976), in 1978 our understanding of the immune systems of birds and ruminants lagged behind that of humans and mice. Different classes of bovine and sheep immunoglobulins and their functions had been identified, some complement factors had been isolated and systems to evaluate T-cell proliferative responses *in vitro* and *in vivo* had been developed; the latter was known as skin testing. However, the description of leukocyte differentiation antigens and cellular functions, including those of antigen-specific T- and B-cells, was hindered by a

paucity of reagents to identify, isolate and characterize specific cell types. The establishment of a well-funded and well-equipped veterinary immunology research programme at ILRAD, as described below, helped to change this.

Technology developed at ILRAD for studying bovine immunology

ILRAD began operations at Nairobi's Kenyatta Hospital in 1975, and its research and support facilities were inaugurated in 1978 on a 70-ha site near Nairobi. In support of its commitment to immunological research, ILRAD recruited faculty members with expertise in what were then cutting-edge technologies – including fluorescence-activated cell sorting (FACS), the production of mAbs, ruminant tissue typing and T-cell cloning – with a view to applying these techniques for dissecting the ruminant immune system in health and disease. The histories of these technologies and their implementation at ILRAD are briefly summarized below.

FACS at ILRAD

Fluorescence-activated cell sorting (FACS) was invented in the late 1960s by a team at Stanford University led by Leonard Herzenberg. Its purpose was to analyse and isolate viable cells using their light-scattering properties and fluorescence emitted by attached fluorochrome-conjugated antibodies or other materials. Although a FACS machine was commercially available from Becton Dickinson Immunocytometry Systems in the early 1970s, at the time of ILRAD's inception, only a few laboratories worldwide had FACS facilities. John J. (Jack) Doyle, one of ILRAD's founding faculty members, established the FACS facility at ILRAD in 1977. The facility became fully operative in 1981, and the first publication from ILRAD using FACS addressed the replicative cycle of bloodstream-stage *T. brucei* and *T. vivax* (Shapiro *et al.*, 1984).

mAb production at ILRAD

Monoclonal antibodies (mAbs) are antibodies of a single antigenic specificity that are produced by a single B-lymphocyte and its clonal progeny. The technology to generate immortal cell lines that produce mAbs against specific antigens was developed by George Kohler and Cesar Milstein at the Medical Research Council Laboratory of Molecular Biology, in Cambridge, UK, and was first described in 1975 (Kohler and Milstein, 1975). Briefly, antigen-stimulated lymphocytes were immortalized by fusion to mutant B-lymphocyte tumour cells (myeloma cells) with an enzyme deficiency that enables hybrid selection. During replication of selected hybrids, called myeloma hybrids or hybridomas, chromosome assortment results in some hybrid progeny that express the genes encoding the immunoglobulin heavy and light chains derived from the lymphocyte partner together with appropriate housekeeping genes and the transforming gene from the myeloma fusion partner. Hybridomas are cloned and grown *in vitro*, and those producing mAbs of the desired specificity are identified by screening culture supernatants for the presence of antibodies reactive with the target antigen. Terry Pearson, one of the founding faculty members of ILRAD, had worked with Kohler and Milstein in Cambridge and brought the mAb technology directly to ILRAD. Samuel Black, who joined ILRAD in 1979, introduced complementary techniques for rapid cloning of hybridomas and screening of leukocyte-specific mAbs using FACS. The first ILRAD mAbs were made against trypanosome and *T. parva* antigens and described by Pearson *et al.* (1980) in a general methodology paper.

BoLA typing at ILRAD

Histocompatibility antigens are cell-surface glycoproteins that have been selected through evolution to present antigens to T-cells. They vary from individual to individual and were initially typed in humans using serum from transplant-rejection patients and multiparous women. The antigens responsible for transplant rejection were named human leukocyte antigens (Rowlands *et al.*, 2003) by a nomenclature committee of the World Health Organization (WHO) in 1968 and are encoded by genes in the MHC locus. Bovine MHC molecules are called bovine lymphocyte antigens (BoLA). BoLA typing was started in Kenya by a small team led by Alan Teale. This group was initially based at the Kenya Agricultural Research Institute (KARI), in Muguga, and used serological methods to identify the MHC antigens of African cattle as part of a study aimed at understanding the problems associated with a *T. parva*-infected cell-line-based vaccine for ECF (see Chapter 6, this volume). The

group moved to ILRAD in 1984, where Steve Kemp soon joined. A strong partnership developed with the immunologists working in both trypanosomiasis and theileriosis to develop a panel of reagents to characterize the MHC diversity of African cattle in order to support vaccine development and to look for associations between tissue type and resistance or susceptibility to disease. This group made important technical contributions to the typing technology and contributed substantially to the international BoLA classification system. BoLA typing was of critical importance in mapping the specificity of cytotoxic T-cells against bovine cells infected with *T. parva*, as exemplified by the 1987 paper demonstrating both MHC and *T. parva* strain restriction (Morrison *et al.*, 1987). In addition, attempts to associate MHC type with disease susceptibility developed into a genome-wide association study, which in turn provided an important impetus to the international bovine genome mapping effort and to the more recent discovery of gene variants associated with resistance to trypanosomiasis in mice (Goodhead *et al.*, 2010).

T-cell cloning at ILRAD

T-cell clones are used to dissect the specificity and functions of individual T-cells participating in cell-mediated immune responses. The cloned cells can be grown as long-term cultures that retain both phenotype and function. Key to the development of T-cell clones was the finding in 1976 by Morgan *et al.* (1976) that interleukin (IL)-2 has human T-cell growth-inducing properties. In 1977, Gillis and Smith (1977) reported that mouse cytotoxic T-cell clones could be grown *in vitro* supported by the addition of medium containing IL-2, which in culture supernatants of stimulated cells was referred to as T-cell growth factor. It was subsequently reported in 1981 by Spits *et al.* (1981) that long-term culture of cloned human T-cells requires frequent stimulation with their cognate antigen in addition to provision of T-cell growth factor. In 1982, Wendy Brown was recruited to ILRAD to generate bovine T-cell growth factor and establish clones of bovine T-cells. This was achieved in 1985 by Brown and Grab (1985) using lectin-stimulated bovine T-cells and in 1986 by Teale *et al.* (1986) using T-cells that proliferate in response to mismatched BoLA molecules. Like antigen-specific human T-cell clones, their bo-

vine counterparts were found for the most part to require T-cell growth factor and periodic antigen stimulation. T-cell cloning facilitated functional dissection of the bovine immune system and analysis of the specificity of T-cell responses to *T. parva*-infected bovine lymphocytes. The T-cell clones also expedited screening of bovine leukocyte-specific mAbs to identify those that react with functionally distinct populations of leukocytes.

Measurements of scientific impact

Quantity of manuscripts

The number of published manuscripts considered for the topic as defined was 400. The manuscripts address bovine immunology and immunoparasitology of theileriosis and AAT and were selected from all papers listed in ILRAD and ILRI annual reports from 1975 to 2013. The manuscripts were grouped initially as those from ILRAD and ILRI that concerned bovine immunology, with a second group concerning bovine immunoparasitology and a third group comprising manuscripts on the mouse model of African trypanosomiasis. This mouse model was included because it was used at ILRAD and subsequently ILRI to inform research in bovine trypanosomiasis.

Citation analyses

Citation data are frequently used for evaluating the scientific productivity of individuals and institutions. Not everyone agrees that this is a useful measure, and much has been written on the topic. However, few would argue against the notion that the absence of citations of a published work that is accessible on PubMed and has been 'out' for some years is a reasonable indicator of low/no influence, while a high citation index is a reasonable indicator of substantial influence. Nevertheless, citation averages vary among fields, and field parameters should be taken into account when considering the citation data. For example, citation averages are much higher in the field of molecular biology than in mathematics (field averages, respectively, of 10.8 and 3.5 citations during the period 2000–2010, based on journal articles indexed by Thompson Reuters in its Essential Science Indicators (ESI) database). Hence,

interpretation of citation data is nuanced. With respect to agricultural sciences and animal science, ESI field averages over the 2000–2010 period were, respectively, 7.1 and 7.7, whereas that for immunology was 21.8. It is not clear how work on ruminant immunology and immunoparasitology should be classified because much of this is not considered to be mainstream immunology. Hence, while the field average comparator for these topics may be imperfect, we consider it worthwhile tabulating citations of the ILRAD/ILRI literature in these areas as an indicator of influence.

Citations (until 2018) from selected ILRAD/ILRI publications from 1975 to 2018 were obtained from Scopus. For bovine immunology and immunoparasitology research, 74% of papers from ILRAD and 56% from ILRI have been cited more than ten times, and 56% of all papers focused on the mouse model of African trypanosomiasis have been cited more than ten times. The lower percentage of papers from ILRI cited more than ten times is partly attributable to the more recent dates of publications included in that group (those published in the last 2 years have been cited less often). All of these would be counted in the i10 index of scientists. As would be expected with publications

from other academic institutions, there are a few highly cited publications (more than 100 times) and many publications with fewer citations. This is a reasonable citation profile for the agricultural sciences and animal science based on average rates of citation by field as discussed above. It is noteworthy that papers with fundamental immunology content tended to be more highly cited (Fig. 4.1) than other more specialist papers, and this is in line with overall expectations for this field.

Impact of highly cited manuscripts

The most highly cited manuscripts are shown in Tables 4.1–4.3 for three thematic research groups. An abbreviated explanation of their impact on the field is given. These publications address immunology and immunoparasitology work from ILRAD/ILRI in journals with broader science readership and high impact factors.

The h-index of scientists

The *h*-index (in June 2015) of 16 key scientists having worked at ILRAD and/or ILRI, and in some cases still working at ILRI, was obtained. These *h*-indices were compared with those from
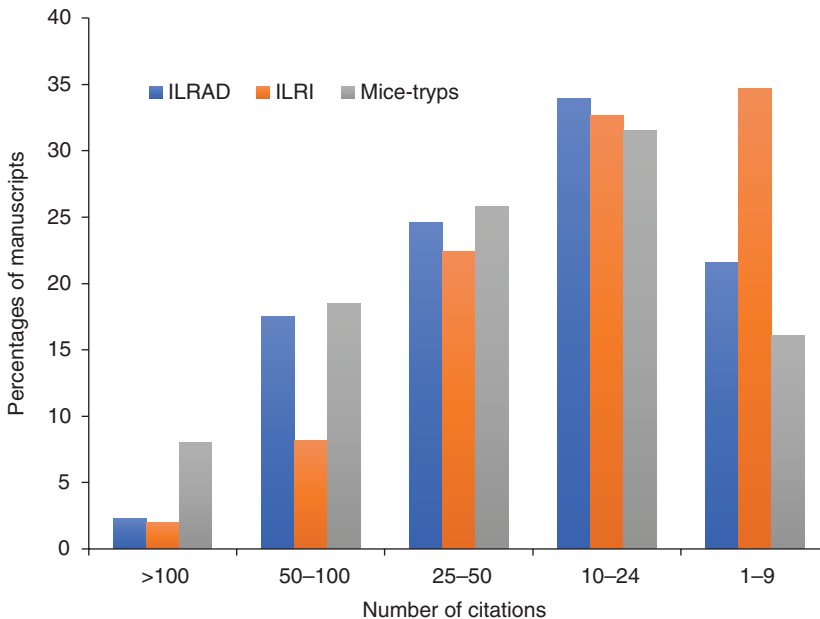
Fig. 4.1. Percentage of manuscripts by citation groups. Mice-tryps trypanosomiasis studies in mice. (Data from www.scopus.com).

Table 4.1. The most highly cited studies on basic bovine immunology.

Scopus citation percentile	Year of publication	Publication	Impact on the field
94	1996	Davis, W.C., Brown, W.C., Hamilton, M.J., Wyatt, C.R., Orden, J.A., *et al.* (1996). Analysis of monoclonal antibodies specific for the $\gamma\delta$ TcR. *Veterinary Immunology and Immunopathology* 52, 275–283.	Still one of the only mAbs that reacts with T-cell receptor (TCR) chains of livestock species
97	1979	McGuire, T.C., Musoke, A.J. and Kurtti, T. (1979) Functional properties of bovine IgG1 and IgG2: interaction with complement, macrophages, neutrophils and skin. *Immunology* 38, 249–256.	First description of the functional properties of bovine IgG1 and IgG2
97	1990	Clevers, H., MacHugh, N.D., Bensaid, A., Dunlap, S., Baldwin, C.L., *et al.* (1990) Identification of a bovine surface antigen uniquely expressed on CD4⁻ CD8⁻ T cell receptor $\gamma\delta^+$ T lymphocytes. *European Journal of Immunology* 20, 809–817.	Study showing that the bovine cells recognized by the mAb to WC1 were $\gamma\delta$ T-cells
98	1986	Baldwin, C.L., Teale, A.J., Naessens, J.G., Goddeeris, B.M., MacHugh, N.D. and Morrison, W.I. (1986) Characterization of a subset of bovine T lymphocytes that express BoT4 by monoclonal antibodies and function: similarity to lymphocytes defined by human T4 and murine L3T4. *Journal of Immunology* 136, 4385–4391.	First mAb to bovine CD4 and demonstration that these cells have a distinct function from CD8⁺ T-cells
95	1986	Ellis, J.A., Baldwin, C.L., MacHugh, N.D., Bensaid, A., Teale, A.J*., et al.* (1986) Characterization by a monoclonal antibody and functional analysis of a subset of bovine T lymphocytes that express BoT8, a molecule analogous to human CD8. *Immunology* 58, 351–358.	First mAb to bovine CD8 and demonstration that these cells have distinct function from CD4 T-cells
92	1986	Goddeeris, B.M., Baldwin, C.L., ole-MoiYoi, O. and Morrison, W.I. (1986) Improved methods for purification and depletion of monocytes from bovine peripheral blood mononuclear cells. Functional evaluation of monocytes in responses to lectins. *Journal of Immunological Methods* 89, 165–173.	A crucial method for both purifying bovine monocytes from blood and depleting them from lymphocyte populations
96	1986	Lalor, P.A., Morrison, W.I., Goddeeris, B.M., Jack, R.M. and Black, S.J. (1986) Monoclonal antibodies identify phenotypically and functionally distinct cell types in the bovine lymphoid system. *Veterinary Immunology and Immunopathology* 13, 121–140.	First mAbs made at ILRAD to T-cell and macrophage populations and some of the first ever made for bovine research

An additional manuscript had 108 citations but is a workshop report and so was not included in the table; however, it demonstrates the importance of the cluster-defined (CD) workshops: Howard, C.J. and Naessens, J. (1993) Summary of workshop findings for cattle (tables 1 and 2). *Veterinary Immunology and Immunopathology* 39, 25–47.

Table 4.2. The most highly cited studies on the bovine immune responses to *T. parva*.

Scopus citation percentile	Year of publication	Publication	Impact on the field
93	1980	Pearson, T.W., Pinder, M., Roelants, G.E., Kar, S.K., Lundin, L.B., *et al.* (1980) Methods for derivation and detection of anti-parasite monoclonal antibodies. *Journal of Immunological Methods* 34, 141–154.	First paper on mAbs produced at ILRAD
88	1992	Musoke, A., Morzaria, S., Nkonge, C., Jones, E. and Nene, V. (1992) A recombinant sporozoite surface antigen of *Theileria parva* induces protection in cattle. *Proceedings of the National Academy of Sciences USA* 89, 514–518.	A major contribution towards developing a sporozoite-neutralizing vaccine
60	1981	Eugui, E.M. and Emery, D.L. (1981) Genetically restricted cell-mediated cytotoxicity in cattle immune to *Theileria parva*. *Nature* 290, 251–254.	First paper to show that *T.parva*-specific cytotoxic T-cells were restricted by host genotype
86	1986	Goddeeris, B.M., Morrison, W.I., Teale, A.J., Bensaid, A. and Baldwin, C.L. (1986) Bovine cytotoxic T-cell clones specific for cells infected with the protozoan parasite *Theileria parva*: parasite strain specificity and class I major histocompatibility complex restriction. *Proceedings of the National Academy of Sciences USA* 83, 5238–5242.	The first paper to show that MHC class I antigens restrict the specificity of *T. parva* parasite strain-specific cytotoxic T-cells
93	1979	Pearson, T.W., Lundin, L.B., Dolan, T.T. and Stagg, D.A. (1979) Cell-mediated immunity to *Theileria*-transformed cell lines. *Nature* 281, 678–680.	First paper to show that *T. parva*-infected lymphocytes induce cytotoxic cells
88	1988	Baldwin, C.L., Black, S.J., Brown, W.C., Conrad, P.A., Goddeeris, B.M., *et al.* (1988) Bovine T cells, B cells, and null cells are transformed by the protozoan parasite *Theileria parva*. *Infection and Immunity* 56, 462–467.	Study showing that all three major lymphocyte populations in cattle (B-cells, CD4$^+$ and CD8$^+$ αβ T-cells, and γδ T-cells) could become infected with *T. parva*
86	1994	McKeever, D.J., Taracha, E.L., Innes, E.L., MacHugh, N.D., Awino, E., *et al.* (1994) Adoptive transfer of immunity to *Theileria parva* in the CD8$^+$ fraction of responding efferent lymph. *Proceedings of the National Academy of Sciences USA* 91, 1959–1963.	Proof that CD8 T-cells mediate protective immunity to *T. parva*
99	1977	Murray, M., Murray, P.K. and McIntyre, W.I. (1977) An improved parasitological technique for the diagnosis of African trypanosomiasis. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 71, 325–326.	Simple and highly sensitive test for the presence of trypanosomes in blood
96	1984	Nantulya, V.M., Musoke, A.J., Rurangirwa, F.R. and Moloo, S.K. (1984) Resistance of cattle to tsetse-transmitted challenge with *Trypanosoma brucei* or *Trypanosoma congolense* after spontaneous recovery from syringe-passaged infections. *Infection and Immunity* 43, 735–738.	Study showing that it is possible to get trypanosome serodeme-specific immunity in cattle

Continued

Table 4.2. Continued.

Scopus citation percentile	Year of publication	Publication	Impact on the field
93	1978	Barbet, A.F. and McGuire, T.C. (1978) Crossreacting determinants in variant-specific surface antigens of African trypanosomes. *Proceedings of the National Academy of Sciences USA* 75, 1989–1993.	Identification of conserved variable surface glycoprotein elements that induce antibodies and are not exposed on intact trypanosomes
97	1998	Nantulya, V.M. and Lindqvist, K.J. (1989) Antigen-detection enzyme immunoassays for the diagnosis of *Trypanosoma vivax*, *T. congolense* and *T. brucei* infections in cattle. *Annals of Tropical Medicine and Parasitology* 40, 267–272.	An important step towards the development of a diagnostic test
86	1993	Authié, E., Duvallet, G., Robertson, C., and Williams, D.J. (1993) Antibody responses to invariant antigens of *Trypanosoma congolense* in cattle of differing susceptibility to trypanosomiasis. *Parasite Immunology* 15, 101–111.	Study showing the presence of wide-spectrum IgG production against trypanosome antigens in resistant animals
93	1982	Akol, G.W. and Murray, M. (1982) Early events following challenge of cattle with tsetse infected with *Trypanosoma congolense*: development of the local skin reaction. *Veterinary Record* 110, 295–302.	Description of the chancre that develops in skin
82	1992	Naessens, J. and Williams, D.J. (1992) Characterization and measurement of CD5+ B cells in normal and *Trypanosoma congolense*-infected cattle. *European Journal of Immunology* 22, 1713–1718.	Study showing that the CD5+ population of B-cells is uniquely high in the spleen of cattle and especially during infection

a cohort of 16 accomplished scientists in similar or parallel fields who worked in Europe and the USA during the same period and who represent the same stages of career development as those from ILRAD/ILRI (Table 4.4). The h-index is based on a formula that yields the highest integer h such that h among the investigator's published papers (N_p) have collected at least h citations, while the remaining papers ($N_p – h$) have fewer than h citations each. Thus, the h-index reflects productivity as well as influence in the field.

Cost comparators

To assess the investment in related fields, rough cost comparisons were made with research on HIV and malaria parasites (*Plasmodium* spp.). The similarities of AIDS and malaria to ECF and trypanosomiasis include the fact that all four causative pathogens vary their antigens recognized by the host's immune system. In addition, both HIV and *T. parva* infect T-cells as their major target. This results in an inability of the host immune system to respond effectively and/or efficiently to the pathogen once the infection is established. *Plasmodium* spp. and *T. parva* are related phylogenetically as well, belonging to the phylum Apicomplexa, and have similar life cycles: both are transmitted by sporozoites delivered in the saliva of ectoparasites and live inside their mammalian host cells as schizonts that develop into merozoites, which are released and infect red blood cells for vector infection with the next ectoparasite blood meal.

Funding for research on African trypanosomiasis and theileriosis has been very limited in comparison with funding on HIV/AIDS and malaria. The funding for HIV research by the

Table 4.3. The most highly cited studies on the immune responses to African trypanosomiasis in the mouse model.

Scopus citation percentile	Year of publication	Publication	Impact on the field
92	1978	Morrison, W.I., Roelants, G.E., Mayor-Withey, K.S. and Murray, M. (1978) Susceptibility of inbred strains of mice to *Trypanosoma congolense*: correlation with changes in spleen lymphocyte populations. *Clinical and Experimental Immunology* 32, 25–40.	Established susceptible/ resistant strains of mice and linked this trait to immune responsiveness
82	1985	Black, S.J., Sendashonga, C.N., O'Brien, C., Borowy, N.K., Naessens, M., *et al.* (1985) Regulation of parasitaemia in mice infected with *Trypanosoma brucei*. *Current Topics in Microbiology and Immunology* 117, 93–118.	Integrated parasite differentiation to non-dividing forms and development of parasite-specific immune responses
93	1982	Black, S.J., Hewett, R.S. and Sendashonga, C.N. (1982) *Trypanosoma brucei* variable surface antigen is released by degenerating parasites but not actively dividing parasites. *Parasite Immunology* 4, 233–244.	Control of *T. brucei* growth (e.g. by a quorum-sensing mechanism or an innate immune response) is a prerequisite for development of an adaptive immune response;
91	1982	Sendashonga, C.N. and Black, S.J. (1982). Humoral immune responses against *Trypanosoma brucei* variable surface antigen are induced by degenerating parasites. *Parasite Immunology* 4, 245–257.	antibodies against the variable surface glycoprotein (VSG) distinguish between exposed and buried VSG epitopes
88	1979	Morrison, W.I. and Murray, M. (1979) *Trypanosoma congolense*: inheritance of susceptibility to infection in inbred strains of mice. *Experimental Parasitology* 48, 364–374.	Study showing that resistance to trypanosomiasis is genetically pre-determined
Not available	1978	Pearson, T.W., Roelants, G.E., Lundin, L.B. and Mayor-Withey, K.S. (1978) Immune depression in trypanosome-infected mice. I. Depressed T-lymphocyte responses. *European Journal of Immunology* 8, 723–727.	Early description of T-regulatory cells (now known as Tregs) potentially contributing to chronicity of infection

Table 4.4. Estimated *h*-indices of scientists as a measure of research productivity and impact. (Data from author interviews with ILRI scientists.)

Scientist category	Range of *h*-indices	Median *h*-index
ILRAD/ILRI	14–39	26
Comparators	17–44	29

USA's National Institutes of Health (NIH) alone was approximately US$2.6 billion in 2016 and in 2017 (www.hiv.gov/federal-response/funding/budget; accessed 6 February 2020), and this does not include AIDS research spending by other governments and international organizations. A global mapping of research funding found that malaria funding averaged US$1.8 billion

annually over the period 2006–2010 (Pigott *et al.*, 2012).

The funding research on bovine immunology and immunoparasitology and on African trypanosomiasis and theileriosis is estimated as 50% of the annual budget of ILRAD and 20% of the annual budget of ILRI (see Introduction, this volume). In the mid-1980s, the budgets for the ILRAD laboratories working on immunology and the flow cytometry facility were not more than US$2.5 million per year per disease, which in today's terms would still be only US$20 million per year or less than 1% of the current HIV or malaria yearly budgets.

There is still no effective vaccine for malaria, HIV or African trypanosomiasis (Table 4.5). For ECF, there is the original multi-strain ITM vaccine known as the Muguga cocktail, which was developed at the Kenya Agriculture Research Institute, at Muguga, Kenya (see Chapter 6, this volume). This was refined and characterized at ILRAD and subsequently ILRI, the latter in partnership with the Global Alliance for Livestock Veterinary Medicines (GALVmed). The vaccine is now marketed as a stop-gap theileriosis control measure with anticipation of a more effective subunit vaccine in the future.

Historic overview of fundamental and translational immunological research

This section asks the following questions:

1. Was the original research direction appropriate?
2. Was the original research successful?
3. Does the published work show step-by-step progression of knowledge through key papers in top journals?
4. Were the results published in a timely manner?

Bovine immune system

Fundamental knowledge of the bovine immune system was needed to unravel the immune responses to bovine theileriosis and AAT so that protective and non-protective immune responses could be defined. Such knowledge is needed to craft vaccines based on logic rather than on trial and error. Thus, the task of describing the bovine immune system started coincidently with evaluating the immune responses to the two diseases.

ILRAD research started when our understanding of the mammalian immune system was rudimentary compared with current knowledge. At the inception of ILRAD, several fundamental advances were made in immunology. These were the invention of the FACS and the development of mAb technology followed closely by the ability to grow individual T-cells into populations (a method known as 'cell cloning'). This was coincident with the burgeoning field of molecular biology, from which techniques were soon applied to immunology, allowing cloning of genes that encoded cell-surface differentiation antigens of lymphocytes and monocyte/macrophages and genes encoding products of these cells, such as antibodies of several classes or isotypes. These four technologies allowed the replacement of older, clumsier methods for studying the roles of individual lymphocyte populations

Table 4.5. Comparisons of diseases for which a vaccine is sought.

Disease characteristic	HIV/AIDS	Malaria	Trypanosomiasis	Theileriosis
Antigenic variation	✓	✓	✓	(Antigenic diversity)
Apicomplexa	×	✓	×	✓
Lives inside host cells	✓	✓	×	✓
Lives in T-lymphocytes	✓	×	×	✓
Taken up by ectoparasites	×	✓	×	✓
Research investment to develop a vaccine	US$2400 million at NIH in 2014	US$2550 million globally in 2010	US$2.5 million a year at ILRAD in 1980s	US$2.5 million a year at ILRAD in 1980s

and their products with more precise methods that allowed identification and isolation of individual lymphocyte populations and evaluation of the roles of their molecules (antibodies and cytokines) in protective immune responses.

To understand the importance of the new technologies for improving the ability to study bovine cells and their products, we need to look at immunology in the late 1970s. As an example, in the 1970s, bovine lymphocytes were separated into T- and B-cell populations by passing lymphocytes over nylon wool packed in plastic columns such that the T-cells flowed through and the B-cells and monocytes stuck to the fibres. This technique was first applied to separation of bovine lymphocytes in 1974 (Rouse and Babiuk, 1974). Bovine T-cells were identified by their ability to interact with sheep red blood cells in a method known as erythrocyte (or E) rosetting, first applied to bovine cells in 1976 (Grewal *et al.*, 1976). The red blood cells interacted with a T-cell surface molecule that was later designated CD2 and to which mAbs were made at ILRAD (Baldwin *et al.*, 1988b). B-cells were identified by their ability to interact with sheep red blood cells coated with antibodies and complement in procedures known as erythrocyte–antibody rosetting and erythrocyte–antibody–complement rosetting in 1977 (Takashima *et al.*, 1977) and using polyclonal antiserum that contained antibodies to surface immunoglobulins (Takashima *et al.*, 1977).

These methods of identifying bovine T- and B-cells lent themselves to crude separation techniques, such as density-gradient separation of the rosetted and non-rosetted cells or 'panning' by coating antibodies specific for surface immunoglobulins on to plastic dishes or beads and allowing the reacting cells to adhere while other cells were washed away (Usinger and Splitter, 1981). A variety of lectins were employed in 1979 to stimulate the T- and B-cells to grow in culture (Pearson *et al.*, 1979b). In addition, in 1981, peanut agglutinin was conjugated to a fluorescent tag and used to identify T-cells, i.e. those cells that bound peanut agglutinin were considered T-cells (Usinger and Splitter, 1981); this was a harbinger of the fluorescently tagged mAbs that would soon be developed to allow efficient identification and isolation of cell populations.

Details of the human and mouse immune systems were just being worked out in the early to mid-1980s, with ruminant immunology closely following and occasionally preceding the human and mouse work (Fig. 4.2). In 1980, mAbs specific for bovine immunoglobulin classes were produced (McGuire and Musoke, 1981) (Fig. 4.2 and Table 4.6) and these were used to identify bovine B-cells and their antibody products. These different classes of antibodies were shown to have different functions in 1979–1980 at ILRAD and by others elsewhere in the world. The T-cell receptor complex that interacts with foreign antigen was defined at this time, along with the encoding genes. While there was some understanding that T-lymphocyte subpopulations exhibit a variety of functions (cytotoxic T-cells lyse infected host target cells; helper T-cells assist B-cells in making and secreting antibodies), it became apparent that T-cell subsets with these functions could be largely divided into cells that bore the CD8 and CD4 markers, respectively. In addition, their ability to respond to antigen was dictated by the type of MHC on the presenting cells or target cells that they interacted with. This was defined in humans in 1982 after prior work in mice. As can be seen in Fig. 4.2, this understanding was emulated by work at ILRAD on the bovine immune system published in 1986 (Baldwin *et al.*, 1986; Ellis *et al.*, 1986; Goddeeris *et al.*, 1986a,b,c). This advance was made possible by the ability to clone bovine T-cells, as reported at ILRAD the preceding year (Brown and Grab, 1985), and by the generation of mAbs at ILRAD that reacted with bovine CD4 or bovine CD8 (Baldwin *et al.*, 1986; Ellis *et al.*, 1986). Functional studies were performed on these CD4$^+$ and CD8$^+$ cell populations using the FACS to purify the cells, eventually confirming that those bearing the CD8 molecule were those that had been identified as having the ability to kill parasite-infected host cells in 1982 (Fig. 4.2) (Emery *et al.*, 1982).

The mAbs described in the preceding paragraph also allowed scientists at ILRAD and elsewhere to identify a large population of lymphocytes in ruminant (cattle and sheep) blood that did not fit into either of these T-cell subpopulations (CD4$^+$ or CD8$^+$), nor were they B-cells, and thus were called null cells (Baldwin *et al.*, 1988a). This observation was made simultaneously with the discovery of a second type of T-cell antigen-specific receptor (TCR) composed of γ and δ chains in the mouse and human systems (Fig. 4.2).

Flow cytometry invented late 1960s – at ILRAD in 1977

mAbs developed1975 – at ILRAD in 1978

T-cell clones derived 1977 – at ILRAD in 1985

| 1970 | 1979/80 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1992 |

E-rosetting (CD2) to identify T-cells

TCR γ gene locus; CD5 found

4th TCR gene

CD4⁺ cells react with MHC class II-bearing cells;
CD8⁺ cells react with MHC class I;
CD6 identified;
mAb to CD25-Tac

CD3 and TCR interact;
TCR ☐ and ☐ genes;
novel TCR gene (TCRγ);
mAb to human CD2

Cells expressing TCRγ complex with CD3, γδ heterodimer

TCR γδ genes used by **sheep** and **cattle** T-cells

Suggested that T3 (later CD3) is associated with an as yet unknown antigen-specific receptor

The nature of the δ protein, γδ molecule is a second TCR

mAb to human CD3; TCR peptide mapping

Third major T lymphocyte population described in **sheep**

Bovine IgG1 and IgG2 functions; mAb to bovine IgM

Bovine cytotoxic T-cells

Bovine IL-2; bovine T-cell clones

mAbs to bovine CD4⁺ and CD8⁺ and monocytes

Bovine WC1⁺ cells identified; mAb to bovine CD2 and CD6; bovine CD1 characterized

Caroline comes to ILRI

Adoptive transfer of T-cells between calves shows protective role against *Theileria*

Bovine MHC class II types with T-cell clones

mAb to bovine MHC class I's; genes in 2nd bovine MHC class I locus

Clumsy separation techniques for bovine lymphocytes employed:
1974 nylon wool columns to isolate T-cells
1976–7 rosetting for T-and B-cell identification
1981 panning with anti-sIg and gradients for separating rosetted cells, fluorescent lectins to identify T-cells

Key:
Historical for cattle
Human
Ruminants
Bovine developments from ILRAD

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Fig. 4.2. Timeline of fundamental developments in T-cell immunology. TCR, T-cell receptor; sIG, surface immunoglobulin. (Constructed by authors from ILRAD archives).

Table 4.6. Milestones in understanding the bovine immune system.

Year	Milestones	Reference(s)
1979	Functions of bovine IgG1 and IgG2 Cytotoxoic T-cells to *T. parva*-infected cells Survey of lectins that stimulated bovine T- and B-cells	McGuire *et al.* (1979); Pearson *et al.* (1979a,b)
1980	Anti-IgM reagent made mAbs that react with cattle and other Bovidae	Pinder *et al.* (1980a,b)
1981	Adoptive transfer of thoracic-duct lymphocytes to twin calves to prove their role in immunity to *T. parva* T-cells responsible for immunity to *T. parva* Plasma cells from trypanosome-infected cattle make IgM Trypanosome infection suppresses lymphocyte response to lectins Possible first observation of $\gamma\delta$ T-cells responding in autologous mixed-lymphocyte reaction A subset of T-cells transformed by *T. parva*	Emery (1981); Emery and Moloo (1981); Masake and Morrison (1981); Masake *et al.* (1981); Pinder *et al.* (1981a,b)
1982	Antibodies do not react with cell membrane antigens of *T. parva*-infected cells Bovine antibodies do react with trypanosomes Bovine IgG2 antibodies block sporozoite infectivity Cytotoxic T-cells to *T. parva*-infected cells Cattle immunized with trypanosome glycoprotein and measurement of antibodies and cellular immunity as demonstrated by lymphocyte proliferation	Creemers (1982); Emery *et al.* (1982); Musoke *et al.* (1982); Pearson *et al.* (1982); Wells *et al.* (1982)
1983	Phagocytosis of antibody-opsonized trypanosomes using IgM and IgG1	Ngaira *et al.* (1983)
1985	Bovine IL-2 characterized T-cell clones maintained with IL-2 for 6 months mAb to *T. parva*-infected cells made MHC-restricted alloreactive cytotoxic T-cell lines generated	Brown and Grab (1985); Naessens *et al.* (1985); Teale *et al.* (1985)
1986	Anti-CD4 mAb made and T-cell helper function demonstrated Anti-CD8 mAb made and cytotoxic function showed Monocyte isolation methods Cytotoxic clones are MHC restricted Alloreactive T-cell clones are CD8+ and MHC restricted Anti-monocyte mAbs made	Baldwin *et al.* (1986); Ellis *et al.* (1986); Goddeeris *et al.* (1986a,c); Lalor *et al.* (1986); Teale *et al.* (1986)
1987	CD4+ T-cell clones specific for *T. parva*-infected lymphocytes *T. parva*-infected T-cell clones retain function and MHC specificity Monocytes stimulate autologous and allogeneic mixed-lymphocyte reaction Non-lymphoid cells in afferent lymph present antigen to T-cells $\gamma\delta$ T-cells respond in the autologous mixed-lymphocyte reaction MHC class II molecules typed with CD4+ T-cell clones	Baldwin *et al.* (1987); Baldwin and Teale (1987); Ellis *et al.* (1987a); Emery *et al.* (1987); Goddeeris *et al.* (1987); Teale *et al.* (1987); Teale and Kemp (1987)
1988	mAb (IL-A29) to a unique surface-determinant WC1, on $\gamma\delta$ T-cells Bovine CD4+, CD8+ and $\gamma\delta$ T-cells and B-cells are infected with *T. parva* Anti-CD2 and anti-CD6 mAb made BoLA class I characterized on cells CD1 characterized Ig allotypes	Baldwin *et al.* (1988a,b); Bensaid *et al.* (1988); Ellis *et al.* (1988); MacHugh *et al.* (1988); Naessens *et al.* (1988); Brown *et al.* (1989a,b)

Continued

Table 4.6. Continued.

Year	Milestones	Reference(s)

1989	T-cell lines and clones used to characterize *T. parva* antigens
	Alleles of CD5
	In vitro activation of bovine B-cells
	WC1$^+$ γδ T-cells described
	mAb IL-A25 characterized
	Haemopoietic stem cell cultures
		Brown *et al.* (1989a,b);
		  Howard *et al.* (1989); Olobo
		  and Black (1989)

1990	mAb to polymorphic determinants of BoLA class I MHC
	  molecule
	Young calves resist *T. parva*
	mAb to mature B-cell antigen made
	Second MHC class I locus gene cloned
	Panel of mAbs reactive with monomorphic and polymorphic
	  antibody epitopes
		Clevers *et al.* (1990);
		  Dobbelaere *et al.* (1990);
		  Fritsch and Nelson (1990);
		  Kemp *et al.* (1990); Koch
		  et al. (1990); Naessens
		  et al. (1990); Toye *et al.*
		  (1990); Williams *et al.*
		  (1990); Bensaid *et al.* (1991)

1991	γδ T-cells kill *T. parva*-infected cells
	Distinction of naïve and memory CD4$^+$ T-cells
	CD8$^+$ and γδ T-cells suppress CD4$^+$ T-cell responses shown
	Veiled cells present antigen efficiently
		Goddeeris *et al.* (1991);
		  Howard *et al.* (1991); Lutje
		  and Black (1991);
		  McKeever *et al.* (1991)

1992	Anti-tumour necrosis factor (TNF)-α mAbs made that neutralize
	  TNF
	Limiting dilution analysis for cytotoxic T-cells established
	Response by CD5$^+$ B-cells (B1 B-cells) in trypanosome-infected
	  cattle
		Naessens and Williams
		  (1992); Sileghem *et al.*
		  (1992); Taracha *et al.*
		  (1992)

1993	WC1 gene family and mAbs analysed Bovine B1 cells defined	MacHugh *et al.* (1993); Naessens (1993)
1994	WC1$^+$ γδ T-cells respond to invariant trypanosomiasis antigen	Flynn and Sileghem (1994)
1997	Role of CD5$^+$ B-cells in trypanosome-infected cattle	Buza *et al.* (1997)
1999	γδ T-cells respond to *T. parva*-infected host cells	Daubenberger *et al.* (1999)
2007	The adjuvant CpG enhances CD4$^+$ T-cell responses	Graham *et al.* (2007)
2011	The adjuvant Flt3L + granulocyte–macrophage colony- stimulating factor as adjuvant for CD4$^+$ T-cell responses	Mwangi *et al.* (2011)

It was fortuitous that lambs and calves have such a large proportion of γδ T-cells in their peripheral blood mononuclear cell (PBMC) populations, making the likely relevance of this new type of TCR to ruminant immunology immediately apparent.

It was postulated that the large 'null' cell population of lymphocytes within the PBMC populations were cells expressing this newly discovered TCR (i.e. γδ T-cells). The 'null cell'-specific mAb T19 of sheep and another for cattle made at ILRAD precipitated molecules ranging from 180 to 240 kDa (Mackay *et al.*, 1989). The molecules turned out to be part of a multigene family whose members were eventually designated Workshop Cluster 1 (WC1) by an international workshop held to group mAbs according to similar reactivity with bovine antigens (Morrison and Davis, 1991; Sopp *et al.*, 1991). (Such work-

shops for mAbs to human antigens gave rise to the cluster-defined (CD) antigens of humans. These workshops were held at intervals of several years to designate mAbs to human cell-surface antigens, while those studying other species followed suit, conducting species-specific workshops and naming their genes in parallel to the human CD system.)

The presence of mAbs defining various members of this family of γδ T-cell-unique cell-surface antigens facilitated the isolation of γδ T-cells. The mAbs include those pan-reactive with all or most WC1 family members as well as others that are specific for a subgroup of WC1 gene products and which thereby define subsets or subpopulations of WC1$^+$ γδ T-cells (Chen *et al.*, 2009). This was followed by the formal demonstration that cells reactive with the WC1-specific mAbs were in fact T-cells expressing the γ and δ

TCRs in both sheep and cattle from studies at ILRAD and others (Mackay and Hein, 1989; Mackay *et al.*, 1989; Clevers *et al.*, 1990). Further studies showed that not all γδ T-cells bear this lineage-specific marker. Thus, in organs such as the spleen, the majority of γδ T-cells do not express WC1, i.e. are WC1$^-$ (MacHugh *et al.*, 1997), and in the uterus no γδ T-cells express WC1 (Tuo *et al.*, 1999). In contrast, as few as 1% of the peripheral blood γδ T-cells in cattle are WC1$^-$ (Baldwin *et al.*, 2000), although this can change with the conditions under which the cattle are held. For example, in one study, it was shown that the proportion of the WC1$^+$ relative to the WC1$^-$ population decreased when the cattle were moved from open grazing at the ILRI Kapiti Ranch to a Biosafety Level 2 (BSL2) facility on the ILRI campus (Baldwin *et al.*, 2000), suggesting that the WC1$^+$ population was maintained at a high level by stimulants such as ticks and undefined environmental antigens not found in a BSL2 facility.

Such studies provide models for understanding expansion of particular γδ T-cell populations in otherwise apparently healthy animals and provide a useful comparison to the response of γδ T-cells to both *T. parva*-infected host cells and trypanosome components, discussed in later sections of this chapter. The simultaneous progress in understanding basic bovine immunology and immune responses to disease is noted in Table 4.6. At times, the advances obtained using the infection systems preceded our definition of the immune system; in other cases, the elements defined in the basic immunological studies were subsequently applied to infection pathology and immunity.

Because these studies showed that the bovine immune system was fundamentally similar to that of humans, knowledge from one is reasonably applicable to the other (i.e. one can assume with optimistic caution that the same principles apply to both). While only a limited repertoire of tools may be required to develop the 'big picture' in the context of disease and vaccine efficacy in livestock species, tools that identify unique aspects of the ruminant immune systems relative to that of mice and humans are also needed, as these species-specific immune response elements may be important in vaccine design and efficacy (e.g. to include the responses of γδ T-cells).

The participation of ILRAD scientists with scientists from around the world in characterizing the bovine immune system through the mAbs generated was crucial for advancing institutional research in the early stages and defining the fundamentals of the bovine immune system (e.g. CD4$^+$ and CD8$^+$ T-cells, immunoglubulin functions, monocytes and efficient antigen-presenting cells), as well as bovine peculiarities relative to mouse and human systems (WC1$^+$ γδ T-cells). Simultaneous with studies at ILRAD, the ruminant immune system, including that of cattle, was being evaluated at the Basel Institute of Immunology, the Walter and Eliza Hall Institute in Melbourne, the John Curtin School of Medicine in Canberra, and Washington State University, among other institutions. As part of this work, many more mAbs were developed. Findings by the various groups regarding mAbs and their targets coalesced in a number of international workshops in which ILRAD scientists played fundamental and leadership roles. ILRAD/ILRI scientists were key leaders and organizers as well as active participants in 'mAb workshops' that were held every few years to compare reagents against bovine immune system molecules (Morrison and Davis, 1991; Howard and Naessens, 1993; Naessens and Howard, 1993). These workshops involved scientists exchanging reagents and then analysing them in a pre-agreed manner in a number of assays and comparing their results. ILRAD hybridomas (the transformed cell lines that produce mAbs) were also generously distributed around the world.

As determined by the literature review here, immunological research at ILRAD/ILRI has had a substantial impact worldwide. The right approach was taken, and appropriate tools were developed to allow further understanding of the ruminant immune system in support of vaccine development and efficacy testing according to the mandate of ILRAD. Moreover, the research team that undertook these studies was reflective and creative in generating a vast number of tools to study the bovine immune system using the most modern technologies and following closely the discoveries informing the fundamentals of the murine and human immune systems. In addition, in some cases, knowledge about the components and function of the bovine system preceded that in either mice or humans. These studies resulted in a substantive body of work, as shown by the examples in Table 4.6 of dozens of peer-reviewed publications. The timeline in Fig. 4.2 indicates that key findings during the nascent period of molecular immunology were

published in a timely manner, being interwoven with those in humans and mice or occurring in the same scientific era. Most of this work was published in international peer-reviewed journals of immunological scientific societies as follows: *Journal of Immunology* (American Association of Immunologists), *Infection and Immunity* (American Association of Microbiology), *Immunology* (British Society of Immunology), *European Journal of Immunology* (European Federation of Immunological Societies) and *Veterinary Immunology and Immunopathology* (American Association of Veterinary Immunologists). So, while not necessarily published in the highest-impact journals, in part because of its iterative nature, the work was nevertheless published in well-respected journals. To a lesser extent, ILRAD/ILRI contributed to making reagents or tools to measure the products of macrophages and T-cells (i.e. cytokines). The production of mAbs to tumour necrosis factor (TNF)-α at ILRI was notable, especially since this particular cytokine is associated with anaemia, which is a characteristic of AAT in cattle. Generating anticytokine mAbs for cattle and other ruminants was addressed more thoroughly by groups at Compton (UK), Namur (Belgium) and Melbourne (Australia).

The measurable outputs and impacts from the generation of reagents to study the bovine immune system can be found in the global exports of the mAbs to other parts of the world including the USA and Europe. In 1990, a group of US-based scientists working in bovine immunology paid for safety testing of the ILRAD mAbs to allow their importation into the USA. This meant that the hybridoma cell lines had to be sent to a US government containment laboratory (Plum Island, New York) and tested in livestock before being allowed on the USA mainland. The group of hybridomas included those that secrete antibodies specific for MHC class I and II (IL-A19 and IL-A21), CD4$^+$ and CD8$^+$ T-cells (IL-A11, IL-A12 and IL-A51), macrophages (IL-A15) and others. Some of these imported mAbs were sold by the Washington State-based company Veterinary Medical Research and Development (VMRD), which continued to offer these until a few years ago. Serotec sells ILRAD/ILRI-made mAbs in Europe and the USA, and the American Type Culture Collection holds a few hybridomas that were generated at ILRAD available for purchase. Currently under way is the importation into the USA (again to Plum Island) of a large collection of ILRAD/ILRI mAbs, where they are being tested for safety.

Immunoparasitology of theileriosis

Before ILRAD was established, research at KARI, at Muguga, some 15 km from ILRAD, had shown that *T. parva* sporozoites derived from infected tick salivary glands can be cryopreserved (Cunningham *et al.*, 1973), that the sporozoites can transform bovine lymphoid cells *in vitro* (Brown *et al.*, 1973) and *in vivo*, and that cattle can be immunized by infection with these parasites in combination with long-acting tetracycline or other drugs (Radley *et al.*, 1975; McHardy *et al.*, 1976). Immunization by simultaneous infection and chemotherapeutic treatment was effective against homologous challenge, and a cocktail of parasites had been established, called the 'Muguga cocktail', which protected against several strains of *T. parva* that are endemic in East Africa but not against all strains of *T. parva* and not against many strains of Cape buffalo-derived *T. parva* (subsp. *lawrencei*). Knowing that cattle could be immunized against *T. parva* subsp. *parva* strains, ILRAD set out to identify the protective immune response, the nature and diversity of host-protective *T. parva* antigens and the best administration of these immunogens to induce broad host protection. The seeming modesty of these aims was belied by the concomitant need to define cells and function in the bovine immune system, as discussed above, to determine the respective roles of antibody-mediated immunity and cell-mediated immune responses in protection. Scientists needed to determine not only the identity of the protective parasite antigens but also their antigenic stability and their utility in vaccination protocols.

In addition to these goals, fundamental gaps in knowledge cried out for resolution. What types of lymphocytes are infected and transformed by *T. parva*? Does the cell type infected affect the induction of protective immunity, i.e. do the infected cells retain functional specialization and release molecules that misdirect the immune responses? What prevents infected cattle from achieving immunity in the absence of drug intervention? These were and are reasonable questions that inform strategies to better control theileriosis in cattle, but were they the right questions? Would it perhaps have been better to

have invested a larger amount of effort in typing *T. parva* strain diversity and improving the ITM, which has obvious immediate translational value, or in focusing on prophylactic immunity against tick infestation?

The *T. parva* sporozoite ITM developed at Muguga was addressed at ILRAD under the leadership of Tony Irvin and continues today under the guidance of Philip Toye. To effectively understand the efficacy of ITM as a potential vaccine, *T. parva* strain diversity needed to be defined and was addressed at ILRAD by many investigators using mAbs against schizont antigens, bovine T-cell clones specific for *T. parva*-infected cells and molecular genetic approaches. Immunization against theileriosis by ITM has some notable successes, e.g. protection of 97.6% of immunized cattle in two districts of northern Tanzania against field challenge (Lynen *et al.*, 2012). This 'live' vaccine continues to be produced at ILRI, with nearly two million cattle immunized with the ILRI-produced vaccine. With assistance from GALVmed, a not-for-profit global alliance that provides livestock treatments in developing countries, ILRI has registered the vaccine in Kenya, Malawi and Tanzania.

While the live vaccine approach serves as an interim disease control measure, it remains less desirable than a killed or subunit vaccine because of the requirement for infective particles (sporozoites) with the concomitant problems associated with the need for a reliable cold chain, carefully titrated infecting particles and renewable propagation of stabilates to sustain the infection regime, which is not straightforward given their genetic diversity (Patel *et al.*, 2011). Indeed, cocktail combinations appropriate to a given treatment area must be developed. Because of live infection, the *T. parva* sporozoite ITM also carries the danger of establishing carrier status in the treated animals. In addition, it is relevant to note that ILRAD was mandated to perform intensive immunological research on trypanosomiasis and theileriosis leading to improved control of disease, a call to action that required more than an intensified focus on the ITM.

With regard to the tick vaccine approach, it can reasonably be argued that the induction of an antibody response against a conserved and physiologically relevant tick salivary protein might be sustained by natural boosting and hence prevent both tick infestation and *T. parva*

transmission. Stuart Shapiro and others at ILRAD obtained some evidence using immunized rabbits to support this approach (Shapiro *et al.*, 1989), but this was not pursued in depth because elucidating and testing possible protective antigens in tick saliva and their polymorphisms was considered a less-assured investment than identifying protective *T. parva* antigens. However, interest in an anti-vector approach, while not a focus of ILRAD's attention, has received renewed attention in Europe, where investigators from several countries are using proteomic and transcriptomic approaches to identify candidate vaccine antigens in the saliva of *Ixodes ricinus* (Sprong *et al.*, 2014). It can be hoped that these studies will be successful and will accelerate development of an effective vaccine against *Rhipicephalus appendiculatus*, the vector of *T. parva*, which is also an ixodid tick. However, even if candidate anti-tick vaccine antigens are identified, these may be polymorphic and protective immune responses difficult to sustain through natural challenge alone, making the success of this approach not assured. Before leaving the discussion of anti-vector immunity, it is noteworthy that ILRI staff have recently identified and cloned tick gut proteins that, when repeatedly administered to cattle, significantly decrease the moulting success of *R. appendiculatus* nymphal ticks to adults (Olds *et al.*, 2012). While this approach has relevance to vaccine-based vector control, the need for repeated immunization and the absence of a natural boost impose constraints to its efficacy. The scientific consensus in ILRAD's early years was that the focus on immune responses against *T. parva* and not on the tick vector was the most promising approach.

Thus, towards the question of whether the ILRAD team indeed asked the right questions in the right way, including being creative and with a focus on translational outcomes and taking advantage of advances in understanding the bovine immune systems made at ILRAD and elsewhere, and whether they further implemented new technologies in a timely manner to achieve its goals of generating a subunit *T. parva* vaccine, we turn to the quantitative impact analysis presented above. It makes a case for solid and even prolific productivity of ILRAD investigators, evidenced through the body of their published work and, moreover, through continued focus on the fields of veterinary immunology and immuno-

parasitology in post-ILRAD careers, including on theileriosis vaccine development. Hence, we will highlight what we consider substantive findings in theileriosis research and their temporal relationship to each other and to discoveries in ruminant immunology made at ILRAD.

Rapid progress was made in identifying candidate mechanisms of protective immunity. Terry Pearson and colleagues in 1979 showed that *T. parva*-infected leukocytes stimulate autologous peripheral blood lymphocytes (PBLs) from naïve and primed cattle to proliferate *in vitro* and, in the case of PBLs from primed animals only, induce the generation of cytotoxic cells that lyse *T. parva*-infected cells but not uninfected lymphoblasts (Pearson *et al.*, 1979a). This work established as research priorities the identification of cytotoxic cells and elucidation of both their role in mediating protective immunity *in vivo* and the identity of their target antigens. A few years later, Tony Musoke and colleagues showed that antibodies of the IgG2 class in serum from cattle that had recovered from ECF, and in serum from rabbits immunized with *T. parva* sporozoites, prevented sporozoites from infecting and transforming bovine PBLs *in vitro* (Musoke *et al.*, 1982). This finding identified the sporozoite coat protein as a candidate vaccine antigen and heralded an additional set of research priorities, namely, characterizing the protein, its neutralizing epitopes and their genetic stability, and ways of immunizing to induce sustained production of sporozoite-neutralizing antibodies.

Table 4.7 lists findings that led to the identification of *T. parva*-specific T-cell epitopes that stimulate protective immunity, while Table 4.8 lists the progress towards identifying B-cell epitopes on the *T. parva* sporozoite coat that stimulate neutralizing antibodies. These tables illustrate the steady and sustained progress towards development of a subunit vaccine that stimulates production of antibodies that neutralize sporozoites and induces primed MHC and *T. parva*-restricted CD8+ T-cells that mount recall responses to and lyse *T. parva*-infected cells, and CD4+ T-cells that expedite development of the cytotoxic T-cell response. Many of the aims of the *T. parva* immunology programme have been achieved, but development of an effective subunit *T. parva* vaccine remains a challenge, even in 2020.

With respect to T-cell immunity, it was elegantly shown that CD8+ T-cells kill *T. parva*-infected cells in a parasite strain- and host MHC class I-restricted manner (Goddeeris *et al.*, 1986c), that CD4+ T-cells expedite priming of the *T. parva*-specific CD8+ T-cells (Taracha *et al.*, 1997) and that adoptive transfer of CD8+ T-cells from an immune to a non-immune chimeric twin conveys protective immunity to homologous parasite challenge (McKeever *et al.*, 1994b). In addition, *T. parva* sequences encoding protective CD8+ T-cell epitopes have been identified and shown to induce *T. parva*-specific cytotoxic T-cells (Graham *et al.*, 2006, 2008). Work from Kariuki *et al.* (1990) showed that immunization of full-sibling cattle by infection with Cape buffalo-derived *T. parva lawrencei* and subsequent pharmacotherapy generated cytotoxic T-cells that recognized common T-cell epitopes of *T. parva*-infected lymphocytes, which is good news for *T. parva* vaccine development, since inclusion of these common epitopes in the vaccine are likely to increase its efficacy. However, work by MacHugh *et al.* (2011) showed that immunodominant T-cell epitopes on *T. parva*-infected lymphocytes showed genetic diversity consistent with antigenic variation, which raises issues with respect to the selection of candidate vaccine epitopes.

With respect to a sporozoite-neutralizing vaccine, the gene encoding the *T. parva* sporozoite surface coat, p67, has been cloned, and immunization with baculovirus expressing the p67 recombinant protein has been shown to induce production of sporozoite-neutralizing antibodies (Kaba *et al.*, 2003) and to protect immunized cattle against syringe challenge with *T. parva* sporozoites (Kaba *et al.*, 2005). However, immunity against tick-transmitted sporozoites appears to be considerably lower (Vish Nene, ILRI, 2015, personal communication), raising the possibility that components of tick saliva might antagonize interactions between neutralizing antibodies and sporozoites.

While the *T. parva* vaccine programme has not yet resulted in full disease control, contributing scientists have identified, cloned and expressed recombinant *T. parva* proteins that stimulate protective T-cells and antibody responses (Nene *et al.*, 1992, 1995; Graham *et al.*, 2006). They have further provided evidence that a subunit vaccine, perhaps comprising a sporozoite p67 subunit that elicits sporozoite-neutralizing antibodies together with schizont epitopes that stimulate appropriate CD4+ helper T-cells and CD8+ cytotoxic T-cells in cattle, is a realistic possibility.

Table 4.7. Immunity to *T. parva*-infected lymphocytes and identification of candidate vaccine antigens: timeline of substantial findings.

Year	Finding	Reference
1979	PBLs from *T. parva*-immune animals are shown to mount *T. parva*-infected cell-specific proliferative and cytotoxic responses upon stimulation with *T. parva*-infected lymphocytes *in vitro*	Pearson *et al.* (1979a)
1981	*T. parva*-infected cell-specific cytotoxic cells are shown to arise in the blood and lymph of *T. parva*-immune cattle following reinfection and are restricted by host polymorphic antigens	Eugui and Emery (1981)
1981	Resistance to lethal challenge with *T. parva* (Muguga) is shown to be transferred from immune to non-immune chimeric twins by cells in thoracic-duct lymph	Emery (1981)
1986	Cytotoxic lymphocytes specific for *T. parva*-infected cells are shown to be restricted by target-cell class I MHC antigens	Goddeeris *et al.* (1986b,c); Morrison *et al.* (1987)
1987	Proliferation and production of T-cell growth factor(s) by cloned bovine CD4+ T-lymphocytes, putatively helper T-cells, that are specific for *T. parva*-infected cells are shown to be both *T. parva* strain and host-cell MHC class II restricted	Baldwin *et al.* (1987)
1989	*T. parva*-specific helper and cytotoxic bovine CD4+ T-cells are shown to proliferate in response to macroschizont membrane and infected-cell extract high-speed supernatant processed by antigen-presenting cells	Brown *et al.* (1989b); Baldwin *et al.* (1992); Brown *et al.* (1989a)
1994	Transfer of bovine CD8+ T-cells from efferent lymph of immune *T. parva*-infected cattle into their non-immune monozygotic twins is shown to convey immunity to lethal *T. parva* sporozoite challenge	McKeever *et al.* (1994b)
1997	*T. parva*-immune bovine CD4+ T-cells are shown to expedite development of *T. parva*-restricted bovine CD8+ cytotoxic T-cells *in vitro*	Taracha *et al.* (1997)
1999	Bovine γδ T-cells proliferate in response to and lyse *T. parva*-infected lymphocytes and are not restricted by class I or class II MHC antigens	Daubenberger *et al.* (1999)
2006	Candidate *T. parva* vaccine antigens that stimulate bovine CD8+ cytotoxic T-cells are identified by screening antigen-presenting cells transiently transfected with cDNAs of selected *T. parva* schizont genes encoding secretory proteins and schizont membrane antigens	Graham *et al.* (2006)
2008	Cytotoxic lymphocyte epitopes on candidate *T. parva* vaccine antigens are identified by immunoscreening on peptide-pulsed fibroblasts and transfected COS-7 cells and confirmed as relevant using cytotoxic lymphocytes from cattle subjected to *T. parva* sporozoite ITM	Graham *et al.* (2008)
2009	The MHC haplotype of responder cattle determines the *T. parva* epitopic bias of bovine CD8+ cytotoxic cells and hence specifies immunodominance	MacHugh *et al.* (2009)
2011	An immunodominant *T. parva* epitope is shown to undergo antigenic variation	MacHugh *et al.* (2011)

From this promising work, the *T. parva* vaccine project has been revitalized by support from the Bill & Melinda Gates Foundation (2005) awarded to a consortium comprising mostly ILRAD alumni and current ILRI faculty. Work at ILRI has shown that *T. parva*-infected cells stimulate the development of cytotoxic γδ T-cells (Dauben-berger *et al.*, 1999), indicating the presence on *T. parva*-infected cells of *T. parva*-induced or -derived antigens that are not MHC restricted and which should be identified and considered for inclusion in a subunit vaccine.

While not of direct importance to the development of a *T. parva* vaccine, several grace notes

Table 4.8. Timeline of substantial findings in immunology of theileriosis: humoral immunity.

Year	Finding	Reference
1982	ECF immune serum and serum of rabbits immunized with *T. parva* sporozoites contain neutralizing IgG2 anti-sporozoite antibodies	Musoke *et al.* (1982)
1985	Infection of bovine lymphocytes by *T. parva* sporozoites is inhibited by a mAb that recognizes a 68 kDa circumsporozoite protein	Dobbelaere *et al.* (1985)
1992	The gene encoding a 67 kDa *T. parva* circumsporozoite protein is cloned and antibodies against recombinant proteins containing residues 9–316 and 397–709 neutralize sporozoite infectivity *in vitro*	Nene *et al.* (1992)
1992	A recombinant fusion protein of *T. parva* sporozoite protein p67 and a non-structural gene of influenza A virus induces sporozoite-neutralizing antibodies in cattle	Musoke *et al.* (1992)
1998	The antibody response of cattle to the p67 sporozoite antigen is enhanced by fusion to the C-terminal secretion signal of *Escherichia coli* haemolysin and expression in *Salmonella enterica* Dublin	Gentschev *et al.* (1998)
1998	Immunization with live attenuated *S. enterica* Dublin expressing sporozoite p67 confers partial protection against syringe injection of *T. parva* sporozoites	Heussler *et al.* (1998)
2003	Expression of sporozoite p67 N- and C-terminal domains fused to the baculovirus envelope glycoprotein GP64 results in retention of native antigen conformation	Kaba *et al.* (2003)
2005	Immunization with a baculovirus-derived sporozoite p67 subunit induces sporozoite-neutralizing antibodies and provides up to 85% protection against syringe challenge with *T. parva* sporozoites	Kaba *et al.* (2005)

enrich the legacy of ILRAD's contributions to theileriosis research. With respect to the biology of theileriosis, bovine CD4+ T-cells, CD8+ T-cells, null cells (now known to be γδ T-cells) and B-cells were all shown to be targets for infection and transformation by *T. parva* sporozoites (Baldwin *et al.*, 1988a), and infected cloned T-cells were shown to retain function for some months after infection (Baldwin and Teale, 1987), although this was not the case with infected B-cells. Host-cell invasion by *T. parva* sporozoites was shown to result from an initial energy-independent zippering of the sporozoite coat (later to be identified as p67) and host-cell plasma membrane receptors, and subsequent energy-dependent removal of the host endocytic membrane that prevents lysosomal fusion and confounds intracellular defences (Fawcett *et al.*, 1984). Work by ILRAD alumna Dirk Dobbelaere and colleagues uncloaked much of the mystery surrounding how *T. parva* transforms host lymphocytes and usurps the host-cell mitotic apparatus to ensure partition of schizonts into daughter cells (von Schubert *et al.*, 2010). In addition, relatively recent work at ILRI has rediscovered an old unsolved mystery involving the development of large num-bers of non-specific cytotoxic cells in the lymph node draining the site of *T. parva* infection in naïve cattle (Houston *et al.*, 2008). This response does not arise in *T. parva*-immune cattle, which instead generate large numbers of *T. parva*- and host MHC-restricted cytotoxic T-cells. It is possible that this poorly understood non-specific cytotoxic response contributes to the inability of the infected cattle to control *T. parva*-infected cells, for example by killing responding *T. parva*-specific T-cells. If these non-specific cytotoxic cells are activated by conserved *T. parva* antigen, such antigens might provide additional targets for an anti-pathology vaccine.

Immunoparasitology of trypanosomiasis

As with *T. parva*, a good deal of information regarding African trypanosomes was available to researchers seeking to develop a vaccine against AAT. It was known at the inception of ILRAD that there are several species of mammal-infective African trypanosomes, all of which can be transmitted in the saliva of tsetse flies, and that there are several species of tsetse that can serve as vectors and are adapted to different habitats. In

addition, methods to cryopreserve bloodstream-stage African trypanosomes and to use these to infect other animals had been described (Herbert *et al.*, 1968), as had methods to purify the parasites from host blood (Lanham, 1968). It was also known that bloodstream-stage trypomastigotes are killed by antibodies specific for their immunodominant variable surface glycoprotein (VSG), and that the parasites undergo antigenic variation by differential expression of VSGs. Furthermore, the VSG from a *Trypanosoma brucei* variant had been isolated and characterized (Cross, 1975, 1977). While research towards a *Theileria parva* vaccine at ILRAD/ILRI continues to progress, this is not the case with research to develop a vaccine effective against AAT. In the case of AAT, high variation in protective antigens blocked the development of an effective vaccine from the outset and led to the programme's closure in 2001.

When ILRAD work began in 1974, there was evidence that metacyclic trypanosomes, which are the mammal-infective forms derived from tsetse, revert to one or a few basic antigen types when transmitted to cattle. However, by the time ILRAD's campus at Kabete was inaugurated in 1978, this view had changed, and it was no longer considered likely that trypanosome infections could be prevented by prior immunization of hosts with a few basic variable surface antigens (reviewed by Vickerman, 1978). Indeed, only 11 years later, ILRAD's Peter Gardiner wrote 'the feeling has arisen that antigenic variation, as demonstrated by the *Trypanozoon* and *Nannomonas* subgenera of trypanosomes, is too extensive, the number of serodemes too large, and the coexistence of different species in many areas too complicated, to allow any immunoprophylaxis based on antibodies to variable antigens' (Gardiner, 1989). Gardiner held out hope that the case might be simpler with *Trypanosoma vivax*, which belongs to the *Dutonella* subgenera. However, there is still no proof that the antigenic repertoire of *T. vivax* is particularly limited, either in metacyclic or bloodstream-stage VSGs.

Concern about the development of a trypanosomiasis vaccine was implied in a presentation made by I.E. Murithi, then Director of Veterinary Services in the Kenya Ministry of Agriculture, at the 1978 ILRAD inauguration symposium. Murithi stated with respect to the trypanosomiasis vaccine that 'our research effort must be planned in such a manner that an authentic answer is obtained at a relatively early stage in our research'. Murithi suggested that if the answer turns out to be 'no', it might be better to invest research effort into other areas of trypanosomiasis research, such as chemotherapy and vector control. At the same time as the inauguration symposium, A.J.S. Davies, of the Chester Beatty Research Institute, raised an additional issue. After commenting on the cost-effective development of earlier vaccines, which resulted from empirical testing of attenuated organisms or organisms that induce cross-protective immunity, he summarized the immunological focus of current disease research as follows, 'Rather to the chagrin of older parasitologists... the immunologists have crept into the [vaccine development] act with little but their enthusiasms and wish to do something useful to support this'. He rightly pointed out that immune responses are complicated and that the study of immune responses per se might not reveal ways to manipulate them to ensure control of highly antigenically variable pathogens. Notwithstanding this oblique cautionary note and bolstered by the institution's mandate to address the immunology of parasitic infections, the ILRAD faculty working on the immunology of AAT pressed ahead with a 'let's have at it anyway' attitude.

Thus, through the 1980s, investigators at ILRAD continued to study trypanosome VSG antigenic variation and genetic mechanisms underlying this process, under the leadership of Jack Doyle and Dick Williams, and to examine the extent to which cattle could be immunized against AAT by injection of dead or dying trypanosomes, or components of trypanosomes, or by ITM under the leadership of Max Murray. The latter investigations showed that immunization of cattle with lethally irradiated trypanosomes with or without their VSG surface coat, with so-called 'uncoated' insect (procyclic) forms of the parasites, or with trypanosome membrane, or by infection with an assembly of metacyclic parasites from various isolates followed by trypanosome pharmacotherapy, did not prevent or reduce the severity of disease upon challenge with heterologous trypanosomes. Instead, immunization with VSG-coated trypanosomes induced immunity to homologous challenge (Emery *et al.*, 1982) – as in some circumstances did infection with tsetse-transmitted *Trypanosoma congolense* metacyclic forms – followed at an appropriate time by trypanocidal chemotherapy. Resistance

of animals made immune by ITM to the tsetse-transmitted metacyclic parasites was coincident with the presence in serum of antibodies that neutralized the metacyclic parasites (Akol and Murray, 1985; Dwinger *et al.*, 1987b), suggesting that protection against homologous tsetse challenge was, at least in part, based on the development of antibodies specific for expressed VSGs. While these studies, which are summarized below, contributed valuable information on the ruminant host immune response to trypanosomes, the findings were not viewed at the time as supporting the possibility of vaccine development because of the absence of immunity to heterologous infection.

With the loss in enthusiasm for effective immunization against AAT using a composite VSG-based vaccine or by tsetse-transmitted ITM, researchers at ILRAD chose two main approaches to try to affect immunological control of the disease. The first was a search for immunoprotective conserved antigens expressed by trypanosomes, an approach based on the knowledge that bloodstream-stage African trypanosomes require lipids and iron and hence may have antibody-accessible receptors for their macromolecular carriers; the second was a search for mechanisms of trypanosomiasis tolerance expressed in animals with genetically acquired resistance to the disease, which is discussed below.

Optimism that non-variant immunoprotection could be induced by immunization with conserved nutrient receptors has proven unfounded, at least so far, although the idea that trypanosomes require macromolecular nutrients was confirmed using axenic cultures of bloodstream-stage *T. brucei* developed at ILRAD. The parasites were shown to require serum lipoproteins (low, intermediate or high density) from any of several mammal species to replicate *in vitro*, and their sustained replication also required the iron-carrying molecule transferrin (Black and Vandeweerd, 1989). Reasoning that receptors for these macromolecular nutrients would concentrate in endocytic vesicles, Stuart Shapiro assessed immunization with purified clathrin-coated vesicles from *T. brucei*. However, this immunization regime did not induce non-variant immunoprotection in a mouse model (Shapiro, 1994), a disappointing result that was later confirmed by immunization of rabbits and mice with tomato lectin-purified parasite components (Guirnalda

et al., 2007). These molecules were predominantly poly-*N*-acetyllactosamine-bearing endosomal proteins that contain the receptor for transferrin, a putative receptor for serum low-density lipoprotein and most likely other receptors (Nolan *et al.*, 1999). Selective immunizations of mice with the putative receptor for low-density lipoproteins (Bastin *et al.*, 1996) and with a receptor for transferrin (Steverding, 2006), performed by scientists unconnected to ILRAD, also failed to elicit non-variant immunoprotection under nutrient-sufficient conditions. Despite the lack of success of the nutrient receptor vaccine approach so far, the choice to take this approach still seems reasonable to the chapter authors.

The remaining approach taken by scientists working on the immunoparasitology of trypanosomiasis at ILRAD was to identify mechanisms of trypanotolerance in Cape buffalo, N'Dama cattle and certain inbred strains of mice, with a focus on control of parasitaemia and anaemia. Understanding cell and molecular mechanisms of trypanotolerance was viewed as a route to identify ways to decrease the trypanosomiasis susceptibility of livestock, such as through the development of an anti-pathology vaccine, if key trypanosome pathology-inducing ligands could be identified, or by selective breeding, or, as only dreamed then, by genetic engineering if key resistance genes could be identified. Trypanotolerance in both livestock and Cape buffalo was shown to be a genetically acquired trait in two magnificent experiments. The first was the importation of N'Dama embryos from a herd in West Africa and their successful implantation into surrogate mothers at the ILRAD farm adjoining the ILRAD campus (Jordt *et al.*, 1986), thus realizing the vision of ILRAD scientists Max Murray and Jack Doyle, and ILRAD's then Director General, Ross Gray, to establish a research herd of N'Dama at ILRAD. These animals, which were born from mothers that had never experienced trypanosomiasis and that were raised and bred on the ILRAD campus (i.e. in a tsetse- and trypanosomiasis-free area) expressed the trypanotolerance traits of their breed, as shown by their superior control of parasitaemia and anaemia after tsetse or syringe infection with African trypanosomes when compared with similarly infected trypanosomiasis-susceptible Boran cattle (several references are provided in Table 4.9). The second approach was taken by

Table 4.9. Findings about the immunology of AAT in ruminants.

Year	Finding	Reference
1981	PBLs from Boran cattle infected with *T. congolense* have decreased responses to mitogens (lipopolysaccharide, phytohaemagglutinin) compared with PBLs from uninfected cattle	Masake *et al.* (1981)
1982	Development of a chancre at the site of infected tsetse bites is due to the metacyclic trypanosome and is not a response to the fly bite	Akol and Murray (1982)
1982	Trypano-destructive antibodies bind to a subset of VSG epitopes that are exposed on the surface of the parasites	Emery *et al.* (1982)
1982	Cattle, particularly N'Dama, that survive trypanosome infection make antibodies against a broader repertoire of trypanosome antigens than those that die	Shapiro and Murray (1982)
1983	Infection of cattle with *T. congolense* suppresses their antibody response to vaccination with *Brucella abortus*	Rurangirwa *et al.* (1983)
1985	Immunity to metacyclic *T. congolense* is induced by infection and Berenil treatment. A chancre does not develop upon second exposure to homologous reinfection	Akol and Murray (1985)
1985	Trypanotolerant breeds of cattle are better able to control trypanosomes in the skin and to generate protective antibody responses than trypanosusceptible cattle	Akol and Murray (1985)
1987	Goats infected with *T. congolense* resist secondary infection by tsetse bite but do not develop immunity to the secondary infection. Infected animals may develop non-specific immunity to skin trypanosomes	Dwinger *et al.* (1987b)
1987	*T. congolense*-infected N'Dama cattle are better able to control anaemia and parasitaemia than similarly infected Boran cattle and have higher numbers of B-cells in peripheral blood before and during infection than Boran cattle	Ellis *et al.* (1987b)
1989	Ayrshire cattle infected with haemorrhage-causing *T. vivax* develop auto-antibodies to normal red blood cells and platelets	Assoku and Gardiner (1989)
1991	Macrophages in lymph nodes of *T. congolense*-infected cattle suppress mitogenic responses of T-cells from infected and naïve cattle	Flynn and Sileghem (1991)
1992	The inability of lymph-node T-cells from *T. congolense*-infected cattle to respond to mitogen is associated with impaired expression of the α-chain of the IL-2 receptor	Sileghem and Flynn (1992)
1992	Splenic CD5+ B-cells, putatively bovine B1 B-cells, increase in the spleens of *T. congolense*-infected cattle	Naessens and Williams (1992)
1993	*T. congolense*-infected N'Dama but not Boran cattle generate IgG antibodies to a 33-kDa parasite parasite cysteine protease, congopain	Authié *et al.* (1993)
1993	N'Dama cattle primed to *T. congolense* antigens by ITM mount superior IgG recall responses to the antigens upon reinfection than similarly treated Boran cattle	Authié *et al.* (1993)
1994	γδ T-cells are selectively depleted from the afferent lymph of responding lymph nodes of Boran cattle exposed to *T. congolense*-infected tsetse	Flynn and Sileghem (1994)
1994	CD8+ T-cells and γδ T-cells, including γδ T-cell clones, of infected N'Dama but not Boran cattle proliferate *in vitro* in response to a 100-kDa complex trypanosome invariant antigen	Flynn and Sileghem (1994)
1994	VSG-primed CD4+ T-cells from cattle immunized with purified VSG and adjuvant recognize non-conserved areas of the molecule	McKeever *et al.* (1994a)
1994	Serum from trypanosome-infected Cape buffalo contains a 133-kDa trypanocidal protein	Reduth *et al.* (1994)
1994	The severity of anaemia in *T. vivax*-infected cattle correlates with *ex vivo* production of TNF by monocytes	Sileghem *et al.* (1994)
1995	N'Dama cattle primed by *T. congolense* ITM retain memory T- and B-cells specific for trypanosome antigens in lymph nodes for at least 3 years	Lutje *et al.* (1995)

Continued

Table 4.9. Continued.

Year	Finding	Reference
1995	Depletion of CD8^{+} T-cells from *T. congolense*-infected cattle does not affect parasitaemia or anaemia	Sileghem and Naessens (1995)
1996	*T. congolense*-infected N'Dama cattle have significantly more VSG-specific IgG in blood than Boran cattle during infection	Taylor *et al.* (1996)
1996	Antibody responses against surface-exposed VSG epitopes are similar in *T. congolense*-infected N'Dama and Boran cattle but N'Dama mount higher-titre IgG1 responses against cryptic VSG epitopes	Williams *et al.* (1996)
1997	CD5^{+} B-cells are the main source of antibodies reactive with non-trypanosome antigens in *T. congolense*-infected cattle	Buza *et al.* (1997)
1998	Monocytes from *T. congolense*-infected cattle produce IL-10 but not nitric oxide when stimulated with interferon-γ *in vitro*	Taylor *et al.* (1998)
1999	Serum of *T. congolense*-infected cattle contains polyreactive IgM antibodies	Buza and Naessens (1999)
(2002)	Depletion of CD8^{+} T-cells and WC1^{+} $\gamma\delta$ T-cells from *T. congolense*-infected cattle does not affect parasitaemia or anaemia	Referred to in Naessens *et al.* (2002)
(2002)	Depletion of CD4^{+} T-cells from *T. congolense*-infected Boran cattle reduces VSG-specific antibody responses and results in increased parasitaemia but does not affect antibody responses or parasitaemia in infected N'Dama cattle	Referred to in Naessens *et al.* (2002)
2003	Depletion of CD4^{+} T-cells from *T. congolense*-infected cattle results in significantly reduced size of chancre	Naessens *et al.* (2003b)
2003	Studies in *T. congolense*-infected chimeric Boran/N'Dama twin calves and singletons indicate that the severity of anaemia is a function of haematopoietic tissue whereas the level of parasitaemia is regulated by non-haematopoietic tissue	Naessens *et al.* (2003a)
2006	*T. congolense*-infected N'Dama cattle are more capable of early T-helper 1 T-cell proinflammatory responses than similarly infected Boran	O'Gorman *et al.* (2006)
2009	Gene expression profiling of PBLs from *T. congolense*-infected N'Dama and Boran cattle show a rapid tenfold higher level of expression in the former	O'Gorman *et al.* (2009)

Jan Grootenhuis who, with the support of the Dutch government and some support from Tony Alison, then Director General of ILRAD, established a captive herd of Cape buffalo on the campus of the veterinary school at Kabete, neighbouring ILRAD. These animals, which were also bred in captivity in a tsetse- and trypanosomiasis-free area, were shown by the ILRAD faculty to be highly tolerant to trypanosomiasis induced by tsetse or syringe challenge.

Trypanosome-infected Cape buffalo controlled trypanosome parasitaemia after one or a few parasitaemic waves, whether they were infected by tsetse or by syringe. Thereafter, they suppressed parasitaemia to a cryptic level with few or no signs of disease but carried enough parasites in their blood for several months to infect feeding tsetse. Post-infection, Cape buffalo serum was shown to contain protein of about 133 kDa that lysed all bloodstream-stage African trypanosomes, irrespective of trypanosome species, serodeme or variant antigen type (Reduth *et al.*, 1994). This molecule was later identified as xanthine oxidase (Muranjan *et al.*, 1997). In fact, trypanosomes were killed by hydrogen peroxide, to which they are highly sensitive, generated during catabolism of hypoxanthine and xanthine by xanthine oxidase and facilitated by an infection-induced decline in Cape buffalo blood catalase, which decreased catabolism of the hydrogen peroxide (Wang *et al.*, 1999). The processes controlling expression of xanthine oxidase and catalase in blood plasma proved complex, with no obvious translational component (Wang *et al.*, 2002), and this line of research was discontinued. However, subsequent work by Sam Black and colleagues at the University of Massachusetts and ILRI showed that the

infection-induced decline in Cape buffalo plasma catalase and non-specific killing of trypanosomes was short lived, whereas parasitaemia in the infected Cape buffalo remained cryptic for months, which correlated with the accumulation in blood of IgG antibodies against VSGs of successive antigenic variants (Guirnalda *et al.*, 2007). While correlation does not denote causation, it was observed that trypanosomes harvested from the blood of infected Cape buffalo during cryptic parasitaemia and cultured in the absence of serum antibodies multiplied every 6 h, while those cultured in the presence of the serum antibodies died or barely multiplied. Mechanisms leading to the highly efficient development of protective VSG-specific IgG antibody responses in the infected Cape buffalo were not resolved.

Comparative studies in trypanosome-infected N'Dama and Boran cattle showed that N'Dama cattle developed smaller chancres than those arising in similarly infected Boran cattle (Akol *et al.*, 1986). Chancres are trypanosome-induced inflammatory sites that arise at the site of infected tsetse bites and are populated by metacyclic-derived trypanosomes, neutrophils and subsequently lymphocytes. Their size is a function of metacyclic dose (Dwinger *et al.*, 1987a); hence, their smaller size in tsetse-infected N'Dama compared with Boran cattle is consistent with the possibility that N'Dama better control the growth of metacyclic-derived trypanosomes in the skin. In addition, levels of parasitaemia were significantly lower in infected N'Dama than in infected Boran cattle, suggesting that the N'Dama are better able to control systemic infection. In this regard, infected N'Dama were found to respond to a wider range of trypanosome antigens (Shapiro and Murray, 1982), and to mount high-titre IgG responses against those antigens, than similarly infected trypanosomiasis-susceptible Boran cattle (Taylor *et al.*, 1996, and other references listed in Table 4.9). These studies suggest that the capacity to generate IgG antibodies specific for trypanosome antigens during infection correlates with, and may contribute to, trypanotolerance. Subsequent studies by Williams and colleagues at ILRI (Williams *et al.*, 1996) showed that *T. congolense*-infected N'Dama and Boran cattle develop similar titres and isotypes of antibodies against exposed (i.e. protective) VSG epitopes on intact trypanosomes in blood serum, but the N'Dama develop higher

titres of serum IgG1 antibodies specific for cryptic VSG epitopes, suggesting differential regulation of these responses. In addition, the infected N'Dama cattle were found to develop lower levels of IgM antibodies reactive with non-trypanosome antigens than the infected Boran. These IgM antibodies, which include polyreactive IgMs, are most likely the products of B1 B-cells (Buza *et al.*, 1997), a B-cell type that does not require help from T-cells to mount an antibody response. The skewing of antibody responses in infected N'Dama cattle towards IgG isotypes suggests robust T-cell-dependent immune responses because production of IgG antibodies in response to antigen challenge or infection is, for the most part, dependent on help from CD4^{+} T-cells and the cytokines they produce. Consequently, the elevated levels of trypanosome antigen-specific IgG antibodies in trypanosome-infected N'Dama versus Boran cattle are consistent with the stronger trypanosome antigen-specific T-cell responses that arise in *T. congolense*-infected N'Dama compared with Boran cattle (Flynn *et al.*, 1992). *T. congolense*-derived cysteine protease, called congopain, is among the trypanosome proteins recognized by IgG antibodies produced by infected N'Dama, and there is some evidence that specific immunization with these proteins modulates infection-induced pathology (Authié *et al.*, 2001).

T-cell-specific antibodies developed at ILRAD were used by Jan Naessens at ILRAD/ILRI to determine the impact of T-cell depletion on immune responses to African trypanosomes. Using this procedure, Naessens and colleagues showed that CD8^{+} T-cells play little or no role in defence against the parasites, but CD4^{+} T-cells are required to control (reduce) the size of chancres (Naessens *et al.*, 2003b) consistent with inhibition of trypanosome growth in the skin, (e.g. by T-cell amplified innate immune responses). In addition, in the absence of CD4^{+} T-cells, antibody responses against trypanosome antigens were decreased and levels of parasitaemia increased compared with those arising in intact cattle (discussed by Naessens *et al.*, 2002). These observations indicate that CD4^{+} T-cells play a central role in controlling protective immune responses in trypanosome-infected cattle and hence the severity of trypanosomiasis, a notion that has support from studies conducted in the mouse model of human African trypanosomiasis by John Mansfield and colleagues at the University

of Wisconsin at Madison (Hertz *et al.*, 1998). The specificity of the putative protective CD4^{+} T-cells needs to be established. In this regard, Mansfield and colleagues have shown that CD4^{+} T-cells in infected mice and in mice immunized with intact VSG respond to the variable but not the more conserved epitopes of trypanosome VSGs (Dagenais *et al.*, 2009). This was also found to be the case in cattle by scientists at ILRI (McKeever *et al.*, 1994a). However, although *T. b. rhodesiense*-infected mice do not develop CD4^{+} T-cells that react with conserved VSG epitopes, Mansfield and colleagues have now shown that they can be induced to do so by immunization with conserved VSG C-terminal peptide and, indeed, T-cells in the immunized animals mount recall responses against conserved T-cell epitopes of the peptide upon trypanosome infection. In addition, this procedure results in effective control of trypanosomes in tissues and greatly reduces infection-associated pathology. These important findings bring into play the possibility of developing a VSG-based anti-pathology vaccine, based on assemblies of conserved VSG T-cell epitopes. It is an appealing notion that such immunization would increase control of tsetse-transmitted trypanosomes in the skin as well as in other tissues, which has been proposed as a goal of trypanosome vaccination by Henry Tabel and colleagues at the University of Saskatchewan (Tabel *et al.*, 2013).

Work at ILRAD/ILRI showed that the efficacy of T-cell responses in trypanosome-infected cattle, which might underpin mechanisms of trypanotolerance, may be regulated by immunosuppressive monocytes/macrophages (Flynn *et al.*, 1994), which prevent their expression of the α-chain of the IL-2 (T-cell growth factor) receptor and thus T-cell activation (Sileghem and Flynn, 1992). Immunosuppressive monocytes/macrophages have also been identified in trypanosome-infected mice, although their mechanism of action, which is dependent on prostaglandins and nitric oxide (Mabbott *et al.*, 1995), is distinct from that arising in infected cattle. Species-specific differences in suppressor effector mechanisms do not necessarily rule out similarities in the mechanism of induction of the suppressor cells, but this has not been resolved in either species. However, the VSG glycosylphosphatidylinositol (GPI) has been shown to be a potent activator of monocytes in mice (Magez *et al.*, 1998) and

hence is a candidate pathology-inducing antigen. The GPI glycan is poorly immunogenic, and it remains an intriguing question as to whether GPI glycan-specific antibodies could be induced by appropriate immunization, and if so, whether the antibodies would block infection-associated pathology.

Attempts to dissect mechanisms of trypanotolerance in ruminants and mice at ILRAD/ILRI were paralleled by analysis of quantitative trait loci (QTLs) responsible for the trait. Studies in mouse models at ILRI and the University of Liverpool, UK, identified three QTLs called 'trypanosome immune response' (*Tir*) loci that control survival after infection with *T. congolense*. *Tir1* was identified as the major trypanotolerance QTL with *Pram1* being the most plausible candidate *Tir1* QTL gene (Goodhead *et al.*, 2010). *Pram1* encodes an adaptor protein that regulates adhesion-dependent oxygen intermediate production and degranulation in mature neutrophils (Clemens *et al.*, 2004) and thus aspects of the innate immune response. Three subregions were identified within *Tir3*, with *2B4* being the most plausible *Tir3c* QTL gene. The 2B4 molecule is a receptor expressed by natural killer (NK) cells. It recognizes CD48, which is expressed on and regulates the activation and differentiation of lymphocytes and dendritic and endothelial cells. Ongoing work in the Black laboratory, in Amherst, Massachusetts, shows that splenic NK cells in *T. brucei*-infected mice suppress protective antibody responses by depleting splenic B2 B-cells by cell-mediated cytotoxicity (Frenkel *et al.*, 2016). These NK cells express 2B4, which is encoded by the *Tir3c* candidate QTL gene. NK cells are also implicated in trypanosome pathology in infected cattle, with elevated recruitment/activation of liver NK cells being a common feature of trypanosomiasis in *T. congolense*-infected N'Dama and Boran cattle (Noyes *et al.*, 2011).

Studies of the mechanisms of trypanosomiasis susceptibility and tolerance at ILRAD/ILRI covered a wide field and left a legacy of infection-induced immune response data in cattle but did not identify candidate vaccine antigens or definitively identify resistance genes for introgression into the gene pool of desirable Boran livestock. Nevertheless, this work made some notable contributions to our understanding of trypanosome biology and immunology. It is particularly noteworthy that CD4^{+} T-cells were found

to play a key role in directing host-protective immune responses in the skin and blood of infected cattle. The chapter authors consider that further study of their specificity and mechanism of action is warranted. It is also noteworthy that strong IgG antibody responses directed against numerous trypanosome antigens is a serological signature of infected trypanotolerant compared with trypanosomiasis-susceptible livestock, as it is in mice. It seems likely that this phenotype could be used together with body condition to identify potentially trypanotolerant Boran cattle for selective breeding in herds subjected to ongoing trypanosome and tsetse challenge in trypanosomiasis-endemic areas. With a new focus on priming CD4+ T-cells against conserved VSG epitopes and possibly a straightforward way to select trypanotolerant livestock under natural challenge on the horizon, fundamental studies on AAT, to which ILRAD/ILRI has made many contributions, might yet yield important translational outcomes.

Beyond Nairobi and Kabete: outreach to other diseases and places

The information and analyses found in this section are based on survey results. They include an analysis of the work environment at ILRAD/ILRI and its influence on subsequent work as well as a survey of the tools and techniques applied outside the ILRAD/ILRI campus and the additional diseases to which they were applied. A survey was sent to scientists in the fields of immunology, including basic immunology, immunoparasitology and vaccinology, from the following categories:

- Employed at ILRAD/ILRI as a scientist, post-doctoral fellow, graduate student or technician who subsequently went on for a graduate degree
- Collaborators on the ILRAD/ILRI campus (short term or sabbaticals) in those fields
- Administrators or advisory board members of ILRAD/ILRI
- Opinion leaders in these fields not associated directly with ILRAD/ILRI

Analysis of work environment and subsequent influence

The results of the survey are shown in Fig. 4.3. The first four questions give a reflection of the work environment and how being involved in important work impacted the growth of the scientists (from technicians to senior scientists):

1. I had a productive period working at ILRAD/ILRI.
2. While working at ILRAD/ILRI, I was exposed to areas of science/techniques that I was previously unfamiliar with.
3. Working as part of a team was important to me at ILRAD/ILRI.
4. Working at ILRAD/ILRI helped me to grow as a scientist.

The next question showed whether the person voluntarily engaged in capacity building, as training students was not part of the mandate:
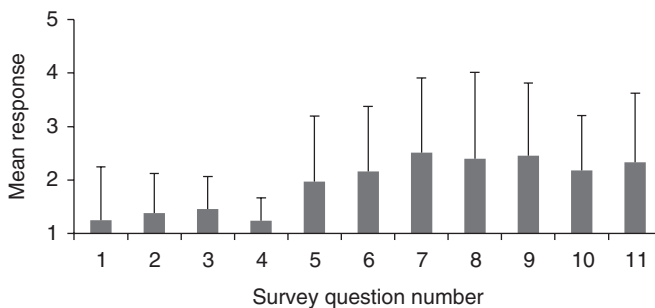
Fig. 4.3. Graph showing the survey responses. A rating of 1 is 'agree completely', 2 is 'strongly agree', 3 is 'moderate agreement', 4 is 'weak agreement' and 5 is 'not at all'. This reflects answers from 35 survey respondents who were employed at ILRAD/ILRI.

5. I trained other scientists/graduate students at ILRAD/ILRI.

The last questions reflect the longevity of the influence the environment had on future scientists:

6. Working at ILRAD/ILRI helped me to obtain my current position.

7. My current research is related to my previous studies at ILRAD/ILRI.

8. I train graduate students/post-doctoral fellows in veterinary immunology/immunoparasitology.

9. My graduate students/post-doctoral fellows plan to work in veterinary immunology/immunoparasitology.

10. I have maintained contact with colleagues from ILRAD/ILRI.

11. Contacts that I made at ILRAD/ILRI have helped me succeed in my career.

There was uniform strong agreement for the first four questions, indicating that the working environment at ILRAD/ILRI was conducive to productive scientific research and scientific growth. The results for question 5 showed that most individuals voluntarily trained other more junior scientists. The answers to questions 6–9 ranged between strong and moderate agreement, indicating that the longevity of the influence was more moderate, suggesting that the bias is still towards continuing in the field engaged in at ILRAD/ILRI (although not irrevocably so) and towards training the future generation of researchers in the field. Answers to questions 10 and 11 suggested that contacts have been maintained among the majority of ILRAD/ILRI alumni and that these have proven fruitful, even after leaving ILRAD/ILRI.

Applications of tools and techniques

Application or transfer of tools such as mAbs and BoLA MHC typing and techniques such as T-cell cloning were used outside of ILRAD/ILRI.

Additional disease research that benefitted

The tools, protocols (techniques) and approaches generated at ILRAD/ILRI were applied to other diseases, and thus research on these diseases benefitted from or was impacted by the work performed at ILRAD/ILRI. These external beneficiaries are summarized in Table 4.10 along with

the geographical placement of the research and/or disease. All are important in world food production.

Conclusions

This chapter has assessed the relevance and impact of ILRAD and ILRI's basic bovine immunology and immunoparasitology as conducted in their trypanosomiasis and theileriosis programmes. Questions were posed and more quantitative measurements were applied, as outlined in the main chapter and in the summary (Table 4.11). The two livestock diseases that were the focus of research at ILRAD and to some extent ILRI still appear, some 40 years later, at or towards the top of priority lists regarding the impediments they raise to raising cattle in sub-Saharan Africa. The investment made at ILRAD/ILRI to develop vaccines for these diseases is a tiny percentage of that invested in research to combat HIV and malaria over the same time period, for which vaccines also do not exist. According to one early ILRAD research participant, Bruno Goddeeris, the tools developed and research undertaken 'gave worldwide a tremendous push in veterinary immunology research and made veterinary immunoparasitology known to the medical world'. This is validated by Fidel Zavala (2015, personal communication), a leading malaria researcher at John Hopkins University, who indicated that ILRAD research on theileriosis in cattle showed the way for studies on human malarial vaccine research that continue to this day.

Immunological research at ILRAD/ILRI has had a substantial impact worldwide. The right approach was taken and appropriate tools were developed to allow further understanding of the ruminant immune system in support of vaccine development and efficacy testing according to the mandate of ILRAD. Moreover, the research team that undertook these studies was reflective and creative in generating a vast number of tools to study the bovine immune system using the most modern technologies and following closely the discoveries informing the fundamentals of the murine and human immune systems (Table 4.12). In addition, in some cases knowledge about the components and function of the bovine system preceded that in either mice or humans.

Table 4.10. Diseases not targeted at ILRAD/ILRI but benefiting from tools and techniques and approaches developed there; unless stated, they are diseases of cattle.

Disease/causative organism	Country or region (of research or disease location)	Scientist involved
African swine fever (pigs)	USA	Mwangi
Anaplasmosis	USA	McGuire, Brown
Avian pathogenic *Escherichia coli* infection (poultry)	Belgium	Goddeeris
Bluetongue virus (sheep)	Canada	Ellis
Bovine babesiosis	USA	McGuire, Brown
Bovine herpes virus (sheep)	USA	De Martini
Bovine herpes virus-1 (cattle)	Canada	Ellis
Bovine respiratory syncytial virus	Canada	Ellis
Bovine viral diarrhoea virus	UK, USA	Graham, Mwangi
Brucella abortus and *B. melitensis* (cattle and goats)	USA, India, Israel, Brazil	Baldwin, Splitter
Middle East respiratory syndrome coronavirus (camel)	East Africa	Jores
Caseous lymphadenitis (sheep)	Canada	Ellis
Chlamydia abortus (sheep)	Scotland	Rocchi
Contagious bovine pleuropneumonia	Kenya	Jores, Naessens
Cowdriosis (heartwater)	USA, Zimbabwe, South Africa	Barbett, Mahan, McGuire
Fasciola hepatica	UK	Williams
Foot-and-mouth disease virus	Scotland	Morrison
Haemonchus contortus	USA, Scotland	McGuire, Ballingal
Histomonas spp.	Belgium	Goddeeris
Leishmania spp. (humans)	Canada, USA	Pearson
Leptospira interrogans serovar Hardjo	USA	Baldwin
Malignant catarrhal fever	USA, Europe, South America, Africa	De Martini
Mycobacterium avium paratuberculosis (cattle and sheep)	UK, USA	Glass, Shields, Davis, Ballingal
Mycobacterium bovis	UK, Italy, USA	Glass, Shields, Rocchi, Baldwin
Nematodes	Australia, UK	Emery
Neospora caninum	UK, Italy	Williams, Rocchi
Newcastle disease virus (diagnostic test on same principle as the trypanosome test) (poultry)	Austria	Dwinger
Ostertagia spp.	Belgium	Goddeeris
Porcine diarrhoea and oedema disease (pigs)	Belgium, Cuba, Vietnam	Goddeeris
Pulmonary adenocarcinoma	Scotland	Ballingal
Retroviruses (pulmonary carcinoma) (sheep)	USA	De Martini
Small ruminant lentiviruses	USA, Europe, South America, Africa	De Martini
Streptococcus agalactiae (camels)	East Africa	Jores
Theileria annulata	UK, India, Turkey, China	Glass
Theileria orientalis (buffalo)	Belgium, Vietnam, Indonesia	Goddeeris
Trypanosoma equiperdum (dourine) (horses)	Belgium, Ethiopia, Switzerland	Brun, Goddeeris
Trypanosoma evansi (horses)	Switzerland	Brun
Trypanosomiasis (trypanosome diagnostic tests)	Austria	Dwinger
Trypanosomiasis (camels)	East Africa	Masake

Table 4.11. Answers to questions about impact of immunology research.

Quality of research	Overall	Basic bovine immunology	*T. parva*	Trypanosomes in cattle	Trypanosomes in mice
Did what was found by the research and assumed to be 'true' at the time of formal publication remain true for years to come?	Yes	Yes	Yes	Yes	Yes
Was the research built upon or taken up by other scientists (i.e. influenced others)	Yes	Yes	Yes	Field analysis of parasitaemia and anaemia continue, but little additional immunological work has been done	Yes
Were the right things being done regarding the research direction according to the mandate of ILRAD/ILRI?	Yes	Yes	Yes	Yes, although research on $CD4^+$ T-cell responses to the parasites may have been stopped prematurely	Additional effort should have been directed at the regulation and specificity of $CD4^+$ T-cell responses; however, this was effectively followed up by the Mansfield laboratory (USA)
Was the team successful, i.e. was the research reflective and creative?	Yes	Yes	Yes	In hindsight, it can be seen that some avenues of research remain open	In hindsight, it can be seen that some avenues of research remain open

Table 4.12. Assessment of immunology and immunoparasitology. (Data compiled from surveys.)

Manuscript questions	Assessment
Was there a substantive body of work that showed the step-by-step progression of knowledge in addition to key papers in top-tier journals?	Yes, ~20 peer-reviewed manuscripts per year
Were the results published in a timely manner?	Yes
Citation indices	More than 50% had >25 citations
i10 index (ten or more citations)	77% of peer-reviewed manuscripts met this criterion
Journal impact factor of top-cited manuscripts	Moderate-level journals for >95% of manuscripts; 2% in top-tier journals
Quality of staff:	
As a group, were the scientists who conducted the research at ILRAD/ILRI highly respected and accomplished (*h*-index)?	Yes – equal to their peers relative to career length
Did the experience at ILRAD/ILRI influence the field of research that these scientists subsequently engaged in?	>30% continued to work directly on the topics researched at ILRAD; <5% do something totally unrelated

Continued

Table 4.12. Continued.

Manuscript questions	Assessment
Was the knowledge gained at ILRAD/ILRI and the tools generated expanded or continued to be used to evaluate other important infectious diseases of ruminants that affect food safety?	Yes
Impact:	
Commercialization of products	mAbs in Europe and North America, ITM vaccine in Africa
Other disseminated tools not commercialized	BoLA typing
	Simple point-of-care technique for detecting African trypanosomes – the most sensitive parasitological technique available for animals, widely used throughout Africa
Did their availability change the landscape?	Yes, for both research and the vaccine

The Future

The immunology and immunoparasitology research at ILRAD and later ILRI had high scientific and technical impacts on a very limited budget compared with spending on human diseases of similar immunological complexity. Output from this research was primarily publications and mAbs specific for bovine leukocytes and immunoglobulins, which are still being used in many laboratories throughout the world. Despite its academic/scientific successes, this immunology/immunoparasitology research did not affect the incidence or economic impact of theileriosis or trypanosomiasis in any substantial way, other than the benefits that have accrued from the ITM method of immunizing cattle against ECF. However, scientific opinion believes that the fundamental research on bovine immunology and the immunoparasitology of theileriosis and trypanosomiasis carried out at ILRAD/ILRI will ultimately have significant development outcomes beyond those it has already had on scientific capacity development.

Future research priorities should be as follows:

- In addition to current research aimed at developing a subunit vaccine for ECF based on an assembly of immunodominant *T. parva* T-cell epitopes, identify antigens that are shared among *T. parva* and *T. parva lawrencei* strains and that stimulate αβ and γδ T-cells for inclusion in the subunit vaccine.
- Identify trypanosomiasis-tolerant individuals in herds of Boran cattle subjected to natural trypanosome challenge, based on the serum signature of IgG antibodies reactive with trypanosome polypeptides, body condition and blood packed cell volume, and determine whether these traits can be improved by selective breeding.
- Determine whether immunization of cattle with conserved VSG components will enhance control of parasites in the skin and tissues and reduce infection-associated immunopathology, as discussed by Black and Mansfield (2016).

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5 Veterinary Epidemiology at ILRAD and ILRI, 1987–2018

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Contents

Executive Summary

The problem

The effectiveness of detecting and controlling animal diseases is dependent on a solid understanding of their dynamics and impacts through scientifically sound qualitative and quantitative methods by trained personnel. Veterinary epidemiology is the systematic characterization and explanation of patterns of animal diseases and the use of this information in the resolution of animal and human health problems. This discipline exploits an increasing inventory of tools for effective data gathering, assembly and analysis, modelling and reporting, all targeted at decision making by producers, governments and international development agencies. Furthermore, the integration of epidemiology with agricultural economics and other social sciences provides a uniquely effective tool for evaluating disease as a constraint to broader development agendas, for assessing the absolute and relative economic importance of diseases, and for evaluating the costs and benefits of alternative intervention options, at different levels ranging from farm to national to global. Furthermore, veterinary epidemiological and economic impact sciences are key components in a number of the global grand challenges relating to disease control, climate change and food security.

ILRI's role in the global context

The International Livestock Research Institute (ILRI) and its predecessor, the International Laboratory for Research on Animal Diseases (ILRAD), have played an important international role in identifying and developing epidemiological tools for the investigation and resolution of animal health constraints to livestock production. When the group was formed in 1987, it was charged with addressing the two diseases considered the priority in Africa, namely East Coast fever (ECF) and trypanosomiasis, to support the development of vaccines against these two diseases, which was the mandate of ILRAD.

Following the transition from ILRAD to ILRI, the institution has been a leader in exploring new epidemiological approaches, and in widening the disciplinary spectrum of epidemiological investigations. However, arguably most important

of all, ILRI has played a facilitating role in collaborating with countries, institutions and organizations in Africa, Asia and Latin America to respond to requests for both short- and long-term partnerships and support at international, regional, national and local levels, and in extensive capacity building in epidemiological tools, techniques and approaches.

Initially, ILRAD and ILRI focused almost exclusively on the dynamics and impact of tick-borne pathogens of livestock in Africa, but during the 1990s, the geographical focus, disciplinary make-up and range of tools used broadened substantially, tackling multiple diseases in Africa, Asia and Latin America and building capacity in epidemiological and economic impact assessment techniques.

For a period of 15 years (1987–2002) ILRAD/ILRI's epidemiology and socio-economic impact assessment capacity was assembled in one team serving a range of institutional and externally commissioned needs and was recognized internationally for its focus of health issues affecting development and poverty reduction. Through a major study of animal health research priorities commissioned by UK Department for International Development (DFID), the team made a substantial contribution to the design of ILRI's new strategy, which emerged in 2002, and to the poverty-focused agendas of other organizations such as the Food and Agriculture Organization of the United Nations (FAO) and the Wellcome Trust.

Impact of ILRI's research

Veterinary epidemiological and economic impact sciences at ILRAD and ILRI have left a valuable legacy of publications in peer-reviewed journals, strategic reports and policy documents, as well as methodologies and approaches that have been applied in virtually all corners of the world, and many trained epidemiologists now serving different institutional needs in Africa, Asia, Latin America, Europe and Australia.

The range of diseases subject to epidemiological and economics research has been wide, and included the viral infections rinderpest, foot-and-mouth disease (FMD), Rift Valley fever (RVF) and highly pathogenic avian influenza (HPAI), and the context of impact assessments has been applied to trade, livelihoods and poverty reduction. ILRI has worked with a multitude of partners around the world and has contributed substantially to research and development networking in many areas of animal health, including tick-borne diseases, rabies, and the fundamental tools of epidemiology and socio-economic impacts.

Scientific impacts

The group brought the science of structured epidemiological analysis to the institute in methodological terms (particularly in observational field studies), and also expanded the disciplinary contributions to include social, economic and environmental considerations in the analysis of disease impacts, and the impacts of disease control interventions.

Economic impact assessment

Most of the earlier economic impact assessments carried out by ILRAD and ILRI were disease specific, such as on ECF, rinderpest and FMD, and built on evidence derived from underlying epidemiological data. Economic impact assessments gained increasing momentum as ILRI's mandate broadened. The epidemiology group concluded that no longer should studies of the economics of diseases of production animals be limited to animal scientists seeking the collaboration of agricultural economists to affix prices to estimated productivity losses, and the new discipline of animal health economics emerged in which the quality of economic evaluations depended on integrating the products of good epidemiological studies into economic frameworks.

In 1998, the World Organisation for Animal Health (Office International des Epizooties, or OIE) approached ILRI to compile and edit a special edition of the OIE *Scientific and Technical Review on Animal Health Economics*, which comprised nine chapters on various topics such as the demands of economic impact knowledge, and seven case study chapters addressing specific diseases and different scenarios affecting the validity of the economic studies.

Developmental impacts

While we cannot ascribe higher productivity to ILRI's veterinary epidemiology research per se, the research has increased our understanding of infection dynamics, which has influenced disease control and the role of interventions in different settings.

Capacity development

Over the years, epidemiology has gone through both administrative and locality changes, seen as a unified entity for 15 years, and later under the new ILRI strategy it was fragmented and diminished. However, during the 15-year period from 1987 to 2002, the institution had supported approximately 15 MSc students and 37 PhD students with approximately 50 scientists predominantly from African countries. In addition, there have been several postdoctoral fellows who have been trained. As most of the epidemiology is conducted under a specific disease, it is difficult to determine how many more have been trained to date.

Partnerships

ILRI has worked with a multitude of partners around the world and contributed substantially to research and development networking in many areas of animal health, including tick-borne diseases, rabies and the fundamental tools of epidemiology and socio-economic impacts. In 2007, the Participatory Epidemiology Network for Animal and Public Health (PENAPH) was developed to connect groups and individuals who apply participatory epidemiology in controlling emerging and existing diseases.

Impacts on human resources capacity in veterinary epidemiology

During the 15-year period from 1987 to 2002 a substantial number of MSc and PhD students were trained through incorporation into ILRI's research activities; these were predominantly from African countries.

Impacts on national animal health departments and services

The epidemiology group provided a role model of investigative problem solving, which was picked up, copied and adopted by some institutions in African countries.

Impacts on animal health constraints in developing countries

ILRI's epidemiology research has made substantial contributions to our understanding and control of ECF and trypanosomiasis in Africa, to the preparedness and responses to RVF in eastern Africa, to a greater understanding of the economic impact of rinderpest in Africa and of FMD in Africa, Asia and Latin America, and to regional understanding of the drivers of rabies control. More recently, epidemiology research at ILRI has contributed substantially to our understanding of food safety risks in formal and informal markets and to the dynamics and risks of zoonotic diseases. The research has also contributed to the global understanding of the importance of these and other diseases to African livestock systems and to the particular animal health constraints facing the poorer sectors of Africa's livestock-engaged communities.

Impacts on ILRI's research and strategy

During the days of ILRAD, the epidemiology and socio-economic programme had little or no impact on ILRAD's research and strategy; rather, it was seen as providing evidence justifying the existence of the laboratory-based vaccine research for the two target haemoparasitic diseases. Nevertheless, after ILRI's birth in 1995, the programme played an important role in providing impact assessment services, which progressively enhanced the engagement of the institution with different national, regional and donor clients. This situation changed dramatically in 2002 following the publication of the DFID-commissioned study on animal research priorities for poverty reduction. The matrix of three 'pathways out of poverty' provided the framework of the new institutional thematic structure, not just for animal health research but also for ILRI's entire programme.

Introduction

Veterinary epidemiology is the systematic characterization and explanation of patterns of animal diseases and, importantly, the use of this information in the resolution of animal and human health problems. It is a subject that exploits an increasing inventory of tools for effective data gathering, assembly and analysis, targeted at decision making in the field of animal disease control and sustainable livestock enterprise development. The integration of epidemiology with agricultural economics and other social sciences provides a uniquely effective tool for evaluating

disease as a constraint to broader development agendas, for assessing the absolute and relative economic importance of diseases, and for evaluating the costs and benefits of alternative intervention options, at different levels ranging from farm to national to global. ILRI and its predecessor, ILRAD, have played an important international role in exploiting epidemiological tools for the investigation and resolution of animal health constraints to livestock production and poverty reduction in many regions of the developing world. Furthermore, ILRI has been a leader in exploring new epidemiological approaches, and in widening the disciplinary spectrum of epidemiological investigations. However, arguably most important of all, ILRI has played a facilitating role in collaborating with countries, institutions and organizations in Africa, Asia and Latin America in response to requests for both short- and long-term partnership and support at international, regional, national and local levels, and in extensive capacity building in epidemiological tools, techniques and approaches.

The introduction of veterinary epidemiology and economics at ILRAD

The fundamental belief at the creation of ILRAD in 1974 was that vaccines against ECF and trypanosomiasis were the mandate of ILRAD. The evidence available to answer these questions at the time was derived almost entirely from African veterinary services and diagnostic laboratories, which had, for the previous 60 or so years, been servicing livestock production enterprises of the colonial powers. There were little if any economic data to quantify the impacts of these diseases, even in commercial systems, and the potential returns from vaccines.

ILRAD alone among the international agricultural research centres of CGIAR had a unique mandate to carry out basic research and as such undertook very little of the technology transfer functions. Pressure progressively increased from partners to quantify the impacts of these two diseases on African agriculture in order to better justify the scientific investment in the study of these two diseases.

Thus, it was some 13 years after the establishment of ILRAD that veterinary epidemiology was introduced into the institute. The Rockefeller Foundation initially for 3 years (and subse-

quently extended for a further 2 years) supported what became the Epidemiology and Socioeconomics Programme. The group was joined in 1992 by an ecologist to explore the environmental impacts of trypanosomiasis control (Reid *et al.*, 1995). The team expanded in the late 1990s to include another staff epidemiologist and two postdoctoral epidemiologists.

The group rapidly laid out a work plan, beginning with the establishment of databases on African production systems at risk from the two diseases and on methodologies for determining their impact. This challenge led to the realization that disease incidence and prevalence data in Africa were scarce and unreliable, notably on the structure and ownership of the livestock populations at risk. The need for structured quantitative epidemiology capacity emerged, which led to a sustained programme of data assembly, digital data documentation and assembly, the development of modelling techniques and, of course, the gathering of field data.

Field studies in Kenya

The first field site of diverse ecosystems and disease impacts was in Kilifi District on the Kenyan coast. A collaborative programme between the International Livestock Centre for Africa (ILCA) and the Kenya Agricultural Research Institute (KARI) was established in 1988 at KARI's Mtwapa Regional Research Centre, near Mombasa.

The smallholder dairy group was setting up a broad study on the constraints to smallholder milk production in the coastal lowlands of Kenya and how extension services covering the areas of feed and health could be improved. Specifically, the study estimated the demand for milk and dairy products, identified technical and policy constraints on production in mixed smallholder farming systems, evaluated dairy cattle breed resources, estimated disease risk to dairy cattle and tested disease control methods, and developed feeding systems appropriate to smallholder dairy production systems.

The ILRAD epidemiology team provided support to the studies on the epidemiology and impact of ECF in the form of design and analysis of studies led by KARI staff. The challenge was a total lack of data on ECF occurrence, and so a series of cross-sectional studies was set up. Key was understanding the link between infection preva-

lence, as measured by antibodies to *Theileria parva* in an indirect fluorescent antibody test, and disease incidence. ILRAD's entry into this research area was at a time when infection prevalence, as measured by antibody prevalence, had not been correlated with disease incidence, and, where prevalence studies had been undertaken, they had often been reported on the basis of administrative boundaries such as the FAO's 1975 study in Kenya (Kariuki, 1988).

In 1983, the *Farm Management Handbook of Kenya* was published (Jaetzold and Schmidt, 1983), which provided a unique landscape synthesis of Kenya's agricultural environment, aggregating a number of variables into a kaleidoscope of colours representing the suitability for different crops and agricultural enterprises. With the knowledge that the epidemiology and impacts of ECF were highly dependent on environmental suitability for the main vector tick, *Rhipicephalus appendiculatus* (the brown ear tick), the zone boundaries provided a new and useful sampling frame that had previously been unexploited.

A series of studies was set up in coastal Kenya to determine the prevalence and incidence of ECF and the other tick-borne infections such as anaplasmosis and babesiosis, and to evaluate the role of immunization against ECF using the infection-and-treatment method (ITM). The studies provided an initial quantitative assessment of antibody prevalence to the spectrum of tick-borne disease parasites in order to assess the epidemiological status of these infections in both indigenous Zebu cattle kept, and in improved dairy cattle in three different agroecological zones (AEZs) (Deem *et al.*, 1993; Maloo *et al.*, 2001a,b,c).

The coast work provided an opportunity to engage at the front line with national partners and to explore impact study design; it also illustrated the need to disaggregate factors affecting ECF epidemiology and impact. However, as the coastal systems were not fully representative of the intensifying livestock systems in the temperate highland areas of eastern Africa, additional studies were set up. The first was in Uasin Gishu, where larger-scale dairy and beef production was rapidly being replaced by small-scale commercial dairy enterprises (Mukhebi *et al.*, 1992a). This work coincided with the introduction of the discipline of human nutrition into the impact equation (Curry *et al.*, 1996).

In 1992, the focus of the ECF epidemiology studies moved to the central highlands of Kenya,

first to Kiambu District, with a 1-year study of the dynamics of theileriosis (O'Callaghan *et al.*, 1998). This was followed in 1994 by investigations in the neighbouring Muranga District, which hosted a range of livestock production systems in diverse AEZs. There were five distinct AEZs within Muranga District, giving the opportunity to investigate the influence of a range of climate, livestock breeds and farming practice variables on ECF dynamics. The work started with a cross-sectional serological study on 750 smallholder dairy farms in Muranga District, selected in a stratified random sample (Gitau *et al.*, 1997), which showed the markedly different prevalences of *T. parva* infection across AEZs. The area was typical of the highland areas of eastern Africa in which the process of smallholder dairy intensification was gaining momentum. The investigation continued with a study that related prevalence with incidence, case morbidity and case mortality (Gitau *et al.*, 1999), and with a study of how these infections affected weight gain in calves (Gitau *et al.*, 2001). The work concluded with a synthesis of the implications of the research on disease risk and on the potential role of vaccination against ECF (Gitau *et al.*, 2000).

The synthesis concluded that ECF risk is low in predominately zero-grazing areas. Thus, tick control or future vaccination programmes will probably only be used by very risk-averse farmers who wish to protect their highly valuable cows from the low risk of ECF mortality. In contrast, for open grazing systems, particularly in the lower-elevation upper-midland 4 (UM4) zone, the risk of ECF is much greater and probably much more variable. In this system, there will be much more substantial direct impact of ECF control programmes. In areas where ECF control will be through vaccination, irrespective of the grazing management system, there will be a greater likelihood of the development of endemic stability. Increased vaccination coverage to enhance the development of herd immunity, combined with modification of acaricide control strategies to allow sufficient challenge, seemed to offer the best prospect for establishing endemic stability. It was quite clear from these studies that attention needs to be paid to the variation in ECF risk, both spatially (as ECF risk changes over relatively short geographical distances) and temporally (seasonally), to develop optimal combinations of

control measures for ECF under different ecological and grazing situations.

It was in 1997 that the ECF epidemiology work expanded into other parts of Kenya, following the submission of a research proposal to the International Fund for Agricultural Development (IFAD). The revised proposal strengthened the epidemiology and impact assessment components and placed them in an *ex ante* context. Vaccine efficacy trials were limited to two sites in Kenya, while the impact assessment broadened into new areas. The impact assessment studies included an evaluation of mechanisms for optimal delivery, adoption and impact of the p67 vaccine (p67 is the major surface protein of *T. parva* sporozoites), determining the impact of a recombinant vaccine on a series of productivity and economic indicators in smallholder dairy systems. The project also included key laboratory studies to support the field studies and disease-modelling work (Ochanda *et al.*, 1998).

Table 5.1 outlines the various studies undertaken in Kenya, illustrating the differences in impacts by region, AEZ and grazing management.

There were a wide variety of products emerging from the IFAD study, ranging from Technical Advisory Notes such as 'Assessing farmer preferences for the provision of livestock health services' to international presentations (Leneman *et al.*, 2000; Kiara *et al.*, 2000, 2003; Ndung'u *et al.*, 2000, 2003; Wanyangu *et al.*, 2000; Di Giulio *et al.*, 2003, Karimi *et al.*, 2003; O'Callaghan *et al.*, 2003; Diaz *et al.*, 2003) to peer-reviewed papers in scientific journals.

In a review article of the ECF work (Perry and Young, 1995), it was postulated that the degree of mortality and production losses from *T. parva* infections were dependent on four key factors, which all exert their influence as a gradient (or cline) of effects:

- The ecological cline, in which the climatic suitability for the tick vector varies with rainfall and altitude; the ecological cline gradient can be affected by differences in vegetation cover.
- The host genetic cline, in which purebred taurine cattle bred under tick-free conditions are highly susceptible to disease, and taurine cattle bred in tick-borne infection endemic areas and some Zebu breeds (such as Boran) bred in tick-free conditions are moderately susceptible, but Zebu cattle bred in tick-borne infection endemic areas are of low susceptibility to disease.
- The feeding management cline, which controls the exposure of hosts to the ecological conditions; this can range from no influence, where cattle are herded on natural pasture, to complete influence, where cattle are kept on concrete and fed on cultivated forage grasses, as in the smallholder zero-grazing units of eastern Africa.
- The tick control cline, where tick control ranges from highly effective, regular application through to no tick control at all.

Tick-borne disease dynamics in eastern and southern Africa

At the start of these intense epidemiological investigations in Kenya, a regional meeting on tick-borne diseases was held in Lilongwe, Malawi, in 1988 (Dolan, 1989), which provided

Table 5.1. ECF risks by region, AEZ and grazing management.

Study	O'Callaghan (1998)		Gitau (1998)		Maloo (1993)	
Incidence rate type	Calves (<1 year of age); incidence density		Calves (≤6 months of age); cumulative incidence		Calves (<1 year of age); incidence density	
Grazing management	Zero grazing	Pasture	Zero grazing	Pasture	Zero grazing	Pasture
Number of animals (*n*)	93	108	134	91	38	50
ECF morbidity rate (%)	5.5	10.9	11.8	49	36.4	68.8
ECF mortality rate (%)	0	2.2	1.7	20.6	20.8	49.7
Case-fatality proportion (%)	0	25	28.6	38.1	57.1	72.2
Seroconversion rate (%)	41.4	56.5	58.4	74	0	0
Morbidity proportion (%)	13.3	7.7	12.2	36.1	0	0

an opportunity for sharing of information and understanding on theileriosis throughout the eastern and southern African regions, and where it became apparent that there were significant differences in the disease epidemiology between the eastern and southern regions. The Lilongwe meeting led to a textbook on theileriosis, *The Epidemiology of Theileriosis in Africa* (Norval *et al.*, 1992b). The book was published by Academic Press, with ILRAD supporting the time contributions of the three authors and the preparation of camera-ready copy, and the book became the reference point for all those working on control of the disease. This book remains the only textbook on theileriosis, a product of ILRAD's epidemiology team of substantial impact.

The disease called ECF was said to have been eradicated in southern Africa as a result of an intensive dipping programme, with the last case occurring in Swaziland in 1960. Nevertheless, *T. parva* infections persist, but with the official eradication declared, the names of theileriosis and corridor disease have been used to describe disease outbreaks. This curious confrontation of science and officialdom of disease and parasite nomenclature was reviewed in an article entitled 'The naming game: the changing fortunes of East Coast fever and *Theileria parva*' (Perry and Young, 1993). It is encouraging how these studies have led to our current understanding of theileriosis epidemiology, as illustrated by a recent review by Gachohi *et al.* (2012).

The heartwater studies in Zimbabwe

Through funding from the US Agency for International Development (USAID), a 5-year project on the epidemiology and impact of another important tick-borne disease of livestock in Africa, heartwater (also known as ehrlichiosis; caused by *Ehrlichia ruminantium* infection, formerly *Cowdria ruminantium*) was initiated in 1994[1]. This work subsequently received ILRI's award (and ILRI's nomination for the CGIAR Chairman's Award) for Scientific Partnership, 2000.

The collaborative research in epidemiology and economics between the Veterinary Research Laboratory (VRL) in Harare, the Heartwater Research Project of the Southern African Development Community (SADC), the Universities of Florida (USA) and Warwick (UK), and ILRI determined and quantified the infection dynamics of heartwater in the major production systems and AEZs of Zimbabwe, the economic impact of the disease, and the technical and economic viability of different control interventions, with particular emphasis on the role of inactivated vaccines. The project outputs were as follows:

- Distributions of tick vectors in Zimbabwe were defined and documented. A national survey of 3000 collections determined that *Amblyomma hebraeum* is the dominant tick in the south and that it had spread into central and eastern areas of the high veld. The survey also found that *Amblyomma variegatum* is present mainly in the north-west but that it is also found in central and eastern parts of the high veld, with some overlap of the two species (Norval *et al.*, 1994; Peter *et al.*, 1998, 1999).

- Spread of heartwater was documented and quantified, and factors affecting the spread were determined. *A. hebraeum* had spread far north due largely to movement of cattle (and some wildlife) to the high veld. A gradual reduction in acaricide use, particularly in the communal lands, contributed to the expanding distribution of this tick (Norval *et al.*, 1992a).

- Infection dynamics in the tick vector and mammalian hosts were determined and quantified. Endemic stability, in which population immunity develops, was found to be widespread but not present where acaricides were used intensively to interrupt natural infection. These results suggest that use of inactivated vaccines in many circumstances will allow a reduction in acaricide use with a transition to endemic stability and subsequent natural infection boosting the vaccinal immunity.

- The impact of endemic stability, and carrier infections, on sheep productivity was determined. Studies in sheep revealed that creating endemic stability artificially with vaccines does not harm the health and reproductive performance of breeding ewes or the growth and milk consumption of their lambs (Martinez *et al.*, 1999a,b).

- Infection dynamics models were developed using data generated by the research. A mathematical model of the infection dynamics of the heartwater pathogen, *E. ruminantium*, showed that endemic stability is due principally to the protection of calves and lambs against disease by innate or maternally derived factors (O'Callaghan *et al.*, 1998).

- Economics of livestock production in heartwater areas was determined. Both large- and small-scale livestock production could be increased significantly with more, and more cost-effective, heartwater control methods (Perry *et al.*, 1998; Chamboko *et al.*, 1999).

- The economic impact of heartwater, and of future vaccine use, was determined. The annual total direct losses in Zimbabwe (acaricide costs, milk losses, treatment costs) from heartwater were estimated to be US$5.6 million. A new inactivated vaccine was predicted to have a benefit:cost ratio of 2.4:1 in the communal sectors and 7.6:1 in the commercial sectors (Mukhebi *et al.*, 1999).

- The efficacy of future vaccine use was evaluated in epidemiological models. The timing of vaccination and frequency of revaccination were shown to have greater effects on population protection than vaccine efficacy. In the face of an epidemic, the frequency of administration is critical to a vaccine's success. Vaccines of relatively low efficacy (about 50%) can significantly reduce livestock morbidity and mortality if administered with appropriate frequency (O'Callaghan *et al.*, 1999).

- The economic impact of the disease and of its control through vaccines was evaluated and quantified in the countries of the SADC region. In total, 31 million cattle and 28 million small ruminants were found to be at risk of heartwater in the nine SADC countries affected: Angola, Botswana, Malawi, Mozambique, South Africa, Swaziland, Tanzania, Zambia and Zimbabwe. The total annual losses were estimated at US$47.6 million, of which 61% were production losses and 39% control costs. New inactivated heartwater vaccines could yield benefit:cost ratios of up to 4.4:1, particularly in commercial and emerging market-orientated systems of the region (Minjauw *et al.*, 1998, 2000).

The successes of this collaborative project were considerable, with all objectives met and all findings published within a period of 5 years. The results of the project have given scientists a sound understanding of the factors influencing the distribution of tick vectors, and the infection dynamics and impacts of the disease in different AEZs and production systems, and predictions of the technical and economic impacts of control with a new generation of inactivated vaccines now emerging. The results generated have strong implications for heartwater control in other countries of Africa. Design and modelling features of the study have been used in studies of other tick-borne livestock diseases.

Apart from its technical achievements, the project boosted scientific capacity, particularly in Zimbabwe, through postgraduate training for national scientists. Project members produced 23 papers in peer-reviewed journals, 15 of which were authored by VRL scientists. Project staff produced another 36 publications, including 22 presentations at scientific meetings and ten articles in the project newsletter.

Economic impact assessments of tick-borne diseases

The first opportunity to undertake an economic impact assessment came in the late 1980s with the ILRAD/KARI partnership on the Kenya coast, where an immunization trial was being carried out using ITM to control ECF. Adrian Mukhebi showed greater profitability in immunized cattle compared with unimmunized, through lower mortality and higher weight gains (Mukhebi *et al.*, 1989). This was a solid first piece of evidence, although it was compiled on a state-run Agricultural Development Corporation beef ranch. The authors commented that 'these results and the recommendation apply to one immunization trial on one farm which was under an atypical management system for the region'.

Building on the potential for ITM, Mukhebi *et al.* (1990) then dissected the complicated vaccine preparation process and calculated the costs of establishing a vaccine production facility (at a hypothetical site in Kenya but using a methodology generic to other countries).

These initial forays into the economics of ECF and its control led to an Africa-wide

assessment, presenting the estimated total costs of ECF in affected countries in 1989 as US$168 million (Mukhebi *et al.*, 1992b). The authors calculated benefit:cost ratios for the control of ECF through vaccination of between 8.9 and 16.8, depending on the intensity of post-vaccination acaricide use. The authors warned that 'the input values and hence results presented in this paper are dependent upon sparse and inadequate data and are largely illustrative of the methodology and data needs. Nevertheless, they provide an estimated magnitude of the economic losses attributed to theileriosis, and the economics of its control by the infection and treatment method in the infected region'.

A series of further economic studies of ECF was undertaken by PhD student Hezron Nyangito, who, in a partnership with the Department of Agricultural Economics at Texas A&M University, used a whole-farm simulation model to estimate the financial and economic pay-offs from the use of ITM vaccination, drawing on data collected from Uasin Gishu, Kenya (Nyangito *et al.*, 1994, 1995, 1996).

The study by Mukhebi *et al.* (1999) provided one of the first attempts to truly integrate epidemiology and economics models to predict future economic impacts of different control scenarios under a set of epidemiological scenarios.

Tick and tick-borne disease distribution modelling

The need to understand the geographical scale of impact of both ECF and trypanosomiasis very quickly led into the area of modelling, primarily of the vectors but also to a degree of the disease itself. In the absence of high-quality field data on *R. appendiculatus* distribution, the group first sought data on the key drivers of climate and vegetation, and in late 1987 and early 1988, a contract was drawn up between ILRAD and the Global Resource Information Database (GRID) group led by Harvey Croze at the United Nations Environment Programme (UNEP) in Nairobi. This group was using geographical information systems (GIS) for various African continent-wide

assessments, running the software ARC/INFO from the Environmental Systems Research Institute (ESRI). A memorandum of understanding was set up between ILRAD and UNEP, and two UNEP scientists contributed data assembly and analysis time over the following 18 months, before the epidemiology and socio-economics group at ILRAD obtained core funds to establish its own GIS capacity, led by Russ Kruska. Research in the late 1980s and early 1990s centred on vector-borne disease distribution and impact studies; the group also contributed to the establishment in 1992 of the UNEP/CGIAR partnership on the development of digital datasets for research on a wide range of topics including natural resources, ecology, environment and socio-economic factors.

Efforts to model the potential distribution of *R. appendiculatus* were assisted by two key inputs. The first was the database on tick field samplings assembled by Jane Walker. The second was a climate matching model, Climex, developed by Robert Sutherst, with parameters for the conditions favoured by the brown ear tick (among others). Instead of the model being run on climate data for any given location, it was run for the whole of Africa, in each of the 25 km² pixel cells of an interpolated climate surface for the continent. The results plotted the potential distribution of *R. appendiculatus* (Lessard *et al.*, 1990; Perry *et al.*, 1990, 1991), but when compared with the database of Jane Walker and others of where the tick had been recorded, the potential distribution exceeded the historical records, suggesting that Climex did not tell the whole story. This finding stimulated interest in other predictive modelling approaches to estimate tick distribution (Randolph, 1993), in which much closer attention was paid to the climatic requirements of all three instars of the tick, which eventually led to a more biologically sound spatial prediction platform (Randolph and Rogers, 1997).

In a follow-up case study of predicting outbreaks of theileriosis in Zimbabwe using multiple climatic variables (Duchateau *et al.*, 1997), the methodology for assessing distribution drivers using climate databases was addressed. The database was considered to suffer from collinearity, because most climatic variables share qualities with (or are influenced by) other variables in the database. Fitting logistic regression

models to disease occurrence with highly correlated independent variables can lead to misleading conclusions if the true biological meaning is not clearly understood. This case study used the analysis of principal components to reduce large numbers of variables to smaller sets of variables that more efficiently describe the important features of the database.

An important early stage in the impact assessment process had been to determine more accurately the distribution of diseases and their vectors. This had four major impacts:

1. It enhanced the understanding of disease vector distributions, and factors affecting these, such as climate and vegetation.
2. It enhanced the understanding of the role of GIS in predicting disease and vector distributions, and the need for appropriate high-resolution georeferenced databases, including the use of satellite-derived imagery.
3. It allowed exploration of new methods for improving the predictive capacity of distribution models (illustrated by Duchateau *et al.*, 1997).
4. It alerted Ethiopia, where *R. appendiculatus* had never been recorded, to the climatic suitability of the survival of this vector in certain parts of the country (Norval *et al.*, 1991). This stimulated the Ethiopian government to revise its policy on importation of live cattle from Kenya. A new study confirming the susceptibility of Ethiopia to ECF has since been published (Leta *et al.*, 2013), repeating the warnings made by ILRAD in 1991.

Modelling the infection dynamics of vector-borne diseases

Soon after the observational studies on ECF on the Kenya coast had started, it was felt that there was a need to develop a mathematical model (Anderson and May, 1992) of *T. parva* infection dynamics that could contribute to our understanding of disease impacts and offer a framework to test the effect of interventions, such as vaccination. This started a 15-year collaboration on infection dynamics of tick-borne infections with Graham Medley, which eventually moved from theileriosis to *E. ruminantium* infection (heartwater). This launched a wider

exploration of modelling in impact assessment, and ILRAD, in collaboration with FAO, organized a modelling workshop in Nairobi in November 1992 to explore the approaches being made by different research groups (Perry and Hansen, 1994).

The collaboration with Imperial College London, and subsequently the University of Warwick (where Graham Medley moved), led to the first attempt to develop a quantitative framework of the infection dynamics of theileriosis (Medley *et al.*, 1993). It was able to demonstrate how infection was maintained in cattle populations and quantified the important role of carrier animals. With the progressive understanding emerging from field studies in different regions, the model was updated and reported by O'Callaghan *et al.* (2003).

The principles behind this first model were then applied to heartwater, and a quantitative framework was produced that demonstrated for the first time the concept of endemic stability (O'Callaghan *et al.*, 1998). The approach went on to explore the effects of vaccination against heartwater (O'Callaghan *et al.*, 1999).

The various observational field studies and the supportive modelling initiatives raised many issues, particularly the mechanism for establishment of endemic stability to both theileriosis and heartwater, and the implication of different interventions, particularly tick control, on the development and maintenance of endemic stability. This led to an extrapolation of the findings to other diseases, including malaria, warning that certain interventions might interrupt endemic stability and lead to outbreaks of disease (Coleman *et al.*, 2001). This *Lancet* publication won the ILRI's award (and nomination for the CGIAR Chairman's Award) for the Outstanding Scientific Article of 2002.

Impacts of Trypanosomiasis and its Control

Economic impact of trypanosomiasis

The focus of impact assessment remained largely on tick-borne pathogens until 1997. In the early 1990s, the epidemiology group adapted a model

that had been used for theileriosis impact assessment to quantify the impacts of trypanosomiasis and its control in Cameroon, Gambia, Côte d'Ivoire and Zimbabwe. The model estimated the proportion of the national herd at risk of the disease and the annual economic cost of the disease and produced a breakdown of the costs into production losses and input costs. Work based on this model was reported in Shaw (1992), in Mukhebi *et al.* (1993) and in the later review of Shaw (2009).

Subsequently an *ex ante* model of a potential trypanosomiasis vaccine (Kristjanson *et al.*, 1999) indicated that the potential benefits of improved trypanosomiasis control, in terms of meat and milk productivity alone, were US$700 million per year in Africa. The disease cost to livestock producers and consumers was an estimated US$1340 million annually, without including indirect livestock benefits such as manure and traction. Given an adoption period of 12 years, a maximum adoption rate of 30%, a discount rate of 5%, and a 30% probability of the research being successful within 10 years, the net present value of the vaccine research is estimated to be at least US$288 million, with an internal rate of return of 33%, and a benefit:cost ratio of 34:1.

While praising the estimated returns to trypanosomiasis control, the critics were uncomfortable with these returns being attributed exclusively to the effects of a vaccine. The predicted reduction of trypanosomiasis could in fact be achieved by several different interventions, including some for which technologies were already available. It could also be an evaluation of more effective deployment of tsetse traps, or of genetically engineered livestock resistance to the effects of trypanosomiasis or of effective chemotherapy; the productivity impacts may be similar. What will differ will be the probability of success, the cost of the research/implementation, the time to achieving that success, and the adoption rates. This is important, because there are those who believe that a vaccine will be out of our reach for a long time to come, and while the evaluation demonstrated probable benefits from trypanosomiasis control, it was not specific to a vaccine as the way to achieve this. Notably, 15 years on from this study, there is still no vaccine on the horizon, whereas the results were based on one being available 9 years ago.

The epidemiology of resistance to trypanocides

In the late 1990s, ILRI began research on the epidemiology and impact of trypanosomiasis in several African countries. Field work was undertaken in Uganda, Kenya, Tanzania and Zambia (in collaboration with the national agricultural research system and the University of Glasgow) and Burkina Faso (in collaboration with the Centre International de Recherche-Développement sur l'Elevage en zone Subhumide (CIRDES) and the Free University of Berlin (FUB). Highlights of this work included the following:

- Support from the Bundesministerium für wirtschaftliche Zusammenarbeit (BMZ) for several phases of an ILRI/CIRDES/FUB project on the epidemiology of trypanocide resistance in West Africa (see Chapter 3, this volume);
- Collaboration on trypanocide resistance in eastern Africa (Kenya, Tanzania and Zambia);
- Epidemiology studies of drug resistance in Mukono County, Uganda.
- Support for drug resistance studies undertaken by the Kenya Trypanosomiasis Research Institute (KETRI) in collaboration with Glasgow University.

These studies resulted in a series of multiauthor and multi-institutional publications (e.g. Gall *et al.*, 2004; Knoppe *et al.*, 2006).

The development of a modelling technique for evaluating control options

An area of emphasis was the development of models to understand factors influencing the transmission dynamics of trypanosomiasis and assessing and predicting the impact of control strategies. The objective of this research was to determine whether transition models, as proposed by Diggle *et al.* (2002), could be applied. This modelling approach offered two major advantages over standard methods. The first is that risk factor associations can be assessed simultaneously for both new (incident) infections and recurrent infections after chemotherapy. The second is that such statistical methods can allow monthly rather than weekly or fortnightly

sampling intervals in the field. This latter feature is crucial logistically and would allow the analysis of data from a much wider variety of sampling sites, as monthly sampling is commonly employed. The use of transition models allowed the distinction to be made between key factors influencing both the incidence and persistence of trypanosome infections in cattle in the Ghibe Valley, Ethiopia, over a 12-year period from 1986 to 1998 (Schukken *et al.*, 2004). With an observed average prevalence, based on microscopic examination, of approximately 50%, Ghibe ranked as an area of severe trypanosomiasis impact relative to other tsetse-infested areas in Africa (Snow and Rawlings, 1999). The real benefit of using a transition model to investigate infection dynamics of trypanosomes in cattle is its ability to assess both the incidence and persistence of infections. This was particularly useful because the main factor influencing changes in incidence, namely tsetse control, differed from the factor most likely to be responsible for increased duration of infection, namely resistance to commonly used trypanocidal drugs. Age and the number of previous infections also influenced incidence and duration of infection, raising interesting hypotheses for further investigation (e.g. potential of selection of trypanotolerance in local Ethiopian breeds).

Sustainable trypanosomiasis control in Uganda

The ILRI epidemiology group began work exploring the historical resurgence of human African trypanosomiasis (HAT; also known as sleeping sickness) in Uganda (Fèvre *et al.*, 2001; Welburn *et al.*, 2001) and went on to explore different potential control options using modelling techniques (McDermott and Coleman, 2001).

HAT remains an important disease in Uganda, and cattle are its main reservoir. This project assessed the role of cattle in human disease and how control of cattle trypanosomiasis can be used to reduce the public health burden of *T. brucei rhodesiense* HAT. Activities included: (i) development of tests to differentiate human-infective and -non-infective *T. brucei* spp.; (ii) studies into cattle movement in new outbreaks of HAT; and (iii) studies to evaluate factors that influence HAT risk, burden and under-reporting.

Sustainable trypanosomiasis control in the Ghibe Valley of Ethiopia

The initial modelling work of ILCA's research in the Ghibe Valley of Ethiopia moved on into an environmental impact study, supported by the International Atomic Energy Agency (IAEA), who were at the time exploring the potential role of the sterile insect technique to eradicate trypanosomiasis. While there was general scepticism over the widespread use of this technique, there was at the time substantial political support for wider tsetse eradication under the Programme against African Trypanosomiasis (PAAT) programme. This work also built on previous collaborative ILCA/ILRAD studies of environmental impact of long-term trypanosomiasis control in the Ghibe Valley, including impacts on bird species richness (Wilson *et al.*, 1997).

Spatial modelling of tsetse distributions

Underlying several studies on trypanosomiasis were studies on predicting the distribution of tsetse species. The GIS capacity set up in the late 1980s was subsequently applied to support studies on the impact of trypanosomiasis control (Perry *et al.*, 1994) and later exploited by Robin Reid, who went on to explore various aspects of the environmental impacts of tsetse control (Reid *et al.*, 2000) before moving into broader ecosystems research at ILRI.

The leaders in the use of statistical methods and spatial climate and vegetation databases were David Rogers and colleagues at the University of Oxford (e.g. Rogers *et al.*, 1996; Wint and Rogers, 2000). However, with the greater engagement of ILRI in predicting the effects of climate change on the length of the growing period and the implications this had on livestock production systems, an assessment of the potential for changing tsetse distributions was considered (McDermott *et al.*, 2001). Subsequent research has included work on the economic impact of trypanosomiasis (Robinson *et al.*, 2014a).

Preventing and containing trypanocide resistance in the cotton zone of West Africa

In April 2012, a final report on 'Preventing and containing trypanocide resistance in the cotton

zone of West Africa' was issued, which was one of a series of projects exploring drug resistance in trypanosomiasis control. Previous work had focused on methods to evaluate resistance to trypanocides in north-east Guinea, southern Mali (Affognon *et al.*, 2009; Talaki *et al.*, 2009) and south-west Burkina Faso (Der *et al.*, 2011), and on testing integrated control strategies to reduce the risk of new drug resistance. In the final phase of the project, the project continued to evaluate resistance and raise awareness and capacity to address the problem across much of the rest of the zone and to scale up the prevention strategies developed earlier. Appropriate strategies were also being developed for containing – and, if possible, reversing – resistance in the pockets previously characterized, and a specific study was undertaken to assess the impact of the trypanocide resistance research efforts to date.

This series of projects has generated an important body of evidence for improving the sustainability of trypanosomiasis control in West Africa and elsewhere in sub-Saharan Africa (McDermott *et al.*, 2003; Clausen *et al.*, 2010). The final project focused on four main outputs, with capacity strengthening in the region as a cross-cutting objective. First, national research teams generated evidence that trypanocide resistance occurs in several locations across the cotton zone of West Africa, and the partnership has provided national services improved tools for detecting and monitoring it. Through collaboration with the Institute of Tropical Medicine (Antwerp), progress was made in developing markers for identifying resistance in trypanosomes (Delespaux *et al.*, 2010); this is expected to provide even more rapid and increasingly accurate diagnostics for detecting and monitoring drug resistance.

Second, informational aids, decision tools and media messages targeting farmers and animal health service providers to reduce the risk of resistance were further developed (Grace *et al.*, 2008, 2009). There is a better understanding of how farmers access information about animal health care and of the most important actors in national-level information networks that communicate such information. A third set of activities demonstrated the effectiveness of integrated control strategies for containing trypanocide resistance in a location once it has established. In such situations, the public sector is probably

required to implement tsetse control interventions and strategic treatment of cattle to suppress trypanosome populations. Actions improving cattle health status, such as helminth control, may also help further suppress surviving trypanosomes. Longer-term research is needed to confirm the subsequent dynamics of resistant trypanosome populations if trypanosomes re-establish.

Finally, a preliminary assessment of the potential impact of the investments made to date in research on trypanocide resistance indicates that adequate returns will be achieved to justify the investment (Affognon *et al.*, 2010).

Research findings and outputs from the project have been taken up by continuing efforts in the region to improve control of trypanosomiasis, notably by a network to monitor drug resistance (RESCAO: Réseau d'épidémiosurveillance de la résistance aux trypanocides et aux acaricides en Afrique de l'Ouest), the FAO PAAT and a 5-year, €3.1 million project involving the principal German partners and CIRDES to extend the project approach and findings to new countries (Togo, Ethiopia and Mozambique).

Rabies Research: A Networking and Capacity-building Role in Africa

ILRAD had no mandate in rabies research, but, beginning in the early 1990s, joined the Southern and Eastern Rabies Group (SEARG). Its first contribution was an overview paper on the epidemiology of rabies in Africa (Perry, 1992). As part of the capacity-building function of the epidemiology and socio-economics programme, partnership with the rabies control groups in Kenya and neighbouring countries was established, including the supervision of Philip Kitala in his PhD research on rabies in the Machakos District of Kenya, and a series of papers emerged (Kitala *et al.*, 2000, 2001, 2002). Other strategic contributions emerged from ILRAD and ILRI (Bingham *et al.*, 1993, 1995; Perry, 1993, 1995; Perry and Wandeler, 1993). In addition, the epidemiology team was called in to evaluate the controversy surrounding the role of rabies and rabies vaccination in the demise of the African wild dog packs in the Aitong region of Kenya's Maasai Mara (Macdonald *et al.*, 1992).

The impacts of the engagement with rabies were substantial, and mostly centred on the

building of a rabies epidemiology and control network through SEARG, in capacity building on rabies epidemiology, diagnosis and control throughout the eastern and southern African region, and in highlighting priority research needs. Furthermore, ILRI's work contributed to some of the principles of dog rabies control, such as the need to understand the vaccination coverage required to prevent rabies (Coleman and Dye, 1996), the need for a sound understanding of population ecology (in this case, dog ecology) in order to target vaccination initiatives (Perry, 1993) and the need to exploit community engagement in rabies vaccination campaigns (Perry *et al.*, 1995).

The Economic Impacts of Rinderpest Control

Rinderpest has had a devastating effect on the livestock industries of Africa since its introduction to the continent in the late 19th century. In its classical form, it was responsible for high levels of mortality and its mere presence constrained trade in livestock. During the 1960s, the first coordinated international control programme was put in place, known as the Joint Project (JP) 15. Although largely successful, rinderpest returned in a major epidemic throughout much of the continent after JP15 concluded in the late 1970s. As a result, the Pan-African Rinderpest Control (PARC) programme was initiated under the auspices of the African Union–Interafrican Bureau for Animal Resources (AU-IBAR) funded by the European Union (EU) and national governments to control and ultimately eradicate rinderpest from Africa. A decade after the campaign started in 1986, increasing donor concern about its impact, coupled with an increasing public and private demand for information on the benefits and costs of rinderpest control, prompted the call for an economic impact assessment of the campaign.

Despite Africa being the last bastion of rinderpest before its global eradication in 2011, ILRAD did not become involved in research into its control, although following its eradication, ILRI did exploit the participatory epidemiology and surveillance tools used in the final phases of the campaign during its research into HPAI in Indonesia. Just before the merger of ILCA and ILRAD in 1995, the EU, which at the time was making large investments in rinderpest eradication through the AU-IBAR, approached both institutions. The PARC programme had been planning for some time to undertake an economic evaluation of the rinderpest control programme. However, the funds made available by the EU were not considered sufficient to employ an independent economist. As a result, the task was offered in 1994 to both ILRAD and ILCA, on the supposition that they could supplement the limited funds with their institutional capacities in agricultural economics. ILRAD, with its historical focus on vector-borne haemoparasitic diseases, turned the offer down, while ILCA accepted it. The two institutions were then amalgamated, and ILRI was born, and the newly created Systems Analysis and Impact Assessment Group (SA/IA, the successor to the Epidemiology and Socioeconomics Programme) 'inherited' the project. This provided a new opportunity for ILRI to work with AU-IBAR, and two agricultural economists were recruited under the leadership and supervision of the SA/IA group.

The study indicated that, for a sample of ten sub-Saharan African countries, the rinderpest campaign was implemented in a cost-effective manner, with average per livestock unit costs appearing within the narrow range of US$0.30–0.66 (Tambi *et al.*, 1999). Benefit–cost analysis revealed that the benefits of the campaign in each of the ten countries covered the value of the investment. The estimated average return over the ten countries of US$1.98 for each US dollar invested in the campaign indicated that rinderpest control in Africa has been economically profitable. The net present value of US$32 million indicates that the rinderpest campaign has been a wise public investment decision.

The work by ILRI scientists demonstrated further that rinderpest control has also improved the well-being of livestock farmers in sub-Saharan Africa, as well as that of consumers of livestock products. Analysis of the distribution of welfare gains from rinderpest control between producers and consumers revealed that producers derived the greater share (80%) of the US$64 million in net value of production losses avoided due to rinderpest control in the ten countries, while consumers derived approximately 20% in net benefits from increased supplies leading to lower prices (Roeder and Rich, 2009).

Applying Economic Impact Assessment Tools to Foot-and-mouth Disease Control

With the formation of ILRI, the new institution embarked on the development of an appropriate research role in what was a new sphere of influence for the organization, and an Asia Action Group was established to plan strategic engagement. For the epidemiology group, the first contact with the new region was a strategic attendance at the Federation of Asian Veterinary Associations (FAVA) Conference in Cairns, Australia, 24–28 August 1997, where a series of meetings was held with those attending. The representatives of the Australian Centre for International Agricultural Research (ACIAR; John Copland), and the OIE (Yoshihiro Ozawa) facilitated a discussion with multiple partners on how ILRI could provide added value to ongoing initiatives within the Asian region.

For ILRI to make an effective move into Asia in animal health research, it was considered that it should exploit the generic research capacity it had developed in epidemiology and economic impact, rather than its traditional disease focus of vector-borne haemoparasites of ruminants, as these were not considered to be a high priority in the region. In addition, it was considered that the first phase of ILRI's involvement in the region should be to better define constraints to livestock production and trade, and ways of alleviating these. To this end, it was suggested that enhancing the regional animal disease surveillance and monitoring programme, the Animal and Plant Health Information System for Asia (APHISA), in the field of epidemiological and economic impact assessment would be the most appropriate entry point. ILRI was invited to undertake an initial case study on the impact of FMD in the region, and the impact of alternative FMD control strategies. This provided an opportunity to enhance impact assessment capacity in the region, initiate longer-term disease control priority evaluations and provide immediate support to the newly created OIE-coordinated FMD control and eradication programme that had been set up. The OIE operation was funded by the Australian, Swiss and Japanese governments, with the Swiss Government offering to provide the ILRI portion of the funding.

A regional FMD coordination unit was set up, based in Bangkok, Thailand, led by Laurie Gleason, and an advisory committee was established, on which Brian Perry of ILRI was invited to sit. The first meeting was held in Bangkok on 1 March 1998. This set the scene for the first of the FMD economic impact studies, which focused on Thailand within a South-east Asia regional context. Thai epidemiologist Wantanee Kalpravidh was assigned to the study, and agricultural economics support was provided by Suzan Horst of Wageningen University, the Netherlands. The World Reference Laboratory for FMD (WRL-FMD) in Pirbright, UK, provided the FMD-specific technical support. Later in 1998, after he was recruited to ILRI's epidemiology and impact assessment group, Tom Randolph took over the economic impact analysis components of the initiative.

The first product of this work was presented at the annual meeting of the South-east Asia Foot-and-Mouth Disease (SEAFMD) group, under the auspices of OIE, in Phnom Penh, Cambodia, in February 1999, and emerged as a peer-reviewed publication later the same year (Perry and Randolph, 1999). This group provided a cost–benefit analysis of different FMD control scenarios and different emerging trading opportunities that would result from greater FMD control.

ILRI work on FMD in the Philippines had a significant impact. Randolph *et al.* (2002) developed scenarios, based on the plans and timetable of the Government of the Philippines, and more optimistic and pessimistic assumptions, each discussed in detail with national stakeholders. It also had an additional component, which was an analysis of the distribution of the benefits. It illustrated that, while the FMD control programme was funded entirely from public sector government coffers, in eradication scenarios the major beneficiaries would be the private sector pig producers, traders and marketers; the commercial swine sector was estimated to capture 84% of the benefits generated by the public investment in eradication, versus 4% by backyard swine producers.

ILRI later undertook a collaborative study on FMD on smallholder agricultural enterprises in southern Laos (Perry *et al.*, 2002a). This demonstrated the widespread impacts the disease had on multiple species and enterprises in the smallholder systems of southern Laos and has been often cited as evidence of the disruption to the livelihoods of smallholders globally.

The southern Africa FMD economic impact study

The results of a benefit–cost analysis showed that FMD control would benefit the economy of Zimbabwe (Perry *et al.*, 2003). First, in a comparison between the Baseline Scenario and the pessimistic FMD Control Scenario 3 (in which disinvestments in FMD control by 50% and resultant loss of beef export markets was predicted), it was shown that for every US$1 that Zimbabwe disinvests in the FMD control programme, a further US$5 would be lost by the country. No transboundary effects were taken into account, and the losses calculated were incurred by Zimbabwe alone. However, the association of the outbreak of FMD in south-eastern Botswana in March 2002 (after over 30 years of freedom from the disease) with the outbreaks in western Zimbabwe suggested that the costs to the region as a whole of Zimbabwe's disinvestments could be much greater.

Second, the results showed that if Zimbabwe were to invest further in the fences and the veterinary service infrastructures required to create a much larger and much more secure export zone that was internationally recognized as FMD free by the OIE, there would be returns of approximately US$1.5 for every US$1 invested. As in the disinvestment scenario, this does not incorporate benefits to the region as a whole through greater disease security for FMD control, nor does it include the other benefits that would result from an enhanced national veterinary service. This analysis did not consider whether Zimbabwe would be able to maintain the capacity, in terms of quantity and quality of beef, to supply the export market on a sustainable basis.

Importantly, the distributions of the costs and benefits turned out to be highly skewed. Expenditures from FMD control are borne almost entirely by the public sector, but when losses from trade bans resulting from FMD outbreaks are included, private sector costs are dominant. The majority of impacts of FMD and the benefits from its control are related to the ability to trade internationally, and so most of the benefits accrue to the commercial sector, comprising cattle production, beef processing, and related input industries and services. The Social Accounting Matrix/Computable General Equilibrium (SAM/CGE) modelling indicates that approximately 16% of the increased value of economic activity resulting from trade is eventually transferred as income to low-income households in both rural and urban areas.

The direct impacts on the poor of FMD, and of measures established to control it, are very limited. FMD has not been a problem in communal areas where the majority of the poor live, and its effects on indigenous cattle are considerably less than on commercially orientated herds. Furthermore, despite the fact that about 75% of poor households own or have access to cattle, over 60% of these households own fewer than five animals. Most of these households use cattle for wealth storing and other livelihood functions such as traction, and do not have the herd size capacity to engage actively in commercial cattle marketing. As such, only about 2% of households are engaged in regular marketing of cattle.

This study provided one of the most extensive analyses of FMD impacts carried out, applying new methods such as the SAM/CGE modelling to a most complex subject. Randolph *et al.* (2005) explored further the highly skewed equity impacts emerging from this study.

Economic impacts of FMD in Peru, Colombia and India

In 1995, the Joint FAO/IAEA Division of the IAEA requested ILRI support for an economic assessment of FMD control. An economic impact assessment plan emerged (Romero *et al.*, 2001). Unlike the South-east Asia partnerships, these Andean initiatives did not result in completed benefit–cost analyses; rather, the impacts of these studies in the region were in the field of networking, training, capacity building, awareness raising and methodology development.

Economic impacts of FMD control in endemic settings in low- and middle-income countries

In April 2006, Brian Perry approached the Wellcome Trust and the EU for support for an international workshop on the research needs for better FMD control in endemic settings of many low- and middle-income countries. This was

approved, and the Global Roadmap for Improving the Tools to Control Foot-and-Mouth Disease in Endemic Settings was duly held in Agra, India, in late November 2006 (Perry and Sones, 2007b) and the Global Roadmap was launched in April 2007.

The Global Foot-and-Mouth Disease Research Alliance (GFRA)

ILRI developed a proposal for a GFRA with five research pillars:

1. A detailed understanding of the host immune responses to FMD virus.
2. Development of a new generation of inexpensive and thermostable vaccines that meet the requirements of both endemic and epidemic FMD control and management.
3. A full understanding of the factors that permit the development of virus carrier animals, the risk that they pose and options for managing them.
4. The identification of antiviral compounds to inhibit virus replication and rapidly reduce virus release.
5. Quantitative predictions of the performance of the new technologies developed in different settings through the use of epidemiological and economics models.

The leadership of each pillar was assigned to different institutions, with ILRI taking on this latter pillar. The US$70 million proposal was launched as a Strategic Global Research Partnership for the Control of FMD in April 2004.

The proposal was received with enthusiasm on the scientific side, but participants urged the development of a business plan. This was duly commissioned and in June 2005 representatives of the partnership set out to visit key donors (DFID and the Department for Environment, Food & Rural Affairs (DEFRA) in the UK; the EU; the Canadian International Development Agency (CIDA) in Canada; and various partners in the USA).

Considering the different contexts of FMD control in the developed and developing world, GFRA revised its approach to adopt two complementary programmes. Programme 1 was targeted at the FMD vaccine and diagnostic needs of FMD-free countries, and their trading opportunities, while Programme 2 focused on the needs of endemic settings, principally in developing countries. At this point, ILRI assumed the leadership of Programme 2, and initiated contact with potential research sponsors and development agencies. Programme 1 was assigned to the four participating research laboratories in the USA, the UK, Canada and Australia, funded through national bodies supporting each laboratory. The outcome would be a better set of tools to manage the risk to the four countries currently posed by FMD in endemic areas. This would focus on improved vaccines and diagnostics and the further development of antivirals.

Program 2 was designed to focus on developing better tools for use in endemic areas with the overall aim of a gradual reduction of the disease in endemic areas. It was recognized that targeted research would be needed to develop specific tools for Programme 2 and that this work could occur both inside and outside of the current GFRA partner institutes. It was foreseen that, for Programme 2, much still needed to be done in the area of epidemiology and impact assessment, and that ILRI would take the lead in this, and that it would be a core component of funding under Programme 2.

However, ILRI management was not at the time supportive of ILRI's engagement with GFRA, in part because it was considered that FMD did not rank highly enough in the health constraints facing smallholder producers.

Rift Valley Fever

Research into RVF at ILRI commenced with an evaluation of the impacts of the 2006/2007 outbreak that occurred in eastern Africa. This work was commissioned by USAID and FAO, and focused primarily on the north-eastern region of Kenya, thought to be the epicentre of the epidemic in Kenya. The outbreak occurred between December 2006 and March 2007 and affected more than 700 people; approximately 150 human fatalities occurred throughout the country. It was believed that people suffering severe clinical disease had close contact with infected livestock.

The impact assessment was implemented by a team of epidemiologists, economists and

social scientists. A memorandum of understanding was established with Kenya's Department of Veterinary Services (DVS), enabling the DVS to participate in the project as a key partner. This work was later extended to the Arusha region of Tanzania with additional support from FAO. Surveys conducted in both sites utilized participatory epidemiological tools and the data collected were synthesized and published (Jost *et al.*, 2010). The key observations made were that there were major weaknesses in preparedness and the response to the outbreak, and that pastoralists noticed RVF-compatible events long before official notifications were made by the government. At the same time, economic impact assessments were conducted by Karl Rich and Francis Wanyoike (Rich and Wanyoike, 2010). This demonstrated that the disease induced substantial production losses, employment losses and reductions in operating capital among various value chain actors including producers, livestock traders, animal transporters, and slaughterhouse and butchery operators. It was estimated that the outbreak cost the Kenyan economy US$32 million.

These findings fuelled discussions on the need for improved warning systems and a structured contingency plan for managing the disease. More importantly, timelines developed with local communities showing events that preceded the outbreak were transformed into a decision support tool (Consultative Group for RVF Decision Support, 2010). This is considered a major contribution by ILRI and FAO to RVF contingency planning given that this tool has now been incorporated into the Ministry of Livestock's Contingency Plan for RVF. More work still needs to be done, however, to develop a harmonized contingency plan that unites the public health and veterinary sectors in line with the One Health paradigm.

Economic impact assessment of control options and calculation of disability-adjusted life years (DALYs)

The outputs of the impact study supported the formulation of a new study to assess the cost-effectiveness of RVF control options from a multidisciplinary perspective. This work also aimed to estimate economic costs of RVF in people using DALYs. The estimates generated suggest that the 2006/2007 outbreak caused a total of 3974 DALYs, or 1.5 DALYs per 1000 population. Provisional results further show that strategies to enhance mass vaccination of cattle and camels over a sustained 2-year period would greatly reduce DALYs. It also showed that integrating vector control measures, for instance through the application of larvicides, would yield even better results, although the practicability of implementing such interventions through institutional collaboration has not been fully resolved.

RVF risk maps for eastern Africa

ILRI epidemiologists have developed risk maps for the eastern Africa region that can be used together with the decision support tool to enhance targeting and evaluation of RVF interventions. This work builds on previous studies done by the National Aeronautics and Space Administration (NASA) and other research institutions such as the Centers for Disease Control and Prevention (CDC). Two methods that have been applied for this analysis are: (i) ecological niche modelling based on the Genetic Algorithm for Rule-set Prediction (GARP); and (ii) a logistic regression model, followed by mapping predicted probabilities on a spatial landscape. Both models use historical data on RVF outbreaks from the 2006/2007 outbreak. Statistical analyses demonstrate that RVF risk is significantly associated with exceptionally high rainfall, low altitude, clay soils and high normalized difference vegetation indices. Such maps could also be used to enhance our understanding of ecological niches for the virus, particularly if the existing hotspots can be classified based on their abilities to support disease persistence. More importantly, these maps are being integrated with socio-economic variables to determine areas that are most vulnerable to the disease given their livelihood patterns, capacities to access public health services and literacy levels.

Land-use change and RVF infection and disease dynamics

With increasing awareness of the impacts of RVF epidemics, there is a growing interest in determining processes that cause RVF occurrence

and transmission, as well as those that promote its persistence during inter-epidemic periods. ILRI is currently leading a project in Kenya that seeks to understand RVF drivers from a multidisciplinary perspective. The project is founded on the premise that intact ecosystems can regulate disease epidemics, and that factors that disrupt ecosystem structure and function, such as climate, land use and demographic changes, contribute to disease emergence and spillovers. The project involves local partners such as the Kenya Medical Research Institute (KEMRI), DVS, University of Nairobi and Ministry of Health.

Preliminary observations indicate that there is a great potential for endemic transmission of RVF in irrigated areas established in arid and semi-arid zones, as poorly managed drainage systems and watersheds provide ideal conditions for the development of primary and secondary vectors of RVF. Observations also show that areas that are RVF endemic tend to be vulnerable to other infectious/zoonotic diseases, malnutrition or insecurity, presenting multiple challenges to the implementation of sustainable RVF control strategies.

Epidemiology of Gastrointestinal Parasites

ILRI published a field and laboratory handbook on the epidemiology and diagnosis of gastrointestinal parasites entitled *The Epidemiology, Diagnosis and Control of Gastro-Intestinal Parasites of Ruminants in Africa* (Hansen and Perry, 1990). A second edition, *The Epidemiology, Diagnosis and Control of Helminth Parasites of Ruminants*, was published several years later (Hansen and Perry, 1994).

Priorities in Animal Health Research for Poverty Reduction

In 2000, ILRI began work on animal health and poverty reduction involving scientists and opinion leaders in Africa, Asia, Europe and North America. This eventually delivered one of the highest-impact products of ILRI's epidemiology group (Perry *et al.*, 2002b). The Inter-Agency Donor Group (IADG) had just been born, as part

of a process to bring greater coordination among its membership in the funding of livestock research. As part of this process, it sought to better define the research options and priorities, and DFID proposed that these be placed in the context of poverty reduction. This required first defining poverty and the association with livestock, and then quantifying the association, a process that continues (Robinson *et al.*, 2014b).

There were seven major components to the study (Perry *et al.*, 2002b). The first was to describe and quantify the distribution and extent of poverty in South-east Asia, South Asia and sub-Saharan Africa, and to determine the association of poverty with different agricultural production systems that involve livestock. These two tasks were accomplished in a companion study commissioned by DFID (Thornton *et al.*, 2002), which developed maps to quantify populations of poor livestock keepers and to predict how they would change over the next five decades. The results provided data on the number of poor (people on less than US$1 per day) in each of the major livestock production systems of the world. These figures served as a weighting factor in determining the importance of different livestock diseases to the poor.

The second component was to determine the priority species to the poor in each region and production system. This was undertaken by a literature review and through stakeholder workshops in West Africa, eastern, central and southern Africa, South Asia and South-east Asia.

The third component was to quantify the disease constraints by species. Diseases and syndromes considered to negatively affect the livelihoods, productivity outputs and marketing of livestock products by the poor were identified in a set of stakeholder workshops. The socioeconomic (primarily production losses and control costs incurred by the poor), zoonotic (for those diseases transmissible from animals to humans) and national impacts (a combination of marketing impacts on the poor with public sector expenditures on disease control) were identified and scored.

Published literature on the impact of livestock diseases and of their control in the target regions was scrutinized and synthesized by commissioned reviews. Research opportunities to alleviate these constraints were then identified. First, research needs were identified from the end

users' perspectives by participants in several regional workshops. Second, research opportunities were identified from the upstream perspective by international experts specializing in different diseases. In addition to identifying relevant research opportunities, the experts were asked to estimate the cost, time frame, probability of success and available capacity to undertake such research. To ensure that issues other than technology generation were addressed, additional reviews of research opportunities for the better delivery of animal health services were commissioned. A specific review of the role of research into the genetics of resistance to disease was also commissioned.

The next step was to score the disease impacts (Shaw *et al.*, 2003), synthesize the disease impacts on the poor with the research needed to reduce them and identify priority research opportunities. A conceptual framework matrix was developed to classify different types of disease-specific research: (i) transferring knowledge and available tools; (ii) developing improved tools and strategies that were better delivered; and (iii) developing new tools and approaches by the contribution the research product will make to poverty reduction (by securing the assets of the poor; reducing the constraints to intensification or improving marketing opportunities).

This study has had a lasting impact on research priorities for development and is still the most cited reference in this context. In addition, it set the stage for measuring the association between poverty and livestock, and for applying greater emphasis to the impacts that research in animal health have on the processes of poverty reduction, rather than simply on national agricultural development. The methodology has been further developed (Perry and Grace, 2009).

The Wellcome Trust Epidemiology Initiatives

In January 2002, the DFID-commissioned study entitled 'Investing in Animal Health Research to Alleviate Poverty' was published (Perry *et al.*, 2002b). As described above, this had been commissioned by IADG on pro-poor livestock research and development, of which the Wellcome Trust was a member, and had been represented by Catherine Davies. The ILRI epidemiology group

was again approached by the Trust, and following discussions in London, the group submitted a pre-proposal for a Wellcome Centre for Strategic Veterinary Epidemiology based at ILRI in Nairobi. After deliberations by the Trust, the proposal was not accepted for funding, but it did reopen the door to dialogue. Strongly influenced by the report by Perry *et al.* (2002b), in July 2002 the Trust announced a new funding programme entitled 'Animal Health in the Developing World', under which it set aside £25 million over a period of 5 years to fund researchers to develop methods of predicting and controlling outbreaks of animal diseases.

A large number of research proposals were developed by ILRI in partnership with institutions in the UK and USA, including gastrointestinal parasitism, FMD epidemiology and dynamics, anti-tick vaccines, livestock/disease information platforms for East Africa and African swine fever, among many others. This later led to the Livestock for Life Programme, launched in December 2005.

In January 2007, the Wellcome Trust held a meeting to give scientists funded under earlier grant programmes the opportunity to present research findings, and to consider future needs in the field (the meeting was entitled 'Animal Health Research: Recent Developments and Future Directions'). To coincide with the meeting, a policy review paper was commissioned (Perry and Sones, 2007a), and ILRI presented an invited talk on the challenges of research outputs influencing policy (Perry and Hooton, 2007).

In summary, the epidemiology group at ILRI undoubtedly had a substantial impact on the shaping and development of the Wellcome Trust's programmes of funding for livestock disease control in the developing world, and the impacts were spread to many different research institutions and countries.

The Broader Economic Impact Contributions

Economic impact assessments gained increasing momentum as ILRI's mandate broadened. In a paper prepared as an invited plenary presentation to the 17th International Conference of the

World Association for the Advancement of Veterinary Parasitology, Perry and Randolph (1999) wrote: 'The traditional veterinarian views disease as evil, and often embarks on a career with a "Superman" like determination to destroy it, regardless of how important it is. To the classical healer, economic considerations are secondary. The economist on the other hand sees animal disease as just one, and often an insignificant one, of a great spectrum of constraints to human and societal wellbeing that needs to be put in context.' They concluded that no longer should studies of the economics of diseases of production animals be limited to animal scientists seeking the collaboration of agricultural economists to affix prices to estimated productivity losses. Rather, a new discipline of animal health economics emerged in which the quality of economic evaluations depended on integrating the products of good epidemiological studies into economic frameworks.

In addition, during 1998, the ILRI Epidemiology and Disease Control group leader was approached by the director general of the OIE to coordinate the design, compilation and editing of a special edition of the *OIE Scientific and Technical Review on Animal Health Economics*. This peer-reviewed edition comprised nine chapters on different demands for economic impact knowledge, and seven case study chapters addressing specific diseases and different circumstances affecting the validity of economics studies. This book, in combination with the study by Perry and Randolph (1999) mentioned above, served as important milestones for the integrated science of epidemiology and economics. Rushton (2009) described as it as 'the first book to bring together a number of important themes in animal health economics: farm-level economic assessments; trade implications of sanitary requirements; and veterinary service delivery'.

ILRI later did an economic analysis of the potential costs, benefits and competitiveness of trade in meat from Ethiopia to the Middle East (Rich *et al.*, 2008). This report was further developed for a peer-reviewed publication, presented by Karl Rich at the International Food and Agribusiness Management Association (IAMA) in June 2009 (Rich and Perry, 2009), where it won the Best Paper Award. At the time, it was widely believed that poor countries with abundant livestock were well placed to develop exports to high-value livestock product markets in Europe and elsewhere. The studies in Ethiopia showed that investments in the quarantine and testing required to ensure that beef feedlots were free of FMD were not the limiting factors affecting the economic viability of beef exports to Middle East markets; rather, it was the high cost of feeding animals to ensure that the product arriving in the market was competitive with others coming from Australia, Brazil and other sources.

ILRI later studied the potential role of commodity-based trade on international market access by developing countries (Rich and Perry, 2009, 2011). This work concluded that, on a geographical basis, the benefits of commodity-based trade are much more likely to be felt in countries like Argentina, Brazil and India than in African countries. Opportunities exist for southern Africa but are predicated largely on continued preferential access that may or may not be sustainable in the long term. While there are numerous opportunities for some African countries in niche markets, it is also important to balance this potential with the sound exploitation of livestock resources and a pragmatic understanding of the challenges in marketing and competitiveness. The constraints that complicate market access for Africa are much more those related to infrastructure, productivity and efficiency throughout the livestock supply chain, and it is in these areas that policy attention is urgently required.

The Responses to Highly Pathogenic Avian Influenza

The emergence of HPAI, initially in East and South-east Asia with subsequent spread to Africa, caused disquiet in all animal health research communities and institutions, and ILRI, in collaboration with the International Food Policy Research Institute (IFPRI), initiated a wide-ranging consultation to discuss where research could contribute (ILRI/IFPRI, 2006). It was not a straightforward process, providing the challenge of developing a framework and methods for designing appropriate control strategy interventions, and generating evidence of the potential trade-offs with poverty reduction objectives.

ILRI was active in providing several background guidance and methodological frameworks for the global response to HPAI. In 2009, ILRI was a partner in the production of a manual entitled *Introduction to Participatory Epidemiology and its Application to Highly Pathogenic Avian Influenza Participatory Disease Surveillance. A Manual for Participatory Disease Surveillance Practitioners* (Ameri *et al.*, 2009). ILRI also developed a user guide for initial bird flu risk maps as a contribution to improving the surveillance for bird flu (Stevens *et al.*, 2009). These have recently been built on and updated in a new risk mapping report (Gilbert *et al.*, 2014).

A Nigerian Avian Influenza Control and Human Pandemic Preparedness and Response Project (NAICP) began in July 2006 and invited ILRI to do an independent impact assessment of the project. The evaluation developed ten 'outcome pillars' to depict the benchmark 'gold standard' of best practices against which to evaluate NAICP (as discussed in Perry *et al.*, 2010). The evaluation report was presented to the Government of Nigeria (Perry *et al.*, 2011) and there were also two independent peer-reviewed publications (Henning *et al.*, 2013; Bett *et al.*, 2014).

The ISVEE Experience

The International Symposium on Veterinary Epidemiology and Economics, known commonly by its acronym ISVEE, has been held every 3 years since the inaugural meeting in Reading, UK, in 1976. It brings together directors of veterinary services, disease control planners, quantitative epidemiologists, agricultural economists, modellers and statisticians to present and discuss on a wide range of diseases and issues. Kenya was proposed by ILRAD's epidemiology group and later confirmed as the venue for 1994 at the 6th ISVEE in Ottawa in 1991, with Brian Perry as secretary of the organization (ISVEE, 1991). This provided the first opportunity to bring ISVEE to Africa, and to engage national and regional programmes in presenting their work and participating in the meeting. Through the hard work and commitment of John Rowlands, a statistician at ILCA, the full proceedings were handed to participants as they registered, a

first for ISVEE, in a special edition of the *Kenya Veterinarian*. The full meeting proceedings are now also available online (ISVEE, 1994).

The next ISVEE was held in Paris in 1998 with a strong representation from ILRI and its partners. But from here the level of participation grew substantially, and the 9th and 10th ISVEEs (in Colorado and Viña del Mar, Chile, respectively) brought the research of ILRI's epidemiology group to new levels of recognition; in the Chile meeting of 2003, the group had 29 papers and posters accepted. At this meeting, under joint sponsorship with the International Association of Agricultural Economists, Tom Randolph organized a mini-symposium on Animal Health Economics, which comprised plenary papers, independent papers and a discussion forum. In this, he concluded that animal health economics has established a solid, although remarkably narrow, foundation in the literature, but that it had not exploited its potential (Randolph *et al.*, 2003). While ILRI continues to be represented at subsequent meetings, the commitment to and impact of ILRI seen during the period 1994–2006 has waned.

The Role of Epidemiology in ILRAD and ILRI

Veterinary epidemiology and socio-economic impact research has gone through both administrative and locality changes during its existence over the last 27 years. It was a unified entity for 15 years, but in 2002, when the new ILRI strategy was developed, epidemiology and impact assessment became both fragmented and diminished in human resource capacity.

From 1987 to 1994 under ILRAD, it was the Epidemiology and Socioeconomics Programme, also varyingly referred to as the Epidemiology and Socioeconomics Unit and Socioeconomics Programme in emerging documentation. In the early days of ILRI from 1995 to 1997, epidemiology was accommodated under the newly created Systems Analysis and Impact Assessment Group, placing it under the Production Systems Programme, but this did not last for long, and from 1997 to 2002 it became the Epidemiology and Disease Control group under the Animal Health Programme.

The Impacts of ILRAD and ILRI's Epidemiology

Capacity development in veterinary epidemiology and impact assessment

During the 15-year period from 1987 to 2002, a substantial number of MSc and PhD students were trained through incorporation into research activities; these were predominantly from African countries. In addition, as mentioned in the section on ISVEE, the group and its associated students presented at many international meetings and in most cases published their research findings in peer-reviewed journals.

Impacts on national animal health departments and services

The epidemiology group provided a role model of investigative problem solving, which was picked up, copied and adopted by other institutions. However, this mostly occurred where there was a specific donor-funded project to support the establishment of an epidemiology group and was more common in academic than in public service bodies such as veterinary departments. Many newly trained graduates return to their institutions with a sound training but do not have the opportunity to build on that, often because of institutional weaknesses, with inadequate financial resources for research and for staff development. Veterinary epidemiologists rely on collaboration with colleagues at the bench, in the field and in the planning arena, and particularly with agricultural economists and other social scientists, so may find substantial difficulty functioning in a 'conservative' public sector environment.

Impacts on animal health constraints in developing countries

ILRI's epidemiology research has made substantial contributions to the understanding and control of ECF and trypanosomiasis in Africa, to the preparedness and responses to RVF in eastern Africa, to a greater understanding of the economic impact of rinderpest in Africa and of FMD in Africa, Asia and Latin America, and to regional understanding of the drivers of rabies control. More recently, epidemiology research at ILRI has contributed substantially to our understanding of food safety risks in formal and informal markets, and to the dynamics and risks of zoonotic diseases. The research has also contributed to the global understanding of the importance of these and other diseases to African livestock systems, and to the particular animal health constraints facing the poorer sectors of Africa's livestock-engaged communities.

Impacts on ILRI's research and strategy

During the days of ILRAD, the epidemiology and socio-economics programme had little or no impact on ILRAD's research and strategy; rather, it was seen as providing evidence justifying the existence of the laboratory-based vaccine research for the two target haemoparasitic diseases. Nevertheless, after ILRI's birth in 1995, the group did play an important role in providing impact assessment services, which progressively enhanced the engagement of the institution with different national, regional and donor clients. This situation changed dramatically in 2002 following the publication of the DFID-commissioned study on animal research priorities for poverty reduction (Perry *et al.*, 2002b). The matrix of three 'pathways out of poverty' (see Perry *et al.*, 2002b, Table ES1: securing assets, reducing constraints to intensification and improving market opportunities) and three research and development opportunities (transferring knowledge and available tools; improved tools, better strategies better delivered; and new tools and approaches) provided the framework of the new institutional thematic structure, not just for animal health research but also for ILRI's entire programme. Ironically, while a key product of the epidemiology and disease control group provided the framework for ILRI's new strategy, by the same token it also triggered the decline of epidemiology as an institutional entity in ILRI.

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Notes

[1] It had been conceived at the University of Florida by former ILRAD tick ecologist Andy Norval. On the tragic death of Norval in April 1994, ILRI assumed project leadership.

[2] Currently, the OIE Sub-Regional Representation for South-East Asia (SRR-SEA) is engaged in FMD control in the region. The SRR-SEA evolved from the South-east Asia Foot and Mouth Disease Regional Coordination Unit (SEAFMD RCU), which was created in 1997 for the control of FMD in South-east Asia, coordinating various prevention and control initiatives in countries of the region, in particular Cambodia, Lao People's Democratic Republic, Malaysia, Myanmar, the Philippines, Thailand and Vietnam. In 2010, the OIE and Association of Southeast Asian Nations (ASEAN) supported the membership of the remaining ASEAN countries (Brunei Darussalam and Singapore) and China, which has resulted in a vastly expanded programme, now renamed the South-East Asia and China Foot and Mouth Disease campaign (SEACFMD).

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6 The Management and Economics of East Coast Fever

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Executive Summary

The problem

East Coast fever (ECF) is a fatal bovine disease caused by the protozoan parasite *Theileria parva*. The disease occurs in 16 countries in eastern, central and southern Africa where the vector, the brown ear tick (*Rhipicephalus appendiculatus*), is found. ECF causes major economic losses by affecting both dairy cows and young Zebu cattle in pastoralist systems and ranches. It is among the most serious constraints to cattle productivity in the countries in which it is found.

    The costs of ECF include both direct and indirect losses. Direct losses are due to cattle deaths, the stunting of calves, reduced milk production in survivors, and the costs of preventing and controlling the disease. Indirect losses include the lack of adoption of more productive breeds of cattle and the avoidance of areas of high infection risks. ECF affects households by reducing milk supplies, depleting assets and reducing incomes, all of which harm household food and nutritional security.

    ECF has been controlled predominantly through acaricide application, but this treatment is expensive and not always successful. An alternative option is for farmers to keep local breeds of cattle, which tend to be more disease resistant but less productive than exotic breeds.

It is widely accepted that vaccination is the most attractive control option, and the development of a vaccine to protect cattle against ECF was one of the founding aims of the International Laboratory for Research on Animal Diseases (IL-RAD).

    At about the time of ILRAD's establishment in 1973, a vaccination procedure was being developed at the East African Veterinary Research Organization (EAVRO) at Muguga, Kenya. The infection-and-treatment method (ITM) is an immunization procedure against ECF. It involves inoculation of live sporozoites of *T. parva*, usually in the form of a semi-purified homogenate of *T. parva*-infected ticks, combined with simultaneous treatment with a dose of a long-acting formulation of the antibiotic oxytetracycline. Whilst safe and very effective when administered correctly, production and delivery of this live ECF vaccine is complicated, expensive and time consuming, and at the time of ILRAD's founding, there were doubts as to whether such a procedure was commercially viable.

ILRI's contribution in the global context

The International Livestock Research Institute (ILRI) has played a pivotal role in overseeing ECF management in the affected regions of Africa. From the beginning, ECF and trypanosomiasis

were central to the work of ILRAD. The institute has led activities in various vaccine development strategies, including commercial production of the ITM vaccine. ILRI has also overseen the development and application of molecular tools to characterize the vaccine and to address concerns by veterinary authorities about the risks of using ITM in the field. ILRI has also undertaken major research efforts to develop an alternative (subunit) vaccine and has furthered our understanding of the bovine immune response in support of these efforts.

Impacts of ILRI research

Scientific impacts

ILRI has generated important research findings in several aspects of ECF research. These are outlined as follows.

ITM. Scientific contributions to the development, production and use of ITM immunization have been significant; together, these contributions have enabled the immunization of hundreds of thousands of cattle in both the pastoralist and dairy sectors and have assisted the commercial production, distribution and use of the vaccine in eastern Africa.

IMMUNOLOGY OF T. PARVA INFECTION. In terms of scientific impacts, ILRI scientists provided convincing evidence that a response by cytotoxic T lymphocytes (CTLs) was the main effector mechanism deployed by immune cattle against T. parva infection; this work was important in the broader context of vaccine development as it was one of the first demonstrations that CD8+ CTLs could mediate protection against intracellular protozoan parasites. ILRI scientists made the first successful identification of T. parva proteins recognized by CTLs from immune cattle; the identification of these CTL antigens was a major achievement in vaccine research, and further examination of the antigens and the CTLs directed against them has yielded some very valuable insights into the immunobiology of the host–parasite relationship.

ADVANCES IN BOVINE IMMUNOLOGY. As part of the work investigating the immunology of T. parva infection, significant advances were made in our understanding of the bovine immune system. These are discussed here and in Chapter 4 (this volume).

SEQUENCING OF THE T. PARVA GENOME. Sequencing of the T. parva genome was carried out by Gardner et al. (2005). This was the second apicomplexan to be sequenced and was essential in screening for CTL antigens. A related paper (Pain et al., 2005) compared the genome of Theileria annulata with that of T. parva.

STRAIN CHARACTERIZATION. Scientists at ILRI in collaboration with many other researchers developed DNA-based methods to characterize Theileria spp. parasites, including restriction fragment length polymorphisms of repetitive regions of the T. parva genome, analysis of polymorphisms in ribosomal RNA genes, in telomere regions of the parasite chromosomes and in genes encoding T. parva antigens and the use of microsatellites and minisatellites.

SPOROZOITE SUBUNIT WORK. Scientists at ILRI demonstrated that immunity to T. parva could also be induced through vaccination with the p67 protein, which is present on the surface of the infective sporozoite stage of the parasite. The protection is believed to be mediated primarily by antibodies.

CELLULAR PROLIFERATION. A spillover impact of ILRI's ECF research, which turned out to be important for the medical research community, was the discovery that upregulated casein kinase 2 is the cause of uncontrolled cell proliferation in cattle suffering from theileriosis. This discovery in this 'bovine cancer' research advanced our understanding of the role of this enzyme in the development of certain human cancers, and thus of potential targets for treatment regimes.

Epidemiological scientific impacts are described in Chapters 5 and 8 (this volume). A major ILRAD product was the book *The Epidemiology of Theileriosis in Africa* (Norval et al., 1992). This not only focused on epidemiology but also covered all aspects of the parasite and infection life cycles.

Development impacts

In 1996 at the request of the FAO, ILRI produced 600,000 doses of the 'Muguga cocktail', a version of the ITM vaccine, which was subsequently distributed commercially. In 2007, when stocks of this batch were depleted, ILRI was asked by

AU-IBAR to produce a second batch at its own cost. With no other institutions in the region with the facilities and expertise to oversee this task, ILRI again complied, producing 1.2 million doses of the 'Muguga cocktail' vaccine ('ILRI08' batch), almost all of which has been commercially distributed. In 2008, ILRI addressed concerns of smallholder dairy farmers regarding the large number of doses that were included in each vaccine straw. To make relatively few doses available to those keeping just a few cows, ILRI produced vaccine straws with just five to eight doses. The doses in these straws proved to be as safe and effective as those in the larger-dose straws. Use of the ECF ITM vaccine has had major development impacts. It has protected approximately 1.6 million cattle against the disease from 1997 to 2014, preventing the untimely deaths of some 400,000 animals over that period, assuming a typical annual calf mortality of 40% (Di Giulio *et al.*, 2009). About 80% of the ECF ITM vaccine has been sold in the pastoral production systems of northern Tanzania, about 10% in the pastoral systems of Kenya and the remainder in the smallholder dairy systems of Kenya. ILRI also facilitated the transfer of production of the vaccine to the Centre for Ticks and Tick-Borne Diseases (CTTBD) in Malawi.

Economic impacts

The production and distribution of the ECF ITM vaccine has protected millions of cattle, preventing the deaths of thousands of valuable animals. Use of the vaccine also improved milk production and reduced stunting in calves and the costs of preventing and controlling the disease. Earlier studies estimated that adoption of multi-component ECF vaccines in affected countries would reduce the value of calf mortality annually (by US$10.1 million) and increase the value of milk production (by US$1.7 million), with estimated economic returns of US$9–17 for every dollar invested. Other economic modelling that considers vaccine adoption processes over time and a wide range of economic impacts is presented in this chapter. In Kenya, production of beef and dairy in 2030 is shown to increase by up to 40% and 56%, respectively, compared with baseline conditions of no new investments in ECF management. Changes such as these have potential implications for incomes obtained by farmers and

prices paid by consumers but also on food imports, livestock feed demand, and land use.

Policy impacts

ILRI scientists helped obtain official registration of the ECF ITM Muguga cocktail vaccine in Kenya, Malawi and Tanzania and approval for use in Uganda pending registration. Until the vaccine was registered in each country, it had only been used with special permission given by the national veterinary authorities.

Capacity building

ILRI supported at least 34 graduate fellows in ECF studies, including 20 PhD degrees, 13 MSc degrees and one post-doctoral scientist. ILRI also contributed significantly to vaccine production capacity CTTBD, Malawi.

Partnerships

Development of the ECF ITM vaccine and overall management of ECF in the region has led to several ILRI partnerships with other institutions, including: the Africa Union–Interafrican Bureau for Animal Resources (AU-IBAR), Centre for Ticks and Tick-Borne Diseases (CTTBD, Malawi), Food and Agriculture Organization of the United Nations (FAO), GALVmed (UK), Kenya Agricultural and Livestock Research Organization (KALRO), United Nations Development Programme (UNDP), Vet Agro Limited (Tanzania), VETAID (Uganda) and Vétérinaire Sans Frontière-Germany (VSFG).

Introduction

ECF is a devastating tick-borne disease of cattle caused by a protozoan parasite, *Theileria parva* (Norval *et al.*, 1992, pp. 64–97, on the classification of *Theileria* spp.; Coetzer *et al.*, 1994). The majority of the discussion in this chapter and in Chapter 5 (this volume) is of *T. parva*. The form of theileriosis known as ECF is present in 12 countries in eastern, central and southern Africa where the vector, the brown ear tick (*Rhipicephalus appendiculatus*), is found (CABI, 2020). ECF causes major economic losses by affecting both dairy cows and young Zebu cattle in pastoralist systems and ranches. A clinically

similar disease, Corridor disease, is found in cattle infected with *T. parva* transmitted by ticks which have fed on buffalo. The chief distinguishing feature of Corridor disease is the low number of the piroplasm (blood) stage of the parasite. A milder form of ECF in Southern Africa with strong seasonal occurrence is referred to as January disease in Zimbabwe. It is among the most serious constraints to cattle productivity in the countries where it is found. Development of a vaccine to protect cattle against ECF was one of the founding aims of ILRAD (see Introduction chapter, this volume). *T. parva* also causes corridor disease if buffalo-adapted parasites are transmitted to cattle, and January disease in Zimbabwe. These have similar clinical signs to ECF but last for only a few days, and emaciation and diarrhoea are not seen. Turning sickness is an aberrant infection characterized by neurological signs caused by parasites in cerebral blood vessels.

T. annulata causes tropical theileriosis or Mediterranean Coast fever. Transmitted by hyalommid ticks, it occurs in North Africa, southern Europe, the Near and Middle East, India, China and Central Asia. It causes both mortality and reduced production, and has significant economic impacts as a result.

The Parasite

The *T. parva* parasite has a complex life cycle involving bovine hosts (African buffalo and domestic cattle) and the tick vector (Fig. 6.1).

The tick feeds on the host three times, as a larva, nymph and adult. *Theileria* sporozoites develop in the salivary glands of infected ticks and are passed to cattle along with tick saliva when the ticks feed. In cattle, these sporozoite forms of the parasite attach themselves to the animal's white blood cells (lymphocytes): some sporozoites enter lymphocytes and develop into multinucleate parasite forms called macroschizonts. The infected bovine lymphocytes become enlarged
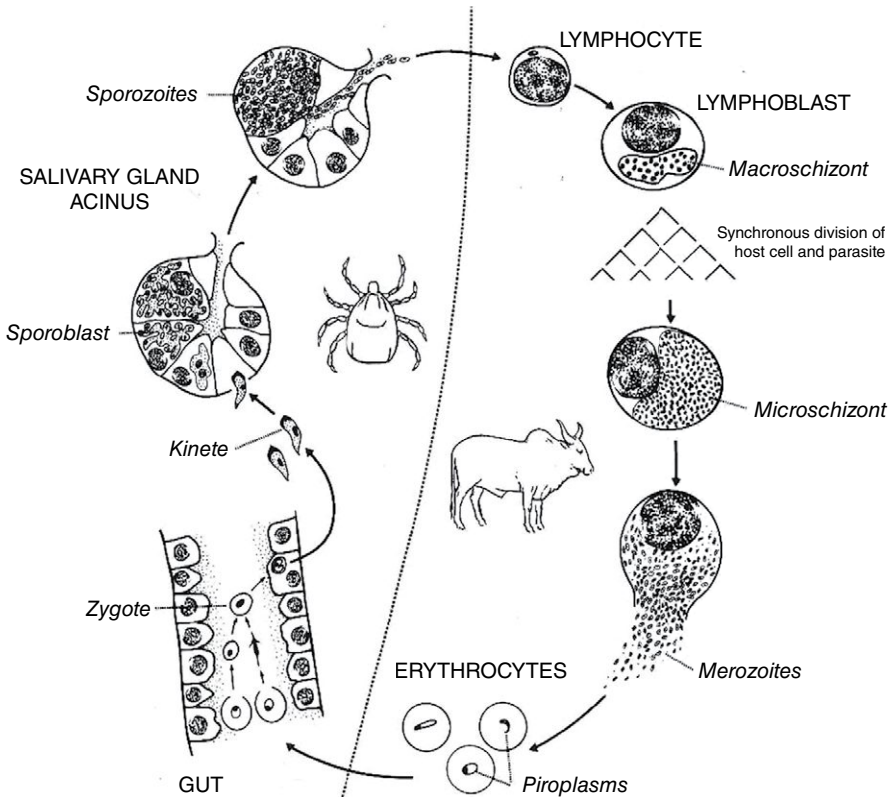

Fig. 6.1. Life cycle of *T. parva* (anon, ILRI).

cells (lymphoblasts) that multiply in synchrony with the parasites, resulting in a rapidly expanding population of infected bovine cells. Some of the macroschizonts differentiate into microschizonts and then merozoites during infection. These merozoites are released into the bloodstream and invade red blood cells, where they further develop into forms called piroplasms. Ticks feeding on cattle become infected when they ingest red blood cells containing piroplasms. In the tick gut, the parasites differentiate into male and female gametes, which fuse to form zygotes. These develop further and eventually migrate to the tick's salivary glands. Here, stimulated by tick feeding, 30,000–50,000 sporozoites develop in an average tick. These are introduced with tick saliva into a new bovine host, initiating a new cycle of parasite development.

The initial clinical signs of infection include pyrexia and enlargement of the superficial lymph nodes, most notably the parotid and prescapular nodes. As the infection progresses, the animals become listless and anorexic and exhibit severe respiratory distress. There is often a progressive loss of white blood cells. On post-mortem examination, infected lymphocytes are found in several organs including the lymph nodes, lungs, liver, kidneys, gastrointestinal tract and sometimes the brain. A particularly prominent post-mortem finding is frothy exudate in the trachea and severe congestion of the lungs (Irvin *et al.*, 1983). In contrast, *T. parva*-infected buffalo show few if any clinical signs of disease.

It is believed that *T. parva* co-evolved with the African Cape buffalo and has undergone a 'host jump' to cattle, where it causes the disease referred to as ECF (reviewed by Norval *et al*., 1992).

Control methods

The dominant method for controlling ECF has been the application of acaricides to cattle to limit their tick infestations. The acaricides are applied as sprays, in dips and more recently as oil-based pour-ons. This control method has several disadvantages. After prolonged use, the ticks can develop resistance to the active ingredient in the acaricides (Abbas *et al.*, 2014) and few if any novel acaricides are expected on the market in the immediate future. Ticks have developed resistance to all known classes of acaricides. The

rate of development of resistance has ranged from 2 years (synthetic pyrethroids) to 40 years (arsenic) influenced by, among other factors, the class of acaricide and the frequency of application. Acaricides also expose users to potential health risks, which are exacerbated by lack of protective clothing and can also cause environmental contamination. Frequent use of acaricides is expensive – in high ECF-challenge areas, application might be needed every 5 days.

A second strategy to reduce the losses associated with ECF is to use less susceptible, but less productive, indigenous cattle rather than improved cattle breeds, which are more susceptible to the disease (Stobbs, 1966; Ndungu *et al.*, 2005). As a third strategy, drugs are available for the treatment of clinical ECF, but to be effective, these must be used at an early stage of the disease and thus require constant monitoring of cattle, which presents difficulties, especially in pastoral systems. In addition, the cost of the drug treatment is high (US$40 per animal), which can be prohibitive, especially for less valuable Zebu animals. More recently, a vaccination protocol known as the infection-and-treatment method (ITM) has become available commercially and is increasingly being used, as discussed below.

Impacts of ECF

The impacts of the disease include direct losses due to cattle deaths, the stunting of calves, reduced milk production in survivors, and the cost of measures to prevent and control ECF. Indirect losses include the lack of adoption of more productive breeds of cattle and the avoidance of areas of high infection risk. ECF affects households by reducing milk supply, depleting assets and reducing incomes, all of which harm household food and nutritional security. Moreover, for smallholder dairy farmers with just one or two animals, the loss of a valuable cow can be a devastating blow. In one pastoralist area in northern Tanzania, overall calf mortality was shown to be 40–80%, with 75% of all deaths due to ECF (Di Giulio *et al.,* 2009). Chapter 5 (this volume) reports more detailed epidemiological and economic studies of the impact of ECF.

It is estimated that 40 million of the 75 million cattle in the eastern, central and southern Africa region are at risk of contracting ECF

(Morzaria and Williamson, 1999; McLeod and Randolph, 2000; FAO, 2014, 2017).

In 1992, an ILRI-led study estimated that ECF caused annual economic losses totalling US$170 million, including more than 1 million cattle deaths a year (Mukhebi *et al.*, 1992). By 2005, cattle deaths alone, at 1.1 million head, accounted for more than US$300 million, based on the unit price of cattle. ECF-related cattle deaths in 2005 thus represented around 44% of the combined value of beef production in Burundi, Kenya and Rwanda in that year (FAO/AU-IBAR/ILRI, 2017).

Various studies have estimated the impact of the disease at national or local levels. In 1999, an ILRI-led study estimated that total losses due to ECF in Kenya were more than US$95 million a year, with mortality accounting for almost three-quarters of this amount; loss of milk production due to morbidity and the cost of acaricides made up most of the balance. For Tanzania, the estimated total annual loss was US$43.8 million, most of which was due to mortality. These estimates can be of significant economic importance. For example, the annual ECF-related losses in Kenya estimated in 1999 would have been equivalent to 11% of the total value of output from the livestock subsector, while the annual losses in Tanzania translated to up to 46% of the same.

The Infection-and-Treatment Method of Vaccination

ITM is an immunization procedure against ECF. The basis for the development of ITM lay in the observations, made shortly after the disease was characterized, that cattle that survived an episode of ECF were unlikely to experience a second clinical episode. Early experiments of Arnold Theiler showed that cattle infected 'artificially' with parasite preparations were subsequently resistant to field challenge. Proof of concept of the ITM approach as a practical means of vaccination was achieved during the 1970s by the group at EAVRO led by Matt Cunningham, as has recently been documented in detail by Perry (2016), and much of the credit for current field application of ITM against theileriosis belongs to these scientists, who long preceded ILRAD and ILRI.

ITM involves inoculation of live *T. parva* sporozoites, usually in the form of a semi-purified homogenate of *T. parva*-infected ticks, combined with simultaneous treatment with a dose of a long-acting formulation of the antibiotic oxytetracycline. Without the antibiotic treatment, the sporozoite inoculation would be lethal. The oxytetracycline suppresses the infection by inhibiting the development of sporozoites to schizonts in lymphocytes (Spooner, 1990). The outcome is an asymptomatic infection or a mild ECF episode followed by the development of a protective immune response. The immunity has been shown to last for at least 43 months in the absence of challenge (Burridge *et al.*, 1972) and it is accepted that a single inoculation confers life-long immunity to the disease under field conditions. Cattle that have been immunized by ITM, or that have survived a natural challenge, may become 'carriers' of a persistent, potentially tick-transmissible, infection.

Adoption of the ITM vaccine has been reported to be associated with a range of benefits. Calf mortality rates have been dramatically reduced, such as in pastoralist areas of northern Tanzania where calf mortality rates dropped from 80% to as low as 2% in a study of 2178 crossbred calves (1434 immunized and 744 controls) in 167 smallholder households in two districts (Lynen *et al.*, 2012). Pastoralists also report that cattle wearing the distinctive round ECF ear tag attract higher prices than non-vaccinated animals of equal size. In another study in Tanzania, it was found that households that had used the ITM vaccine sold twice as many animals as non-adopting households (Homewood *et al.*, 2006).

Although acaricides may still be required for other tick-borne diseases, vaccination by ITM reduces the frequency of acaricide application. In both smallholder dairy and pastoralist areas of northern Tanzania, acaricide application is now often done once a month rather than once a week. Pastoralists also report that when their animals are vaccinated, they no longer have to avoid areas where they know cattle are at high risk of ECF. A study by Lynen *et al.* (2012) reported that 80% of the farmers reduced the frequency of acaricide treatment after immunization, while 38% reduced this treatment by more than 75%.

Other methods of controlling ECF are available. They include treating animals with anti-theilerial drugs when they fall sick. The therapeutic drugs are quite effective but require early diagnosis as the disease progresses very

quickly. The drugs also tend to be expensive, costing US$40–60, and are beyond the reach of many smallholder farmers. This drug treatment also has the disadvantage that once an animal suffers ECF, production losses, including stunting in calves, follow.

In smallholder dairy systems where cattle are kept confined rather than allowed to graze, exposure to ticks, and therefore diseases, is minimized. Where farmers can grow their own fodder, this is quite an effective disease control strategy. Quite often, however, farmers must get feed from outside the farms and this can introduce ticks, leading to disease outbreaks. As mentioned, another approach has been to maintain indigenous cattle breeds that are relatively tolerant to tick-borne diseases, including ECF. However, the local breeds are less productive than improved breeds, so this strategy is unsuitable for intensive smallholder dairy farming.

Development of the ITM vaccine

Work to develop an ECF vaccine began in the 1960s at EAVRO, located in Muguga, Kenya, under the auspices of the East African Community. Following the collapse of the East African Community, it continued at the National Veterinary Research Centre, KARI (now the Veterinary Research Centre, KALRO). This culminated in the introduction of the ITM Muguga cocktail vaccine on a commercial basis in various eastern African countries for various classes of cattle between 1998 (Tanzania pastoral sector) and 2012 (Kenya dairy sector).

For close to 50 years, many partners have been involved in the testing, refinement, re-testing, production, registration and commercialization of the vaccine. Key among this team has been (in alphabetical order): the Africa Union–Interafrican Bureau for Animal Resources (AU-IBAR), CTTBD (Malawi), Food and Agriculture Organization of the United Nations (FAO), Global Alliance for Livestock and Veterinary Medicines (GALVmed, UK), KARI, UNDP, Vet Agro Limited (Tanzania), VETAID (Uganda) and VSFG. Financial support for more than four decades has been provided by many donors and investors, including the Bill & Melinda Gates Foundation (BMGF), Biotechnology and Biological Sciences Research Council (BBSRC), CGIAR Funders through ILRI, Danish International Development Agency (DANIDA), FAO, International Fund for Agricultural Development (IFAD), Netherlands government, Overseas Development Administration/Department for International Development (ODA/DFID) and Wellcome Trust, among others.

The ITM method was built on three key practical developments:

- The demonstration that animals could be reproducibly infected with a ground-up suspension of whole infected ticks.
- The observation that such tick preparations could be stored for extended periods in liquid nitrogen and were infectious when thawed.
- The use of antibiotics, particularly long-acting tetracycline, as a reliable means to prevent the clinical effects of a dose of the tick suspension without impairing the development of immunity.

One challenge that remained was that of parasite strain specificity, or the frequent inability of a single parasite strain when used in ITM to protect against all other strains of the parasite. Researchers at EAVRO assessed the protective capacity of several parasite isolates and showed that a combination of parasites from three isolates – Muguga, Serengeti-transformed and Kiambu 5 – offered the most complete protection to heterologous challenge (Radley *et al.*, 1975). The combination was named the 'Muguga cocktail'. Other forms of ITM have been produced and tested over the years using different *T. parva* isolates. The veterinary authorities in Kenya, Zambia and Zimbabwe favoured the locally derived, single isolates Marikebuni, Boleni and Katete/Chitongo, respectively, while the rest of the eastern African region chose the Muguga cocktail. Kenya later also adopted the Muguga cocktail.

ILRI's contribution to the Muguga cocktail

Production of the ITM vaccine is a long and complicated process, involving artificial infection of 'production' cattle, application of several hundred thousand ticks to the cattle and homogenization of the subsequently infected ticks (Patel *et al.*, 2016). The clean ticks, which come from a selected population of highly susceptible ticks maintained by ILRI's tick unit, are fed on production cattle infected with one of the three component stabilates. Infected ticks are analysed

for infection rates to ensure that equal numbers of sporozoites from each isolate are included when the ticks are combined before homogenization. The Muguga cocktail stabilate is evaluated in extensive *in vivo* trials to ensure that the vaccine is both safe and effective and to determine the appropriate dilution with respect to a fixed dose of oxytetracycline.

Given the complicated production process, one of the perceived obstacles to the widespread use of the ITM Muguga cocktail was the prospect of producing standardized, large-scale batches of several hundred thousand doses of the vaccine. In 1996, ILRI was asked by FAO to undertake this challenge, which resulted in the production of over 600,000 doses of a safe and effective vaccine. At the time, there was no other institution in the region with the facilities and expertise to undertake this task. The vaccine was provided to CTTBD, in Malawi, for subsequent sales and distribution. All the available vaccine was sold unsubsidized on a commercial basis, which provided strong evidence that a commercially viable demand for the vaccine existed.

In 2007, when the stocks of the FAO-requested ILRI batch were about to be depleted, ILRI was asked to produce a second commercial-scale batch. At its own expense, the institute produced a batch of about 1.2 million doses (named 'ILRI08'). These were sold to distributors authorized by the respective national veterinary authorities. As in 1998, no other institution in the region could mass produce a quality-assured ITM Muguga cocktail vaccine, so ILRI's production again ensured continued vaccine supply at a time when demand for the vaccine was gradually increasing across the region, especially in Tanzania. In association with GAL-Vmed, ILRI also compiled the documentation required to support the registration of the ITM Muguga cocktail, which was subsequently officially registered in Kenya, Malawi and Tanzania, and progress was made towards registration of the vaccine in Uganda. Until the vaccine's registration in each country, the vaccine had been used through special permission by the national veterinary authorities, which discouraged private distributors from taking up the vaccine. ILRI scientists also published details of the production process in a peer-reviewed journal to ensure future production of standardized batches of the Muguga cocktail stabilate (Patel *et al.*, 2016).

Further production of the vaccine will be undertaken by CTTBD, in Malawi. In conjunction with GALVmed, ILRI facilitated the establishment of the process in CTTBD and supplied the vaccine seed stabilates, which were made at the same time as the 'ILRI08' vaccine batch, and well-characterized pathogen-free *Rhipicephalus appendiculatus* ticks. ILRI scientists continue to provide technical advice to Malawi.

One of the commonly voiced issues surrounding the ITM vaccine, especially in the smallholder dairy systems, is the number of doses in the vaccine straws (ILRI/GALVmed, 2015). The standard presentation of the ITM vaccine produced at ILRI is plastic straws of 32–40 doses, cryopreserved in liquid nitrogen. Once thawed and prepared for vaccination with diluent, the vaccine has a working life of only a few hours (Mbao *et al.*, 2006); any vaccine unused by that time must be discarded. Whereas this is not a major problem when vaccinating large herds in pastoralist settings, use of the vaccine in smallholder settings, where each smallholder may have only two or three cattle, can lead to substantial wastage of the vaccine. To overcome this, ILRI demonstrated that the vaccine straws can be thawed, diluted, refrozen and repackaged with minimal loss of vaccine viability. An initial experimental production resulted in straws containing five to eight doses (Patel *et al.*, 2019). In collaboration with Vet Agro Limited, in Tanzania, ILRI showed that the vaccine was safe and effective under both experimental and field conditions. Importantly, cattle vaccinated with the diluted vaccine are protected against challenge with the parent stabilate, suggesting that any important antigenic types are not lost during the process.

Development and application of molecular tools

Over the past 35 years or so, ILRI has developed and utilized a series of increasingly sophisticated molecular tools to investigate various aspects of *T. parva* infection. These have taken advantage of, and kept pace with, advances in the fields of immunology, molecular biology, genomics and biotechnology. Some of these tools, which were developed primarily to study the biology and epidemiology of the parasite or to facilitate the pursuit of a subunit vaccine against *T. parva*, have

found subsequent use in the analysis of the ITM vaccine. These tools have improved the quality control of the immunizing stabilate and have provided greater insights into the true genetic complexity of the Muguga cocktail and the efficacy and biological impact of ITM in the field. They have also helped to allay concerns of the veterinary authorities about the risks of using ITM in the field.

Monoclonal antibodies (mAbs)

mAbs were raised against the schizont stage of the parasite specifically to try to define the immunological heterogeneity that had been observed during the early stages of the development of the ITM vaccine. The first set of seven mAbs did indeed show differential reactivity in immunofluorescent assays with a set of schizont-infected cells, especially those derived from buffalo (Pinder and Hewitt, 1980). These observations were confirmed with a further nine mAbs tested on an extended array of parasite isolates (Minami *et al.*, 1983). An additional observation from this work was that immunized cattle were susceptible to heterologous challenge from a parasite of different mAbs reactivity profiles, and that the 'breakthrough' parasites had the same profile as those comprising the heterologous challenge. In a companion publication, it was reported that cattle were protected from heterologous challenge from parasites having a similar mAb profile but not those with a different profile (Irvin *et al.*, 1983).

One of the practical aims of developing the mAbs was to use them to characterize antigenically distinct strains for inclusion in an ITM stabilate for use in field immunization. This has not been possible, primarily because most of the anti-schizont mAbs recognize the same antigen and it is now known that several other antigens are the targets of the protective immune response induced by ITM (see below). A panel of nine of the mAbs was used as part of a study involving several approaches to characterize the component stocks of the Muguga cocktail (Bishop *et al.*, 2001). The results showed that two of the stocks (Muguga- and Serengeti-transformed) displayed identical patterns of reactivity, whereas the Kiambu 5 stock did not react

with three of the mAbs. The original 16 mAbs described above, plus an additional four generated against buffalo-derived parasites, were used to characterize infected lymphocytes from buffalo (Conrad *et al.*, 1987b; Baldwin *et al.*, 1988). Among other things, the results showed that parasites with different mAb reactivity patterns were present in a single isolate and that different parasite types were isolated from the same animal when sampled at different times but that cloned parasite lines did not alter their mAb reactivity profile. Although the possibility of antigenic variation (the ability of a single organism to express different antigens or forms of the same antigen at different times) in *T. parva* had been proposed earlier (Young *et al.*, 1988), the last observation suggested that this was not the case. Thus, it became clear that the same animal can be infected with several parasite types concurrently, and that while an initial infection can result in protection against subsequent disease, it may not necessarily protect against subsequent infections. This observation has important implications in the ability of vaccinated animals to transmit parasites to other, non-vaccinated, animals.

The specificity of several of the mAbs has been determined and all were shown to react with a single antigen known as the polymorphic immunodominant molecule, or PIM (Shapiro *et al.*, 1987; Toye *et al.*, 1991). The differential reactivity with strains of *T. parva* is believed to be due to sequence variation of the epitopes located within the PIM antigen (Toye *et al.*, 1995a). The size variation of the antigen among parasites from different isolates allowed an additional layer of discrimination. It was noted, for example, that analysis of cloned cell lines, all derived from the Marikebuni isolate, revealed four different parasite types (Goddeeris *et al.*, 1990; Toye *et al.*, 1991).

PIM was also shown to be the major antigen recognized by sera from infected cattle, which has led to its use in an enzyme-linked immunosorbent assay (ELISA) developed by ILRI scientists to detect antibodies to *T. parva* (Katende *et al.*, 1998). This ELISA is used extensively during the production of the ITM vaccine to screen cattle to be used for production of the sporozoites for the stabilate and for assessing the safety and efficacy of the final product (Patel *et al.*, 2016). In the field, the assay is relied upon to

assess seroconversion levels following vaccination, and it has been used widely in epidemiology studies (Gitau *et al.*, 1997; Okuthe and Buyu, 2006; Swai *et al.*, 2009; Kivaria *et al.*, 2012; Malak *et al.*, 2012; Toye *et al.*, 2013; Kiara *et al.*, 2014).

Similar ELISAs were developed at ILRI for other tick-borne diseases caused by *Theileria mutans* (Katende *et al.*, 1990), *Anaplasma marginale* (Morzaria *et al.*, 1999) and *Babesia bigemina* (Tebele *et al.*, 2000) and were transferred for commercial distribution to Svanova Biotech AB, now part of Boehringer-Ingelheim Animal Health. The *Theileria* assays were subsequently withdrawn from sale due to insufficient global demand. *T. parva* is limited to parts of eastern, central and southern Africa, and *T. mutans* is generally considered to be non-pathogenic. Nevertheless, the assays are still offered as kits and as a diagnostic service by ILRI.

DNA-based strain identification

Scientists at ILRI in collaboration with other researchers have developed a series of DNA-based methods to characterize *Theileria* parasites, including restriction fragment length polymorphisms of repetitive regions of the *T. parva* genome (Conrad *et al.*, 1987a; Allsopp *et al.*, 1989), analysis of polymorphisms in ribosomal RNA genes (Bishop *et al.*, 1992), telomere regions (Morzaria *et al.*, 1990) and genes encoding *T. parva* antigens (Geysen *et al.*, 1999), and the use of microsatellites and minisatellites (Oura *et al.*, 2003). An early application of these techniques to the ITM vaccine revealed that two of the component stabilates (Muguga and Serengeti-transformed) were remarkably similar and quite distinct from the Kiambu stabilate (Bishop *et al.*, 2001). In a collaborative study with scientists from the University of Glasgow Veterinary School and the UK's Institute of Animal Health at Pirbright, these markers were applied to analyse samples from cattle vaccinated in the field with the Muguga cocktail (Oura *et al.*, 2004, 2007).

With the caution that these markers represent a very small but none the less highly polymorphic segment of the parasite genome, the work showed that the vaccine strains can persist in vaccinated animals for several years. Local parasite strains were also detected in animals after vaccination, indicating that the vaccinated animals can become re-infected but not show clinical disease. The studies also showed that non-vaccinated animals co-grazing with vaccinated animals could be infected with the vaccine parasites. This phenomenon has been put forward as a case against the use of live parasite vaccines, particularly those comprising parasites originating from areas outside those in which cattle are being vaccinated (McKeever, 2007). These concerns are allayed by observations that no deleterious effects from the use of ITM have yet to be reported, that such mixing of parasite strains has been occurring for millennia, particularly through the presumably unrestricted movement of infected buffalo, and that the parasite strains used in the vaccines originate from natural infections and are not 'artificial' or the result of genetic manipulation in the laboratory.

ILRI scientists were also part of a large international team that, in 2005, reported the sequencing of the *T. parva* genome. In the conclusion to the paper reporting this in *Science* (Gardner *et al.*, 2005), the team described the genome data as 'a critical knowledge base for a pathogen of significance to agriculture in Africa'. One immediate use of the genome sequence was the development of a panel of genome-wide mini- and microsatellite markers, which greatly enhanced the power and utility of molecular analyses, as described above. The application of the mini- and microsatellite markers coupled with high-throughput electrophoresis showed that the Muguga cocktail is more complex than previously thought, containing at least 14 different genotypes of *T. parva*, although they express a limited number of alleles (Patel *et al.*, 2011). The study also showed, by comparing the genotypic composition between different batches of the vaccine, that the batches were very similar. High-throughput electrophoresis with the satellite markers has been shown to be a useful and reproducible approach that can be used to monitor the genetic composition of future ITM vaccine batches. Such a tool is essential to facilitate standardized, consistent, quality-assured vaccine production.

More recently, high-throughput sequencing has been used by ILRI scientists and collaborators to characterize the parasite more deeply. Norling *et al.* (2015) analysed the whole-genome

sequences derived from the three component stocks of the Muguga cocktail and showed that two of the stocks (Muguga- and Serengeti-transformed) were remarkably similar. Somewhat surprisingly, the total diversity residing in the three component stocks together represents only a small fraction of the *T. parva* genetic diversity observed in field isolates. This result was supported by satellite genotyping and high-throughput multilocus genotyping of genes encoding antigens recognized by cytotoxic T lymphocytes (CTLs) and believed to be important in the protective immunity seen in cattle (Hemmink *et al.*, 2016). There was very limited diversity in many of the antigen gene or satellite loci and certainly far less than is seen in field populations of *T. parva*. The results raise the intriguing question of how the Muguga cocktail can protect cattle exposed to field challenge from *T. parva*. This is one of many questions yet to be addressed concerning this method of vaccination, as discussed below.

Research to Develop a Subunit Vaccine

A subunit vaccine is one that avoids the use of a whole organism and instead relies on inoculation of those components that can stimulate, and are the target of, a protective immune response. The advantages of subunit vaccines are that they avoid the risk of infection with virulent organisms and, if they are manufactured by 'synthetic' means such as recombinant DNA technologies, are easier and cheaper to produce.

Protection of exposed animals

A fundamental observation that serves as a basis for vaccine development is that animals that survive an infection are immune to the clinical effects of a subsequent exposure. For *T. parva*, this observation was made shortly after ECF was recognized (reviewed by Lawrence, 1992). The key knowledge gained from these and many subsequent experiments is that cattle have the capacity to prevent the clinical effects of *T. parva* infection, thus instilling confidence that an effective vaccine could be developed. What was

required for the rational design of an ECF vaccine was an understanding of the mediators of this immunity and the corresponding parasite components that induced these mediators.

The anti-schizont vaccine

Lack of protection with serum

The initial focus on the mediators of the protection seen in immune animals was on the role of serum. This is not surprising given the state of knowledge of, and tools available to study, mammalian immune responses at the time. The expectation was that infection with the parasite induced the production of protective serum antibodies. However, it was shown early on that cattle with high levels of anti-*T. parva* antibodies were nevertheless fully susceptible to infection (Wagner *et al.*, 1974).

The central role of CTLs

Attention at ILRAD then turned to investigating a direct role for white blood cells as the primary mediators of immunity. The first evidence was obtained by Terry Pearson and co-workers, who showed that infected lymphocytes are specifically recognized and killed by effector cells from immune animals (Pearson *et al.*, 1979). Shortly thereafter, Eugui and Emery (1981) showed that the cytotoxic (killing) activity was genetically restricted. In other words, the killing was only observed when the infected cells and the cytotoxic effector cells came from the same animal or closely related animals. This would be expected with killing mediated by classical CD8^{+} CTLs, where recognition of the infected cell is dependent on presentation of the parasite components by molecules of the class I major histocompatibility complex (MHC), which varies among animals. This was subsequently confirmed by Goddeeris *et al.* (1986a,b) who showed that the killing was mediated by cells of the CD8^{+} lineage and, by using a panel of mismatched and semi-matched target cells, that it was restricted by a class I MHC molecule (KN104). Importantly, it was demonstrated that the killing was specific for strains of the parasite – the immune cells were derived from the Muguga isolate of *T. parva* and did not recognize cells infected with the

Marikebuni isolate. As this reflected earlier *in vivo* challenge experiments, such as the work undertaken in the development of the Muguga cocktail (discussed earlier), it provided convincing evidence that the CTL response was the main effector mechanism deployed by immune cattle. Further confirmation of this was provided by cell transfer experiments where a purified population of CD8^{+} lymphocytes from immune animals was shown to provide protection when transferred into a naïve twin recipient (McKeever *et al.*, 1994).

This work was important in the broader context of vaccine development as it was one of the first demonstrations that CD8^{+} CTLs could mediate protection against intracellular protozoan parasites. The challenge was then to replicate the induction of the protective CTL response by using isolated parasite components (antigens) rather than the whole organism – in other words, a subunit vaccine.

Identification of CTL antigens

By the early 1990s, the techniques to identify, characterize, isolate and administer parasite components that are the targets of antibody responses were well advanced and commonplace. The same situation did not apply to those recognized by CTLs. In general, CTLs are induced by and recognize antigens when they are presented on the surface of infected cells in the context of the class I MHC molecule. The most efficient way to evaluate individual components from infectious organisms for CTL recognition is to introduce the gene that encodes the antigen into a cell expressing the appropriate MHC class I molecule, and one of the technologies that was emerging to do this was transfection technology.

Among the first uses of transfection technology at ILRI was the production of cells suitable for expressing candidate antigen genes. Thus, a widely used mouse cell line was transfected with two bovine class I MHC genes, which, at the same time, provided the first conclusive evidence that a second class I MHC locus existed in cattle (Toye *et al.*, 1990; Bensaid *et al.*, 1991). Transfection technology also proved useful in isolating the gene encoding an early candidate CTL antigen (PIM), which had proved recalcitrant to isolation by the traditional bacterial expression systems (Toye *et al.*, 1995b), and in establishing the specificity of mAbs used to

characterize lymphocyte subsets (Naessens *et al.*, 1992; MacHugh *et al.*, 1993).

The feasibility of using transient transfection technology to screen libraries of genes for candidate CTL antigens was also demonstrated (Toye *et al.*, 1995c). Eventually the use of a random immunoscreen coupled with targeted gene analysis yielded the first successful identification of *T. parva* proteins recognized by CTLs from immune cattle (Graham *et al.*, 2006). In further work, the short (9–11 amino acids) peptide regions precisely recognized by the CTLs were identified, together with the class I MHC molecule that presented the peptides on the cell surface (Graham *et al.*, 2008). Unfortunately, the goal of inducing protective immune responses by using these antigens as vaccines was only partially achieved (Graham *et al.*, 2006), and no method for consistently inducing CTLs in large mammals with isolated proteins is currently available. Nevertheless, the identification of these CTL antigens was a major achievement in vaccine research, and further examination of the antigens and the CTLs directed against them has yielded some very valuable insights into the immunobiology of the host–parasite relationship.

Antigenic diversity

Antigenic diversity is the phenomenon through which parasites and other infectious organisms evade a protective immune response by changing the sequence of the epitope recognized by an existing immune response such that the mutated organism can infect an already exposed host. Evidence for antigenic diversity in *T. parva* was first shown for two of the CTL antigens, Tp1 and Tp2 (MacHugh *et al.*, 2009; Pellé *et al.*, 2011). The diversity was particularly striking in the *Tp2* gene, with single nucleotide polymorphisms identified at 61% of positions in the gene. Equally striking was the finding that there was much greater diversity in the *T. parva* parasites originating from buffalo than those from cattle, suggesting that the *T. parva* population transmitted among cattle may represent only a subset of the entire *T. parva* population, presumably that which is most fully adapted for transmission among cattle. The studies did not detect evidence among the currently identified epitopes that the mutations were driven by positive immune selection (Pellé *et al.*, 2011), although there was a

lack of recognition by naturally derived CTLs of mutated epitope sequences in both Tp1 and Tp2 (MacHugh *et al.*, 2009; Connelley *et al.*, 2011).

Immunodominance

CD8^{+} CTLs recognize antigens presented by class I MHC molecules. The genes encoding the MHC molecules are carried on two genetic regions, or haplotypes, with each parent contributing one of the haplotypes. For CTLs specific for *T. parva*, it was noted very early on that the CTLs were restricted predominantly or even completely by only one of the MHC haplotypes (Morrison *et al.*, 1987). More recent work led by Ivan Morrison at the University of Edinburgh, UK, and in collaboration with ILRI scientists has shown that the great majority of the CTLs in any given responding animal recognize the same peptide presented by the same MHC molecule (MacHugh *et al.*, 2009). The precise peptide that is recognized is governed by the MHC type of the animal. This is a quite remarkable phenomenon, given that *T. parva* is predicted to encode over 4035 proteins (Gardner *et al.*, 2005), each of which could, theoretically at least, contain hundreds of peptide epitopes. The focus of the CTL response on one or two epitopes, termed immunodominance, had been described previously in viral infections, but this was the first description of the phenomenon in a complex organism such as *T. parva*.

Immunodominance has significant implications on the performance of a potential subunit vaccine. The focus of the response on one or two epitopes leaves the animal vulnerable to infection with a second parasite that carries mutations in those epitopes. Given the large number of MHC haplotypes that are likely to be present in outbred populations of cattle, there may be a similarly large number of epitopes presented by those MHC molecules. For there to be a subunit vaccine of practical use, it may rely on the existence of a few antigens of limited diversity that can induce CTLs specific for epitopes present on those antigens when given in isolation and that can still recognize and kill infected cells.

The anti-sporozoite vaccine

While the CTL response was being examined, another approach, led by Tony Musoke, was being taken within ILRI, which was aimed at developing a vaccine to prevent the entry of sporozoites into infected cells. This was based on evidence that sera of animals from endemic areas or animals that had been hyperimmunized against *T. parva* were able to neutralize the entry of sporozoites into lymphocytes *in vitro* (Musoke *et al.*, 1982). The availability of neutralizing mAbs led to the identification of the p67 surface molecule as the target of the protective antibodies (Dobbelaere *et al.*, 1985). These observations culminated in the remarkable demonstration that cattle vaccinated with a recombinant version of the p67 antigen were immune to subsequent challenge with *T. parva*, which raised the prospects of a commercial vaccine against ECF (Musoke *et al.*, 1992). However, subsequent field trials have returned mixed results in terms of the protective ability of the vaccine (reviewed by Nene *et al.*, 2016) and the goal of a vaccine based on the p67 antigen is yet to be realized.

ITM: The Future

ILRI's scientific contributions to the development, production and use of the ITM vaccine have been significant. Together, these contributions have enabled the ITM Muguga cocktail to be used to immunize hundreds of thousands of cattle in both extensive (pastoralist and ranch) and dairy sectors. They have also helped pave the way for commercial production, distribution and use of the vaccine in much of eastern Africa.

New research and development problems must be addressed, however, as discussed below. Many of these challenges and opportunities are also described by Perry (2016), based on a review commissioned by CGIAR.

The buffalo problem

Although the Muguga cocktail appears to provide good protection against cattle-derived parasites in both laboratory and field conditions, the group at EAVRO observed that this protection did not extend to cattle exposed to buffalo-derived parasites (Radley *et al.*, 1979). Breakthrough infections were recently observed in

Kenya, where immunized cattle graze with or near buffalo (Sitt *et al.*, 2015), although the vaccine appeared to perform well in northern Tanzania, where buffalo and cattle graze together (Homewood *et al.*, 2006). To combat this, an obvious solution is to produce a vaccine stabilate containing buffalo-derived parasites, although this presents two additional challenges. First, given the extensive heterogeneity in the parasite population found in buffalo, it may be difficult if not impossible to select a 'buffalo' parasite stabilate that will protect against all buffalo challenges. Second, the very low parasitaemia found in cattle infected with buffalo-derived parasites will increase considerably the number of cattle required in the production process, which may render this approach economically unsustainable. The current alternative is to provide clear guidelines as to where the ITM Muguga cocktail should and should not be used.

Molecular tools

The powerful molecular tools developed by ILRI and other scientists can now be used to track quantitative variation in the parasite composition of stabilates. The availability of these tools means that formal procedures must be developed and documented as standards to evaluate production batches of stabilate to ensure the production of a consistent, standardized, safe and effective product. More sophisticated and powerful molecular tools are likely to be needed in the future, for example to detect parasite components that might be important for immunity or transmission but that are present at low, currently undetectable, levels. Also, more studies are needed to identify which antigens are responsible for the protection conferred by the Muguga cocktail vaccine.

Cold chain

The need for a liquid nitrogen cold chain is inconvenient and logistically challenging. Attempts to date to lyophilize (or freeze-dry) *T. parva* sporozoites to make them stable at or near room temperature have resulted in low and variable rates of recovery of viable parasites. Lyophilization of organisms as large and complex as sporozoites is likely to present a significant challenge and may not be possible with the technology available today.

Vaccine production

The production and testing of batches of stabilate is expensive, demanding and time consuming, and raises animal welfare issues: production of 1 million doses requires 18 months, 130 cattle, 500 rabbits and at least 600,000 nymphal ticks. A further problem in the production of the ITM vaccine is that the process includes the sexual stage of the *T. parva* life cycle. Because of this, recombination can occur, causing stabilates to vary both qualitatively and quantitatively, complicating efficacy and safety testing. Studies have begun at ILRI to develop an *in vitro* correlate of potency, which may reduce or eliminate the need for the extensive *in vivo* testing that is now required. In addition, *in vitro* production (growing of parasites in vessels under laboratory conditions) could minimize the need for cattle, rabbits and ticks, thereby simplifying production and reducing the opportunity for interbatch variation to occur.

Performance monitoring

As use of the ITM vaccine increases, it will be important to continue to monitor the dynamics of local *T. parva* populations and to investigate apparent vaccine failures and breakthroughs. Standard protocols should be developed to guide such studies and the molecular and other tools as well as capacity building and technical support to national laboratories charged with this responsibility.

Irradiation of sporozoites: potential lessons from candidate malaria vaccine

Encouraging results have recently been announced for a malaria vaccine based on malaria sporozoites attenuated by exposure to radiation. The resulting experimental vaccine is similar to the ITM vaccine, although it does not require simultaneous treatment with drugs.

In August 2013, an article in *Science* found that six adult volunteers who received the highest dose of an experimental malaria vaccine, PfSPZ, were protected from subsequent challenge with malaria parasite-infected mosquitoes

(Seder *et al.*, 2013). This is the first time that 100% protection has ever been achieved for a malaria vaccine, albeit in a very small-scale phase I safety trial. This outperforms the results reported in 2012 for the other leading malaria vaccine candidate, RTS,S/AS01, a subunit vaccine, which protected just 31% of young infants and 56% of older babies and toddlers.

The promising result for PfSPZ was achieved using an approach that is similar to ITM: *Plasmodium falciparum* sporozoites are attenuated by radiation and the weakened but live parasites are injected intravenously. Antibodies to other stages in the parasite life cycle were undetectable, indicating that the irradiated sporozoites were effectively attenuated and did not develop beyond the early liver stage. The malaria team believes that the result has established proof of concept for the vaccine and has demonstrated that PfSPZ is safe and meets regulatory standards.

There would be significant advantages in terms of cost and safety if an ECF vaccine comprising irradiated parasites were to be developed. The possibility of using irradiated sporozoites to immunize cattle was explored by Cunningham's group at EAVRO (Cunningham *et al.*, 1973). The experiments were unsuccessful and the EAVRO scientists concluded that vaccination against ECF was unlikely to be achieved using irradiated parasites. Nevertheless, researchers at ILRAD pursued the use of irradiated *T. parva* sporozoites in the late 1980s (ILRAD, 1989). Cattle inoculated with irradiated sporozoites showed weak antibody and cytotoxic responses and were not protected on challenge. Further advances in this area will require methods to quantitate sporozoites with much greater precision and to expose them more uniformly to the irradiation dose.

The issues discussed above raise new questions for vaccination against ECF:

- Is a subunit vaccine attainable or could a better use of available resources be achieved if these were redirected to making the ITM vaccine easier and cheaper to produce and deliver?
- Why are reactors and vaccine failures seen in Kenya in areas where buffalo-derived parasites are present but not in northern Tanzania?
- How does the Muguga cocktail provide such broad protection in the field?

The Proliferative Response in *T. parva*-infected Lymphocytes

Casein kinase 2

ILRI's molecular biology laboratory sought to determine the underlying molecular mechanisms that drove bovine lymphocytes to divide uncontrollably in theileriosis. The goal of understanding the mechanisms was to enhance the ability to create a vaccine against the disease. The results of this investigation, however, had a much broader significance, which became evident only several years later (ole-MoiYoi, 1989, 1995; ole-MoiYoi *et al.*, 1988, 1989, 1992, 1993).

Background

The generation time of *T. parva*-infected lymphocytes *in vitro* varies from 16 to 27 h. The intralymphocytic form of the parasite, the macroschizont, is considered cancerous because it induces uncontrolled growth and clonal expansion of the infected lymphocytes, which are pleiomorphic and show alterations in surface phenotype. The mode of death of the infected animals is very much like that of acute leukaemia in people, i.e. massive tissue and organ infiltration in the lung, kidneys and other organs. *T. parva*, together with its Mediterranean counterpart *T. annulata*, is unique among intracellular protozoan parasites in causing this bovine leukaemia. The disease is unusual because if infected cattle are treated in a timely manner with anti-theilerial drugs, the uncontrolled cell division stops with the death of the parasite. This is the reason why this disease is often described as reversible lymphocyte transformation (leukaemia).

Experimental approach

Initial experiments to determine the driving force for lymphocyte division in theileriosis focused on small segments of DNA known as tumour viruses or oncogenes. Many of these were originally identified in diseases caused by viruses, such as *src* of Epstein–Barr virus associated with Burkett's lymphoma or *v-myc* of bird myelocytomatosis. None of the oncogenes that were available at the time showed any significant hybridization signals with materials

from *T. parva*-infected lymphocytes separated according to their size in gels.

The next set of experiments employed conventional gel electrophoresis, which separates proteins according to their size. Using various inhibitors and activators of enzymes called protein kinases, which attach phosphate groups to certain amino acids in proteins, the researchers could determine the class of protein kinase that was predominant in the *T. parva*-infected cells. There are two classes of protein kinase called tyrosine kinase oncogenes and serine/threonine oncogenes. There was little or no information about serine/threonine oncogenes in the late 1980s when these experiments were carried out. It was therefore surprising to find casein kinase 2 (CK2), which preferentially phosphorylated only serine and threonine amino acid residues in the *T. parva*-infected cells. There were no detectable tyrosine oncogene signals in the *T. parva*-infected materials. CK2 was not known to function as an oncogene at that time. That it was discovered to be the cause of uncontrolled cell proliferation in theileriosis prompted medical studies that confirmed it was also involved in some human cancers, which advanced understanding of their potential treatment. Follow-up experiments could have included the generation of lysates from *T. parva*-infected lymphocytes or such lysates from purified macroschizonts to determine what the parasite may secrete into the cytoplasm of the infected lymphocytes that activates CK2. It would have been interesting to have treated infected animals with a CK2 inhibitor, such as trace doses of heparin, to test whether such charged molecules could enter the cells. However, at this time, ILRAD merged with the International Livestock Centre for Africa (ILCA) to become ILRI and there was a change in the institute's mandate.

Current implications of CK2 overproduction in human medicine

Although the implications of CK2 as an oncogene were not known, and this work did not lead to a vaccine against *T. parva*, CK2 has recently become a major target for the treatment of acute, chronic leukaemia in humans using competitive inhibitors of the adenosine triphosphate (ATP) molecule. These studies are in phase II trials and show promise. In addition, CK2 is also being tested for the treatment of other white blood cell cancers as well as cancers of solid tissues such as those of the breast, lung, kidney and prostate, and metastatic tumours. CK2 has been shown to be a 'pro-life' enzyme. It protects cells from natural death (apoptosis). As such, it minimizes the effectiveness of chemotherapy in many human cancers. Surprisingly, CK2 inhibition also shows great promise in slowing down degenerative neurological diseases such as Alzheimer's disease and Parkinson's disease. Scientists at ILRAD/ILRI were vaguely aware of this potential while doing their experiments because CK2 is the kinase that phosphorylates proteins in the brain that somehow become denatured and precipitate out as fibrillary tangles, compromising brain function.

The Economic Impacts of ECF Research

Earlier studies have estimated various aspects of the economic benefits of ECF disease control. According to McLeod and Randolph (2000), adoption of a multi-component ECF vaccine in small dairy and large commercial livestock systems across endemic countries in southern, central and eastern Africa would reduce the value of cattle mortality by US$10.1 million, while increasing value of milk production by US$1.7 million annually. Mukhebi *et al.* (1992) looked at the economics of immunization using ITM in ECF-affected countries in Africa. This analysis showed high potential economic returns, with a benefit:cost ratio in the range of 9–17 under various assumptions. Minjauw (1999) demonstrated the cost-effectiveness of ITM as an ECF control strategy in traditionally managed crossbred cattle (*Bos indicus* × *B. taurus*) in Zambia. Other work has focused on the economic burden of ECF in the livestock sector and general economy. For example, ECF-related spending in Kenya was estimated at US$10 million in 1987 (Young *et al.*, 1978), while Zimbabwe expended an estimated US$9 million on ECF-related bills in the 1988/89 fiscal year (Perry *et al.*, 1990). Although these costs included control of other tick-borne diseases, ECF is arguably the major disease requiring acaricide application in the region (Cunningham, 1977).

Modelling the economic impacts of ECF

ECF causes a range of economic impacts associated with the morbidity and mortality of animals. Following the classifications of disease impact developed by Rich *et al.* (2014) and expanded by Rich and Niemi (2017), we can categorize the distinct levels of impacts – and associated modelling needs – of ECF to inform our modelling approach. Rich *et al.* (2014) identified impacts taking place from the micro-level (i.e. household or farm level) to different types of meso-level impacts (species, sector and value chain) and to aggregate macro-impacts on the local, regional or global economy. Their framework also considered externalities that could come from control strategies themselves (e.g. the effects of acaricides on the environment) as well as spillovers from regional and international trade.

The impacts of ECF are primarily through high mortality affecting the assets and incomes of farmers. In smallholder settings that are less commercially oriented, this can severely restrict the ability of farmers to cope with market shocks or to meet irregular livelihood needs such as school fees and family emergencies. As with other diseases of livestock, the risk of disease itself can lead to stocking patterns that are suboptimal from the standpoint of market productivity, such as maintaining older, less productive (from a commercial standpoint) herds that are less disease prone. For more commercially oriented farmers, ECF reduces sales of meat and milk and thwarts investment into scale economies, such as fencing for beef and buildings, processing for dairy or expanding herd sizes to meet growing demand. Substitution effects with other sources of protein could also arise, causing changes in supply and demand in other livestock markets.

ECF can induce important spillover effects outside the immediate livestock sector. For instance, where animals are used as draught labour, ECF can have strong, negative impacts on the productivity of staple crops such as maize. Mukhebi *et al.* (1992) estimated that the negative impacts of ECF on animal traction comprised 13% (US$21 million) of the total annual loss associated with ECF in 11 African countries in 1989. This in turn has indirect effects on prices of other food crops. Land and labour markets can also be affected by ECF, the former through the changing use of pasture land and/or reduced land for crops based on the unavailability of draught labour, and the latter from reduced throughput in local abattoirs and milk processors that diminishes the demand for labour (see Rich and Wanyoike, 2010, for a similar discussion of Rift Valley fever in Kenya). While macroeconomic impacts outside the agricultural and livestock sectors associated with ECF outbreaks are likely to be small, important environmental spillovers such as water and land contamination exist with the use of acaricides for dipping (Mukhebi and Perry, 1992).

Most economic analyses of ECF are derived from farm budget data. Various authors estimated the regional impacts of ECF on meat and milk based on a combination of available secondary data on livestock production and primary survey data (Mukhebi *et al.*, 1992, 1995; Martins *et al.*, 2010; Kivaria *et al.*, 2012). An exception to these partial budget approaches is that of Nyangito *et al.* (1996), who developed a whole-farm simulation model with linkages outside the livestock sector, including crops and products derived and used by livestock (e.g. feed, draught power, manure). Financial and economic impacts derived from these simulations were computed over a 10-year horizon. The model allowed the simulation of alternative investments and technologies and was used to develop ECF control scenarios based on combinations of ITM and acaricides. Based on smallholder farm data from Kilifi in Kenya, they found that a control strategy that used ITM alongside a 75% reduction in acaricide use generated an internal rate of return of over 34% and a benefit:cost ratio of 5.18.

A drawback of this approach (and of the partial budget models cited above) is that prices and other market parameters are exogenous to the system and thus fail to capture market dynamics related to disease control. Moreover, most of the available economic analyses do not directly consider the adoption process over the time involved in the implementation of ECF control strategies. Partial or slow uptake of ITM could reduce its impact both on the disease and on markets over time. This suggests the need to use more robust modelling frameworks that capture a wider range of economic phenomena over longer periods.

Methods

To assess the economic impacts of ECF, Rich and Perry (2011) investigated the impacts of ECF on production, prices, trade and livelihoods. First, they used the DynMod model (http://livtools.cirad.fr/dynmod; accessed 13 February 2020) developed by Lesnoff (2007) to assess the impact of ECF on herd demography. DynMod traces livestock herd growth, based on exogenously defined births, fecundity and mortality; exogenously defined purchases and offtake rates; and the initial structure of herd populations by age and gender. These parameters calibrate the evolution of herd growth based on a state-transition (age-cohort) model. Animals move between age cohorts based on pre-defined parameters associated with their time (in months) spent in a particular age class (juveniles, subadults or adults).

Rich *et al.* (2014) used DynMod to develop scenarios of alternative rinderpest control regimes in which varying levels of rinderpest-associated mortality were generated to define herd populations under different control regimes. Rich *et al.* (2014) adopted a similar approach for computing the *ex ante* benefits of ECF control. Based on a review of the literature (Gachohi *et al.*, 2012) and expert consultations, the authors first derived an average of annual incidence and fatality associated with ECF in four different production systems (intensive dairy (ID), open-grazing dairy (OD), agropastoral (AP) and pastoral (P)), as shown in Table 6.1. The product of incidence (I, with units of new annual cases of ECF/total population) and case fatality (CF, with units of annual deaths from ECF/new annual cases of ECF) rates gives the percentage of the population dying annually from ECF. This product was weighted by the population share (w) in each system to give a number for the national ECF mortality (M^{ECF}; Equation 6.1). A triangular distribution comprising a minimum, most likely and maximum level of ECF mortality was generated for sensitivity analysis.

$$M^{ECF} = \sum_{i \in \{ID,OD,AP,P\}} w_i I_i CF_i \qquad (6.1)$$

Next, we developed alternative scenarios of adoption patterns of ECF control through ITM. It is instructive to first review some of the issues governing adoption of ITM to inform our choice of parameters.

The Muguga cocktail ITM vaccine has been commercially available for the past 15 years. Over that period, close to 1.8 million doses of the vaccine have been distributed. About 80% of these have been sold in the pastoral production systems of northern Tanzania and about 10% in the pastoral systems in Kenya. The rest have been sold in smallholder dairy systems across Kenya. Although considerable effort has been put into the intensive dairy systems, adoption of ITM in dairying has been low.

Many reasons have been advanced for this apparent contradiction, because when the vaccine was first developed the main target was smallholder dairy farmers who, it was then believed, had the incentive to protect their high-value dairy animals and were more commercially oriented than other livestock keepers (Perry, 2016).

Some of the reasons suggested include alternative disease control methods in dairy systems. Acaricides are very effective in controlling ECF when correctly used. They are also relatively economical because one can buy enough for just one spray per week, and they also protect against other tick-borne diseases. Curative drugs are also available because most private animal health service providers are in the high agricultural potential areas where most smallholder dairying is located.

The reluctance of the smallholder dairy farmers to experiment with new untested methods on their valuable animals has also played a role. As much as acaricides have their shortcomings, most farmers have used them and know they work. A novel approach would have to prove itself before most farmers want to risk using it.

Strong marketing of acaricides and antitheilerial drugs by pharmaceutical companies in the dairy areas has also contributed. Unfortunately, they may sometimes give incomplete information, and the current distributors of the vaccine are small local companies whose staff may lack capacity to present scientifically correct information.

The packaging of the last several batches of the vaccine in 30–40-dose packages is also a disincentive to smallholder dairy farmers. A single straw of the current batch of the vaccine covers 40 calves, and to collect this number from smallholder farms that on average keep one or two animals is problematic. Had small-dose packages

Table 6.1. Parameters used for deriving population trajectories in DynMod. (Calculations from DynMod.)

System	Cattle population share (%)	ECF incidence (%)			Case-fatality rate (%)			Adoption rate (%)		Predicted adoption by 2026 (%)		
		Base	Low	High	Base	Low	High	2007	2016	Base	Low	High
Intensive dairy	8.7	20	10	30	10	8	15	0	3	20	15	25
Open-grazing dairy	10.5	20	10	30	15	10	20	0	5	40	30	50
Agropastoral	27.3	20	10	30	4	3	5	0	0	20	15	25
Pastoral	22.5	20	10	30	30	20	40	1	15	33	20	40
Not affected by ECF	31.5	0	0	0	0	0	0	0	0	0	0	0
Population-weighted incidence		13.7	6.9	20.6								
Population-weighted case fatality					10.1	7.0	13.6					
Population (number of cattle in millions)	17.5											

been available for smallholder dairy systems, adoption of the vaccine might have been greater.

The reason for the dose packaging is related to vaccine production. Because of the need to maximize on the number of sporozoites and reduce the amount of tick material in the stabilate, ticks with high infection rates are normally selected. The estimation of the sporozoites is also a crude estimate based on the estimated number of infected ticks in a batch and the number of infected acini in an infected tick based on a random sample of ticks assessed. The final dose was therefore only determined at the end of the production run and there was no easy way to dilute the stabilate once it was produced. Recently, Patel *et al.* (2019) demonstrated that, once made, the stabilate can be thawed, diluted and repackaged without loss of efficacy. Another attempt to reduce the number of doses in a straw has been to predilute the stabilate based on the expected concentration (based on the number of sporozoites/ml) and then determine the final dose afterwards. New techniques to more accurately count the number of sporozoites in the stabilate are being developed. If these studies are successful, it may be possible in the future to produce vaccines of a desired number of doses.

ITM price

The price of ITM relative to other veterinary vaccines is quite high. Although smallholder dairy farmers make money from the sale of milk, raising at once US$8–12 for each animal to be immunized is not easy. Unlike pastoralists who can sell one animal to raise enough money to vaccinate all their calves, the smallholder dairy farmer does not have a surplus animal to sell. This can work only in areas where there are strong cooperatives that can advance farmers money for vaccination.

Grazing type

Zero grazing dominates the intensive dairy systems. This involves keeping cattle in stalls and bringing fodder to them. This method reduces the risk of tick-borne diseases, including ECF, because animals move less in tick-infested pastures. In some highland areas where animals are constantly kept in stalls, many farmers can go

for up to 3 months without using acaricides. Only when farmers get external hay do they experience increased tick-borne disease risk.

Many factors that block tick-borne disease in dairy systems are the opposite in pastoral systems. First, pastoralists do not have alternative disease control options. Second, they keep large herds, and any one herd can easily include the 40 calves required for immunization with one straw of the vaccine. Third, whereas the vaccine is relatively expensive, it is easier for pastoralists to sell one animal to raise enough money to vaccinate their calves. Fourth, in many pastoral areas, the risk of ECF is increasing as a result of upgrading indigenous stock with breeds that are more productive but also more susceptible to ECF.

Few studies have investigated adoption trends for ITM, partly because the vaccine has not been used extensively other than in the pastoral systems. Attempts at predicting future adoption trends are therefore speculative, based on projected developments in the three production systems.

Intensification of smallholder dairy farming is likely to increase, driven by population increases and land pressure. As pointed out, the risk of disease declines with intensification. Provision of animal health services in these systems is also likely to improve. Although more acaricide resistance is projected to develop generally, because acaricides are not intensively applied in intensive smallholder dairy systems, acaricide resistance in these dairy systems is unlikely to be a problem in the immediate future. Demand for the vaccine in the intensive systems will arguably remain low in the near future.

In the more open-grazing dairy systems, demand for ITM is likely to rise due to increasing acaricide resistance. However, this will be contrasted by the trend towards intensification and zero grazing in some of the currently medium-sized farms. Overall, there is likely to be a moderate increase in demand for the ITM vaccine in open-grazing dairy systems.

The greatest potential of ITM is expected from agropastoral systems, which have the most cattle and which are spread across areas most suitable for ticks. Currently, the disease risk is low due to an endemically stable situation. The indigenous breeds kept and a scarcity of ticks

due to overgrazing leads to low incidence and rare fatalities. However, many farmers are upgrading their cattle by crossing their local animals with exotic breeds to produce greater amounts of milk that they can sell for high prices. This trend is likely to continue, and as more and more farmers begin keeping ECF-susceptible breeds, the disease risk might rise, and with it, demand for the ITM vaccine.

Demand for the vaccine in pastoral systems is unlikely to change significantly. As more farmers become aware of the vaccine, more are likely to adopt its use until a peak is reached. After that, only newly born calves that have not been vaccinated in the past and very few unvaccinated adults will be vaccinated. The trend towards upgrading animals is also likely to continue, which will lead to more disease-susceptible animals and a greater demand for the vaccine. It is unlikely that animal health services in the pastoral systems will improve significantly in the near future and that there may not be alternative methods for controlling ECF other than vaccination.

Given these dynamics in the different production systems, the authors developed a variety of different paths of adoption that are summarized in Table 6.1 and in Fig. 6.2 in scenarios of low, most likely (shown as 'base') and high levels of adoption. For dairy systems during 2007–2016, it was assumed that adoption took place in the last 3 years only (starting from 1% in 2014), while for pastoral systems, a gradual linear increase in the adoption range was assumed. For 2017–2026, roughly linear rates of adoption were assumed, albeit with slightly slower rates of increase in the first part of the period, rising steadily in the latter part and levelling off by 2026. Each of these adoption levels was weighted in its respective system to obtain a national weighted average.

The estimated impact on ECF mortality of adoption of ITM was then computed. Adoption of ITM in each period (t) was assumed to result in perfect control of ECF, consequently reducing population-weighted ECF mortality by the rate of incremental adoption relative to the first period (2007) of the simulation. This percentage is defined as avoided mortality (AM; Equation 6.2) from ECF for each period:

$$AM_t^{ECF} = \sum_{i \in \{ID,OD,AP,P\}} w_i AR_{i,t} I_i CF_i \qquad (6.2)$$

The new population mortality rate per age class and time step ($M_{1,t}^C$; Equation 6.3) is thus the difference between the original age-cohort mortality rate (M_0^C) and the avoided mortality (AM_t) achieved from the adoption of ITM:

$$M_{1,t}^C = M_0^C - AM_t^{ECF} \qquad (6.3)$$

This new path of mortality rates was subsequently put into DynMod for simulation and compared against a counterfactual (baseline) scenario of control measures.

The International Model for Policy Analysis of Agricultural Commodities and Trade (IMPACT) was then employed to compute impacts on the agricultural economy and livelihoods (the model is documented in Robinson *et al.*, 2015). IMPACT is a system of simulation models incorporating economic, crop, livestock, hydrology and climate change components. IMPACT uses a partial equilibrium economic model that represents global supply, demand and trade of agricultural commodities among open economies. The demand for agricultural commodities is simulated for 159 countries. Agricultural production is modelled at a subnational level known as food production units (FPUs). There are 320 FPUs in IMPACT that represent intersections among 159 nations and 154 water basins. Solving the system of country demand and FPU supply equations in IMPACT produces measures of each country's crop and livestock production and land use, as well as measures of prices and trade of agricultural commodities consistent with trade balances in global agricultural markets. Model results are then translated into indicators of agricultural incomes, food security, nutrition and environmental health, among others.

The IMPACT model has been used to analyse global food security, rural development and natural resource management to 2050, including different scenarios of policy, technological, economic and climatic change. Some of the model's applications are relevant to assessment of transformations in global livestock. These applications highlight the drastically changing roles of developing countries in the demand and production of livestock products globally (Delgado *et al.*, 1999); a more recent study assessing the potential impacts on food prices and the management of natural resources of changing demand and supply of meat and milk in fast-growing regions
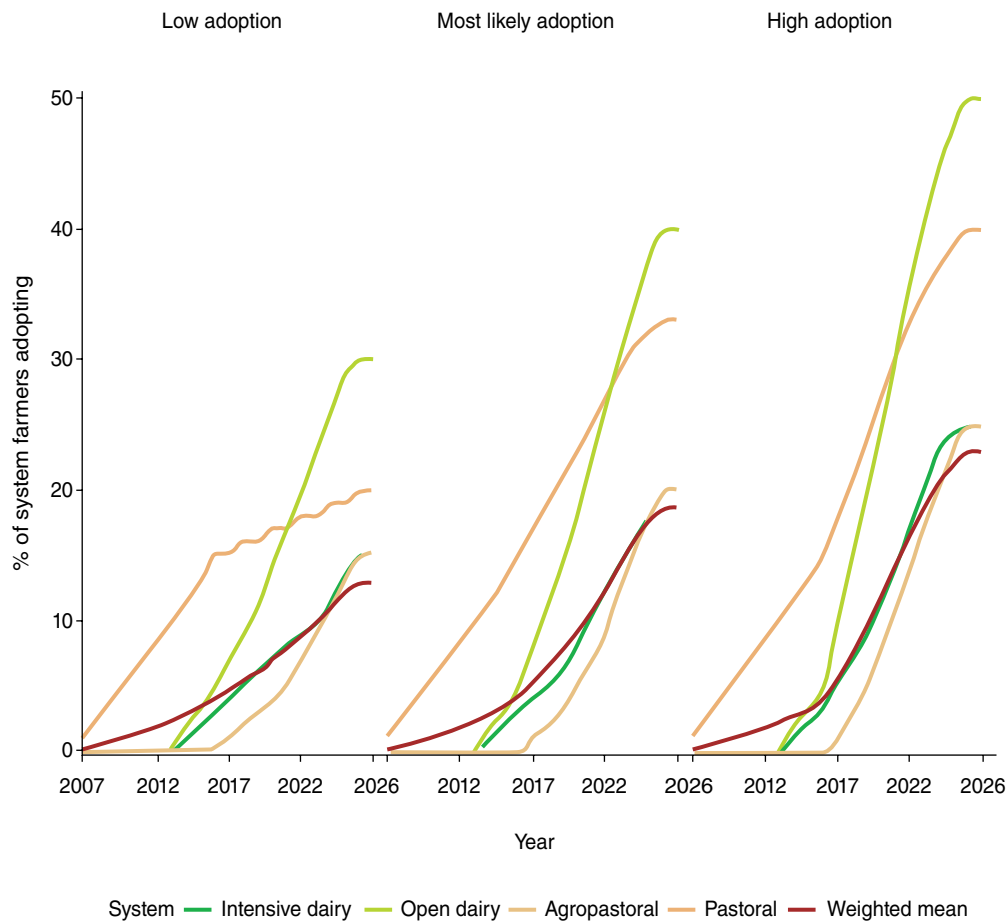
Fig. 6.2. Projected ECF vaccine adoption rates by adoption scenario and production system, 2007–2026. Constructed from DynMod model for ECF in Kenya. Intensive dairy cattle were about 8.7% of the cattle population in 2007, open dairy were 10.5%, agropastoral were 27.3%, pastoral were 22% and cattle unaffected by ECF approximately 31.5% of the national cattle herd of 17.5 million head.

(Rosegrant *et al.*, 2013); and an assessment of trajectories of livestock demand and supply in Africa and South Asia that explores the potential impacts of improving livestock productivity in key livestock-producing countries (McDermott *et al.*, 2013).

The IMPACT model allows for international trade, providing a framework to assess the sub-national factors of ECF and its management that are driving dynamics of the demand and production of livestock products and the global context of food systems. As such, the model is useful in assessing the effects of ECF control on livestock production and food security, and on the potential (including through higher imports) for offsetting shortfalls in the supply of animal-sourced foods. Furthermore, the impact effects are captured over the long run, providing a tool useful for more long-term planning. IMPACT may thus offer a much more comprehensive approach to measuring impacts of ECF control in the affected regions than has been offered by previous approaches (e.g. Mukhebi *et al.*, 1992; Minjauw, 1999). In addition, by introducing reliably informed estimates of the parameters depicting incidence and control of a specific disease, this work builds directly on the earlier analysis of livestock futures by McDermott *et al.* (2013).

The current study applies the IMPACT model to medium- to long-run impacts of the

ITM vaccine for ECF control. Only the main aspects of the model structure that are most relevant to the current context are presented below.

As mentioned, FPU is the unit of analysis in IMPACT, with FPU production of livestock calculated as the product of an assumed 'average' yield (AY) per head and the number of animals in the FPU. Animals are distinguished by species and include beef cattle, dairy cattle, sheep and goats, poultry and pigs, while livestock product types (j) accounted for in the model are beef, milk, lamb, poultry meat, eggs and pork. Livestock yield or production per animal (AY; Equation 6.4) is driven by factors of improved animal and animal management practices that are exogenous (Int) to the system of demand and supply equations in IMPACT:

$$AY_{j,fpu} = AYInt_{j,fpu} \times AYInt2_{j,fpu} \qquad (6.4)$$

Animal numbers (AN; Equation 6.5) are functions of endogenous and exogenous factors. These are species and system specific and are a function of endogenously determined input (c) and output (j) price indices (PNET) and feed costs (PC), country-specific (cty) parameters of feed efficiency (Feeds). The exogenous component of the equation adjusts year-to-year changes in herd populations through a herd expansion rate (ANInt2) that denotes system-level differences.

$$AN_{j,fpu} = ANInt_{j,fpu} \times ANInt2_{j,fpu} \\ \times \left(\frac{PNET_{j,cty}}{PNET0_{j,cty}}\right)^{AN\varepsilon} \times \prod_{feeds}\left(\frac{PC_{c,cty}}{PC0_{c,cty}}\right)^{Feed\varepsilon}$$

$$(6.5)$$

Equation 6.5 provides a convenient entry point for modelling production system growth in the context of ECF, as cattle mortality, a major disease effect, can be factored into the animal population growth rates. The effects of ITM vaccine use were thus simulated in IMPACT using adjustments to the historical and projected growth rates (ANInt2) of beef and dairy cattle herds. These adjustments are based on the mortality and population growth rates generated in DynMod for the different scenarios of ECF control, as described above. Animal mortality rates in turn reflect incidence, fatality and adoption rates related to ECF disease and vaccine use, as presented in Table 6.1.

Returns to ECF Investment

Data from DynMod and IMPACT were used to derive the benefits associated with ECF control under different scenarios. To measure the returns to investment for the ITM vaccine, we compared these benefits with the costs of achieving them to derive benefit:cost ratios associated with investments in ECF control.

Two sets of costs were generated based on two different sources. First, data on expenditures on research by ILRAD/ILRI from 1975 to 2015 were obtained to quantify the sunk costs associated with research expenditures on vaccine development, etc. It is worth highlighting that these costs are global costs that are wholly attributed to the case study of Kenya. As such, they overestimate the costs incurred in Kenya. Second, for each scenario, costs were generated on vaccine delivery based on expert opinions. These costs included the number of doses deployed per scenario, distributor costs and training costs for vaccinators. As delivery costs differ by production system, a weighted-average vaccine cost was derived based on the share of animals in different systems. The weighted-average current cost of vaccine dose plus delivery was estimated at US$6.70. It was assumed that the costs of a new distributor of vaccines was US$100,000 per 250,000 doses administered in the first 5 years of the scenario, and US$100,000 per 500,000 doses from year 6. We assumed these costs were recurrent costs based on the number of vaccines delivered. Finally, we assumed that for every 10,000 doses of vaccine delivered, a training cost of US$300 was incurred. This was assumed as a one-time cost in the year when this occurred. All scenario costs were assumed to increase by a 5% inflation rate annually.

ITM was assumed to confer life-long immunity to ECF. Therefore, the number of doses administered had to account for the natural survival and presence of animals that had been vaccinated in previous years. A simple Markov chain was constructed over the 20-year scenario period to adjust the number of administered vaccinations for animals that had already been vaccinated and either survived or had not exited the system through offtakes. The Markov chain was age-cohort weighted to account for different mortality and sales transitions by age and sex of animal.

Sunk research costs and scenario costs were added to generate a stream of current costs from 1975 to 2026. These were discounted at a 5% discount rate to generate net present values for each scenario. Benefit:cost ratios compare additional agricultural production value derived from IMPACT/DynMod with the added costs from the different scenarios, with the counterfactual assuming no expenditure on ECF at all.

Model results

First, results are presented of the projected paths of cattle production from DynMod under nine scenarios of ECF control. These are contrasted with a baseline scenario that assumes no ITM adoption from 2007, thus providing us with an *ex post* impact of adoption of ITM to date (2007–2016) and *ex ante* projections against such a baseline from 2017 to 2026. As summarized in Fig. 6.3, there are higher impacts on herd growth from ITM adoption than in our most likely and low mortality scenarios. In these scenarios, we see an increase in cattle stocks of 60% over 2007–2026 versus a no-control baseline growth of just over 20% over the same period. Taking our most likely scenarios into account, cumulative herd numbers remain about 10% higher relative to the baseline.

Different rates of animal mortality simulated using DynMod were translated into cattle populations in Kenya for scenarios of ECF control using IMPACT. These scenarios include a
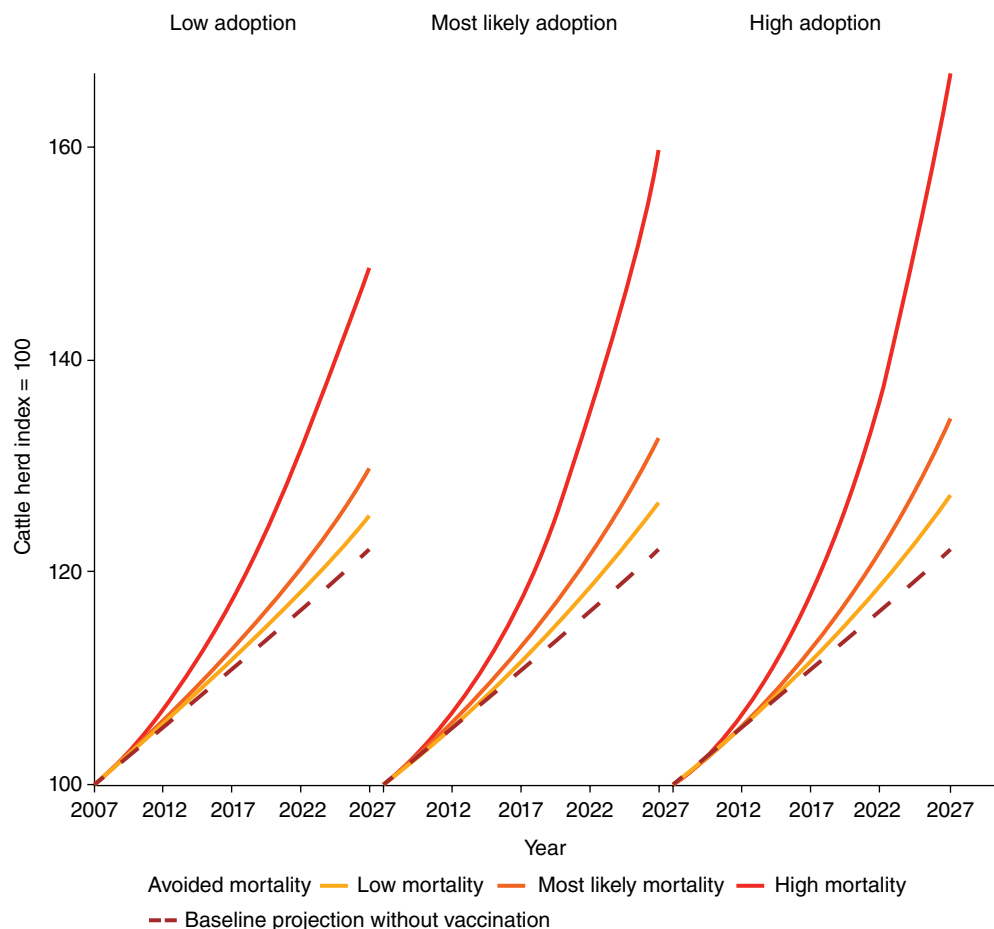

Fig. 6.3. Projected cattle herds by vaccine adoption and mortality avoided, 2007–2026. (Constructed from DynMod model for ECF in Kenya.)

baseline that assumes that current levels of ECF control are maintained over the simulation period (2005–2026) and nine plausible situations of ECF management. The baseline condition accounts for the current management of ECF in Kenya, including acaricides and low rates of adoption of the ITM vaccine. Because future adoption is uncertain, the ECF control scenarios necessarily cover a range of adoption rates. Because there is insufficient information on current rates of cattle mortality due to ECF (particularly as distinct from other disease-related animal deaths), the scenarios also use a range of ECF mortality rates. In applying the data on animal growth rates as input into the IMPACT model, impacts were simulated of interactions among ECF, herd dynamics, markets and socio-economic variables.

Table 6.2 presents IMPACT projections of the supply of animal-source foods associated with the baseline and ECF scenarios in Kenya. Compared with the status quo in which beef production increases from 392,000 t in 2005 to 706,000 t in 2026, beef output in 2026 is projected to increase to between 726,000 and 990,000 t under various assumptions of ECF mortalities. These scenarios correspond to low to high levels of vaccine adoption countrywide. The estimates of beef production under the ECF control scenario represent increases of 3–40% over year 2026 production under baseline conditions. Dairy production similarly increases 6% to 56% in 2026 under alternative ECF management.

Looking at the baseline trend for lamb, eggs, poultry meat and pork, it is observed that national production increases by 80%, 19%, 113% and 44%, respectively, for these product types, from 2005 to 2026. Furthermore, relative to the baseline in 2026, production may decline very slightly under the ECF control scenarios for lamb, for poultry and for eggs, with no change observed in pork production to 2026. The decline in production of lamb, eggs and poultry meat is probably explained by market substitution effects. As cattle meat and dairy supplies increase under ECF management, the prices of these products decline, causing a weakening in the demand (and subsequent production) of comparable products. The market shifts are, however, small. Related to the expansion in cattle production, the aggregate supply of meat, milk and eggs increases by 48% from 2005 to 2026. Compared with the baseline in 2026, supply increases under the ECF control scenarios in a range of 0.5–5%.

Figure 6.4 presents an index of the value of national agricultural production associated

Table 6.2. Production and net imports of selected commodities in Kenya, 2005–2026. (Calculations from DynMod and from IFPRI IMPACT; Robinson *et al.*, 2015).

	2005	2026: status quo	2026: low mortality, medium adoption	2026: medium mortality, medium adoption	2026: high mortality, medium adoption
Production in 1000 t					
Beef	392	706	732	768	942
Dairy	2178	5018	5200	5254	6694
Lamb	77	140	140	140	140
Eggs	61	73	73	73	73
Poultry meat	19	43	43	43	42
Pork	14	21	21	21	21
Feeds[a]	286	461	475	494	590
Net imports in 1000 t					
Beef	0.83	36.68	9.26	0.00	0.00
Dairy	3.30	0.00	0.00	0.00	0.00
Lamb	0.10	0.00	0.00	0.00	0.00
Eggs	0.11	52.33	52.54	52.55	52.56
Poultry meat	0.00	10.76	10.77	10.77	10.79
Pork	0.00	0.00	0.00	0.00	0.00

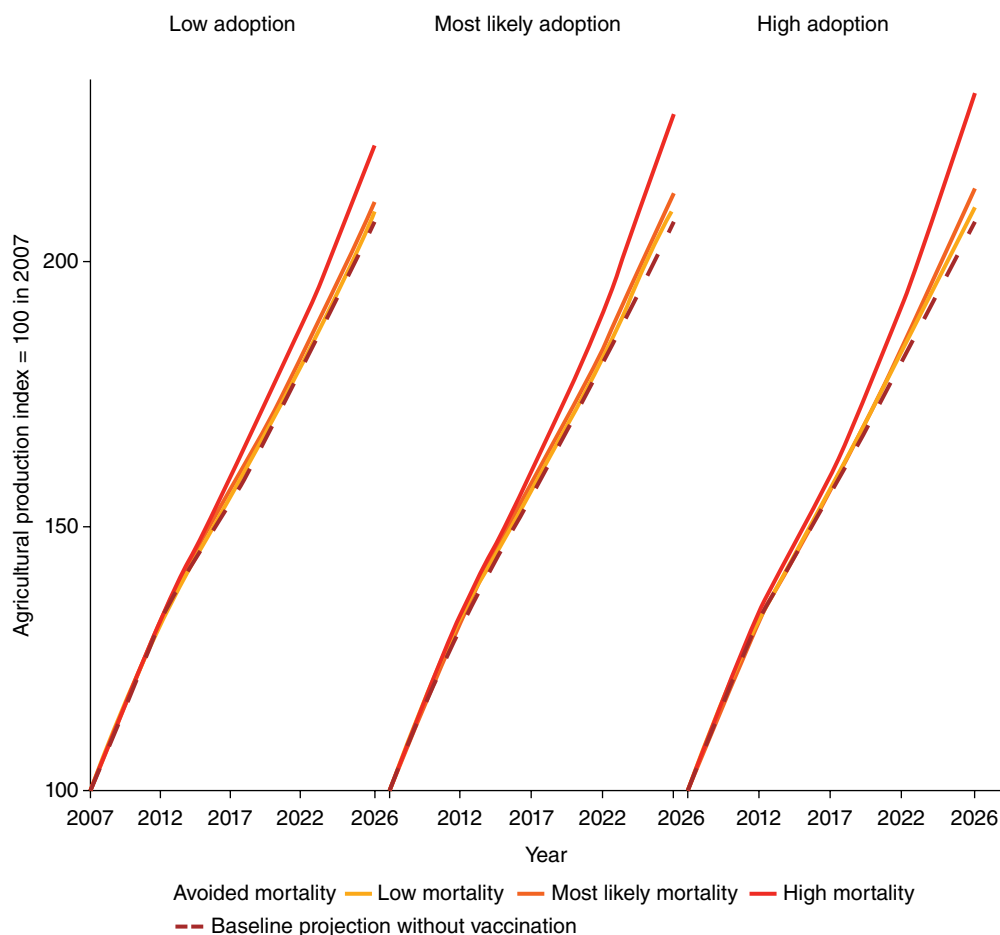[a]Feed grain for livestock production, not quantity of feeds produced.

Fig. 6.4. Index of agricultural production in Kenya by vaccine adoption and mortality avoided, 2026–2027. (Constructed from DynMod model for ECF in Kenya.)

with the vaccination scenarios. Relative to the reference case, agricultural incomes improve by between 0.8% and 12% in 2027. On a commodity-by-commodity basis, revenue from beef and dairy production increases by 3% to 40% over the baseline. Benefits also accrue to the consumers, but these are more modest. Aggregate household expenditures on food are lowered by 0.01% to 0.07% in 2027 under the ECF scenarios compared with the reference case. Food expenditure as a share of national income remains the same or declines (by 0.01% at most) relative to the base case in 2027.

The vaccination scenarios have faint effects on international trade in livestock commodities. The scenarios lead to reduced imports in both volume and value. Under assumptions of low

animal mortality, the net import of beef is between 5000 and 15,000 t in 2026, or roughly 1–2% of the demand in that year. Net dairy imports at 3300 t, are only 0.1% of national demand in 2005. ECF control in cattle does influence the demand and supply of other livestock commodities, probably through competition for feeds, but these effects are also small.

The model projections on crop use for feed are substantial. Baseline feed demand increases 61% from 2005 (285,000 t) to 2026 (461,000 t). Demand for cereals is 29% of this demand in 2005 and 35% of the same in 2016. Under the ECF control scenarios, demand for livestock feeds in 2026 is 2.3–34% higher than the baseline volume. However, there is little or no increase in cultivated area. This suggests that

cropland is being reallocated (e.g. from use as food) to the production of livestock feeds. As cattle production expands and meat and milk prices fall, households are probably able to replace staples in their diets with the higher nutrient animal-source foods, so that no additional land is needed to support the growth in feed demand.

Figure 6.5 illustrates benefit:cost ratios associated with the use of the ITM vaccine in Kenya. The ITM vaccine, under a wide range of hypotheses about vaccine adoption rates across livestock systems and about avoided mortality, would produce a high return to ILRI's historical investment in all types of ECF research. This example of a proven technology against ECF is

unlike the projections of Kristjanson *et al.* (1999) of the returns to a trypanosomiasis vaccine, which does not exist.

Model results indicate modest impacts of ECF control through ITM. There was a steady increase in domestic supply of cattle, meat and milk and an associated reduction in net imports. The value of production in the agricultural sector rises by about 12% relative to the baseline by 2026. Agricultural revenue is increased, mostly through expanded livestock production, while food expenditures are lower in 2026 under the ECF scenarios than in the baseline case. The implication is that producer welfare is improved in the near to medium term but not at the expense
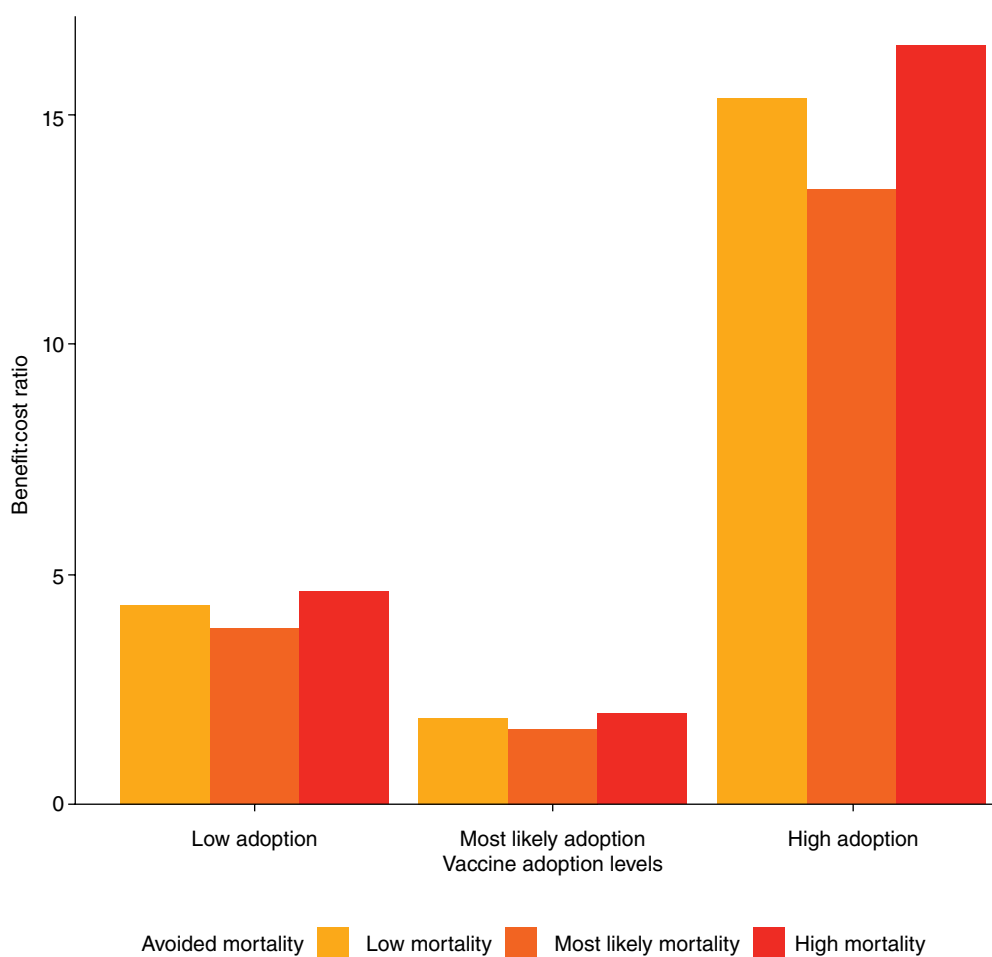

Fig. 6.5. Benefit:cost ratios for ECF vaccination research and development programmes by vaccine adoption levels and mortality avoided. (Constructed from DynMod model for ECF in Kenya.)

of consumer welfare. Impacts on nutrition and food security are relatively small, suggesting that increased production probably reduces reliance on food imports and improves the supply of key macro- and micronutrients in human diets but does not create new food consumption.

Model gaps

An important research gap is ECF's impact on morbidity and productivity. Our analysis focuses on mortality avoided by ECF vaccination and does not consider disease effects on meat and milk productivity or possible rising costs of treatment. We may have therefore understated the potential benefits from ITM in Kenya.

Another model gap is that IMPACT does not consider the power output of cattle. We expect that improved control of ECF would have a positive impact on the use of cattle as an input to crop production, which would raise producer incomes. However, as Kenyan agriculture mechanizes, draught power will become less important and potential benefits from increasing draught power will become smaller, so it is not possible to project a net effect of omitting power benefits from the present model.

A second indirect effect of ITM adoption that we did not capture is the potential benefit of controlling high-mortality diseases such as rinderpest and ECF. This would, in theory, allow farmers to stock herds in a more efficient manner and one less dictated by risk preferences (e.g. stocking older animals instead of more productive younger ones, or keeping less productive but disease-resistant breeds; Rich *et al.*, 2014). These shifts could have significant effects by providing farmers with higher prices for the sales of younger, more productive animals, and might allow farmers greater access to commercial markets that demand younger stock.

Conclusions and the Future

ILRI and its historical partners have had significant scientific and development impact on our understanding of theileriosis and on management of ECF. The demonstration that commercial-scale batches of the ITM vaccine could be produced was a major achievement and underpinned the sale of the vaccine in Tanzania. In a more direct sense, it also resulted in the immunization of more than 1.5 million cattle. The many years of basic research in the search for a subunit vaccine have not only resulted in a greater understanding of the biology and immunology of *T. parva* infection but have also had a much broader scientific impact on our general knowledge of protozoan–host interactions and of the bovine immune system, especially the role and function of the MHC and CTLs. The scientific outcomes unexpectedly found application in human tumour biology. The numerous serological and nucleic acid-based tools that were generated during this time later proved immensely valuable in the characterization and quality control of the ITM vaccine, and in dissecting the functioning of the bovine immune system.

The future for ILRI in the pathology and immunoparasitology of theileriosis will be guided by the degree of success in the uptake of the ITM vaccine, balanced against the evolving prospects for a subunit vaccine. The future in the epidemiology and economics of ECF management will be developing and evaluating current or novel control methods.

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7 Transboundary Animal Diseases

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Contents

Executive Summary

Transboundary animal diseases (TADs) are highly contagious epidemics with the potential for very rapid spread, causing serious economic and sometimes public health consequences while threatening farmers' livelihoods. TADs often cause high morbidity and mortality in susceptible animal populations. Some TADs are also emerging infectious diseases, food-borne diseases and/or zoonoses: these are covered in other chapters. This chapter covers those high-impact, highly contagious animal diseases, such as foot-and-mouth disease (FMD), that do not infect humans but do affect food and nutrition security and trade that the International Livestock Research Institute (ILRI) has been working on since the 1990s. These are: African swine fever (ASF), mycoplasma disease (both contagious bovine pleuropneumonia (CBPP) and contagious caprine pleuropneumonia (CCPP), peste des petits ruminants (PPR) and Newcastle disease (ND). Other TADs, which were to a lesser degree the focus of ILRI research, are briefly mentioned (including FMD, classical swine fever (CSF) and rinderpest).

ILRI's contribution in the global context

ILRI has been involved in ASF research since 2003. Originally, the focus was on diagnostics and molecular epidemiology. A large project in western Kenya broadened this by introducing a multidisciplinary approach. With the start of the CGIAR Research Programme (CRP) on Livestock and Fish in 2012, a major research-to-development initiative started in Uganda. From 2008, ILRI has been a key player in conducting research on the mycoplasma diseases: first, CBPP, and, more recently, CCPP. This research agenda started in response to the African Union's listing of CBPP as the most economically important transboundary livestock disease on the African continent in the post-rinderpest era. ILRI has been significantly involved in PPR research since 2010, with the primary aim of developing appropriate and proven PPR vaccination strategies that can progressively control the disease in developing countries. Finally, ILRI has made small but strategic inputs to the understanding and control of rinderpest, FMD, CSF, ND and some other TADs.

Impacts of ILRI's research

Scientific impacts

Molecular epidemiology highlights include: the isolation and genetic characterization of CBPP and ASF and other pathogens; a better understanding of disease dynamics; and improved understanding of immunity in local African breeds and European breeds.

Technical research contributions to vaccine development for CBPP, CCPP, ASF and PPR have been developing a new challenge model for CCPP for vaccine development, improved diagnostic tests for CBPP and ASF, and construction of biological components using synthetic biology to identify vaccine candidates.

Field epidemiology research highlights include: a better understanding of disease dynamics by mathematical modelling of ASF, CBPP and rinderpest and also using social networks to understand ASF transmission; investigating reservoirs of ASF and rinderpest and the role of carriers in ASF; conducting large-scale studies on the prevalence and risk factors for ASF, showing the importance of this disease; contributing to a major gap analysis of FMD research, shaping the path of FMD control; and a large vaccine trial of an improved mycoplasma vaccine, which did not demonstrate superiority but did show the feasibility of CBPP control. ILRI and partners pioneered the first attempt to describe the entire disease burden of any naturally occurring animal population in the world by a landmark study in which a cohort of several hundred calves were followed for a year and assessed for more than 100 pathogens.

Socio-economic research highlights include: extending knowledge, attitude and practice related to TADs; understanding the economic factors in the adoption of the CBPP and the ND vaccine; the first *ex ante* assessment of the costs and benefits of ASF control through improving biosecurity; developing estimates for the economic benefits of rinderpest, PPR and CBPP control that influenced investment; challenging conventional wisdom that training and awareness were enough to motivate disease control by farmers and traders; and incorporating gender, as a measure of inequality, into the analysis of the distributional effects of most TADs (see Chapter 18, this volume).

Development impacts

Mycoplasma studies at ILRI have been undertaken since the mid-2000s, but the initial focus was on upstream research, which can be expected to bring about development impact several decades later. ASF research became more development oriented with the start of the CRP on Livestock and Fish, and end-user benefits are starting to be documented but not yet on a large scale. Already, ILRI evidence has helped national partners to better target ASF surveillance and response in Uganda, safeguarding smallholders' stock. A thermostable PPR vaccine developed by ILRI is under production in Mali and Kenya and will play a major role in global control efforts as the vaccine does not require a cold chain. ILRI made a small contribution to generating the evidence that motivated the global eradication of rinderpest, one of the greatest successes of global animal disease control.

Policy impacts

ILRI, the Food and Agriculture Organization of the United Nations (FAO) and the African Union-Interafrican Bureau for Animal Resources (AU-IBAR) have been collaborating since 2013 to develop an Africa-wide strategy for the prevention and control of ASF (FAO/AU-IBAR/ILRI, 2017). ILRI evidence has stimulated the local government in Uganda to invest in ASF control.

In 2015, FAO and the World Organization for Animal Health (OIE) launched an international initiative for the progressive control of PPR and its global eradication by 2030. ILRI hosted the second meeting of the Global PPR Research Alliance (GPRA), and ILRI scientists contributed to the development of the first pan-African strategy for the progressive control of PPR.

ILRI developed a policy analysis for the implementation of CBPP control strategies in pastoral regions of sub-Saharan Africa. ILRI has also contributed to a major gap analysis for the Global Foot-and-Mouth Disease Research Alliance (GFRA) and to the Global African Swine Fever Research Alliance (GASFRA) and along with FAO and the African Union helped develop a regional strategy for ASF control.

Capacity building

Several dozen graduate fellows have participated in this research. Farmers, butchers, government veterinarians and scientists in Uganda

have benefitted from training. One manual on ASF has been developed and is widely being used by the private sector in training farmers.

African Swine Fever

African swine fever (ASF) is a haemorrhagic viral disease in pigs resulting in mortality rates approaching 100% (Steinaa *et al.*, 2016). ASF is native to southern and eastern Africa, where it was historically maintained in a wildlife (sylvatic) cycle involving warthogs, the natural reservoir, and soft ticks. It first came to attention when susceptible exotic pig breeds were introduced in the early 1900s to eastern Africa. It spread within Africa and, in the 1950s, to Europe and subsequently to South America and the Caribbean (Costard *et al.*, 2009). In the 1990s, the disease was eradicated from Europe, except in Sardinia (Galindo and Alonso, 2017). However, in 2007, the disease expanded once more out of Africa into the Caucasus (Georgia). ASF was recently confirmed in China (Wang *et al.*, 2018) and in Vietnam and Cambodia.

Unlike many other viral pathogens, ASF is remarkably stable, surviving in pork, pig waste and the environment. No drugs or vaccines exist for treating or preventing ASF. Control relies on biosecurity and surveillance, diagnosis and slaughter, all difficult to apply given the persistence of the virus. Limited diagnostic capacities and poor knowledge about the epidemiology of the ASF virus have long hindered its control.

Research

ILRI research on ASF began in 2003 through collaboration with the European Union Reference Laboratory for ASF diagnostics at the Centre for Animal Health Research (CISA), National Institute for Agricultural and Food Research and Technology, Spain. This worked towards the development of improved diagnostic tests and also assessed viral prevalence and molecular diversity in East and Central Africa using assays developed at CISA, as reported by Bishop *et al.* (2015), Gallardo *et al.* (2009, 2011, 2013) and Okoth *et al.* (2013). The CISA provided staff expertise, intellectual input, diagnostic reagents and use of their Biosafety Level 3 laboratory for viral culture and *in vivo* infections of swine. In 2004, a collaboration with the Friedrich-Loeffler-Institut

(FLI) in Germany started, aiming to develop an ASF vaccine, led by Richard Bishop.

The capacity for diagnosis was used between 2006 and 2008 to further train laboratory technicians and field epidemiologists in Kenya, Uganda, Tanzania, Rwanda and Burundi. Subsequently, diagnostic tests have been validated with national veterinary services in much of East Africa. ILRI and the other organizations made available both facilities and material from recent outbreaks of ASF in the eastern Africa region for this purpose. The work focused on extensive studies of ASF outbreaks and sylvatic (wild pig-based) cycles in Kenya and Uganda.

ILRI was also a partner in a Swedish-led consortium to assess the impact of ASF in Uganda, starting in 2010. This project conducted outbreak investigations and also investigated the role of bush pigs in transmission. It was followed by another Swedish-led initiative, which focused more on interventions.

From 2012, the Biosciences eastern and central Africa-ILRI Hub (BecA-ILRI Hub), in partnership with the Commonwealth Scientific and Industrial Research Organisation (CSIRO), conducted studies in the border region of Kenya and Uganda. This project represented the most comprehensive study of ASF disease yet attempted. Using the biosciences capacity for diagnosis and epidemiological surveillance at the BecA-ILRI Hub and epidemiological research incorporating participatory and quantitative approaches, state-of-the-art diagnostics, molecular biology, genetics and genomics, mathematical modelling and social network studies enabled the development of evidence-based recommendations for disease mitigation. There were important advances in immunology of ASF, and two potential vaccine candidates were produced by deleting a gene in two different ASF viruses – the Kenyan 1033 strain (genotype IX) and the Sardinia strain (genotype I).

In 2011, the CRP on Livestock and Fish identified the smallholder pig value chain in Uganda as a high-potential target to translate research into development interventions (Ouma *et al.*, 2015). ASF was identified by the farmers and pig value chain stakeholders as the major constraint to smallholder pig farming (Dione *et al.*, 2014). This background analysis generated information on the epidemiology of ASF and led to testing of 'best-bet' interventions to manage ASF and other pig diseases (Dione *et al.*, 2018a,b).

In collaboration with Chinese researchers, ILRI has been researching genomic characterization of domestic pigs and wild boars in Asia and the genetic resistance of domestic pigs and wild boars to ASF. With the spread of ASF into Asia, ILRI has been providing support to countries in the region.

Research impact: technologies

Diagnostics

Reliable diagnostics are key to the rapid containment and management of disease outbreaks. As such, ILRI contributed to validation of diagnostic tests developed by their international partner, CISA. However, samples taken from outbreak areas, surprisingly, did not test positive for ASF antibodies using the OIE protocols (Gallardo *et al.*, 2013; Okoth *et al.*, 2013). Analysis of blood and serum samples using a polymerase chain reaction (PCR) assay found positivity to ASF virus (ASFV) of 28% in two independent samplings in south-western Kenya and 0% PCR positivity in central Kenya, but no animals were seropositive in either study site using the OIE indirect ELISA, and none of the animals sampled exhibited clinical symptoms of ASF. Failure of the OIE protocol might be related to the characteristics of African pigs (Gallardo *et al.*, 2013), opening opportunities for further research on host-pathogen interactions.

ILRI scientists were part of a Swedish-led team that evaluated a rapid diagnostic approach using a portable, commercial real-time PCR (Zsak *et al.*, 2005). Trials suggested that it could be used effectively at the pen side or in a field laboratory with performance at a level comparable to sophisticated molecular laboratories (Leblanc *et al.*, 2013). This was subsequently confirmed in Uganda (Liu *et al.*, 2016).

Vaccines

In collaboration with FLI, ILRI studied the immune responses to African ASFV strains and generated additional knowledge of the Kenyan pig major histocompatibility complex (MHC)[1]. Using an experimental animal model with an isolated virulent virus from Kenya, it was found that immunity could be obtained by increasing doses of the virulent strain. This method is now being used for studying the immune response to such isolates. Immune responses were characterized by very low antibody titres but solid cellular immune responses (Steinaa *et al.*, 2016).

Another advance was sequencing MHC molecules from Kenyan pigs to identify which antigens can be used for a vaccine that induces cellular immunity. This revealed new sequences (Sørensen *et al.*, 2017); ILRI has received sequences from approximately 34 other Kenyan pigs, which are currently being evaluated. Of particular importance was the achievement of generating two vaccine candidates by deleting a gene, which should attenuate the virus. Recently, cutting-edge CRISPR/Cas (clustered regularly interspaced short palindromic repeats and CRISPR-associated protein 9) gene-editing technology and synthetic biology approaches for generating ASF vaccine candidates have been introduced to the ILRI ASF research programme. Using CRISPR/Cas9 is faster, cheaper, more accurate and more efficient than other existing genome-editing methods.

Research impact: molecular epidemiology

ILRI used molecular epidemiology to track viruses causing outbreaks, helping to understand the spatial and temporal relationships among them. Complete sequencing of the p54 gene from ASFV isolates revealed regional differences and the value of p54 gene sequencing as an additional, intermediate-resolution, molecular epidemiological tool for typing of ASFV (Gallardo *et al.*, 2009). Whole-genome phylogenetics, including a newly sequenced virulent isolate from Spain, identified two clusters. One contained South African isolates from ticks and warthog, suggesting derivation from a sylvatic (wildlife-to-pig) transmission cycle. The second contained isolates from West Africa and the Iberian Peninsula, suggesting a domestic (pig-to-pig) transmission cycle. This provides valuable insights into control, as disease maintained in a sylvatic cycle is harder to control than disease maintained in a domestic cycle. Comparative genomics revealed high diversity within a limited sample of the ASFV gene pool (de Villers *et al.*, 2010) but revealed that genetically similar ASFVs may be circulating between Kenya and Uganda (Gallardo *et al.*, 2011).

Scientists later enriched the publicly available ASFV genome bank with sequences from East Africa. Genome sequencing and annotation of a recent pig-derived p72 genotype IX and a

tick-derived genotype X isolate from Kenya were carried out using the Illumina platform and this was compared with a Kenya 1950 isolate. The three genomes constituted a cluster that was phylogenetically distinct from other ASFV genomes but 98–99% conserved within the group. There were multiple differences among East African genomes in the 360 and 110 multi-copy gene families (Bishop *et al.*, 2015). This information is not only important in tracking movement of the viruses but also helps with recognition of new viruses being introduced into East Africa, indicating a breach in transboundary disease control. A practical implication of the genetic similarity of the Kenyan and Ugandan viral isolates is that ASF control requires a regional approach to control. There was also a classification of the ASFV genome series of multi-gene families, with the goal of providing standard comparisons and naming schemes, thereby enhancing the capacity to search for novel vaccine targets in ASFV.

Research impact: field epidemiology and control

Transmission dynamics

Understanding transmission dynamics is needed before control is feasible. Recent findings that high levels of detection of ASFV DNA in pigs slaughtered in Kenya during a period with no reported outbreaks provided support for the hypothesis that subclinical, chronically infected or recovered pigs may be responsible for persistence of the virus in endemic areas (Thomas *et al.*, 2016). Other findings indicated that carrier pigs may play a role in ASFV maintenance and help explain the disease outbreaks that have occurred without any evidence of any of the known transmission sources (pigs clinically ill with ASF or adjacent populations of resistant African wild pigs) (Abworo *et al.*, 2017). These findings have significantly increased scientific knowledge of the epidemiology of ASF in the field in Africa, which has contributed to the design of effective surveillance and control strategies.

The role of the ancestral sylvatic cycle of ASFV was not well understood in the endemic areas of eastern Africa. Scientists therefore explored for the first time the coexistence of different ASFV genotypes in the soft ticks found in warthog burrows and adult wild warthogs in Kenya. The data from this and earlier studies suggest that there has been transfer of viruses of at least two different p72 genotypes from wild to domestic pigs in East Africa (Gallardo *et al.*, 2011).

Although warthogs are considered the main wild vertebrate host of the virus in the endemic African setting, they are not the only wild African pigs with a potential role in ASF epidemiology. The bush pig, *Potamochoerus larvatus*, is an elusive, nocturnal pig known to be susceptible to ASF, and might be a link between the sylvatic and domestic cycle. Studies from south-west Kenya showed similarity in viruses in bush pigs and domestic pigs (Okoth *et al.*, 2013), indicating possible transmission between the two species or the presence of an intermediary vector. Initial results following a bush pig with a radio collar revealed close interactions between the species (Ståhl *et al.*, 2014). Other studies have reported an apparent strong association of viral infections with pig breeds, suggesting that some breeds may be resistant to infection and offering opportunities for genetic resistance as a disease mitigation measure as well as encouraging the conservation of tolerant breeds (Mujibi *et al.*, 2018).

Participatory epidemiology studies in three districts of central Uganda found that farmers considered ASF and parasites to be the major health constraint to pig production. They also reported ASF as the primary cause of pig mortality, with epidemics occurring mainly during the dry season (Dione *et al.*, 2014). Other studies have revealed widespread under-reporting of ASF by farmers, traders and animal healthcare professionals and the motivations for this (Atherstone *et al.*, 2019).

Risk factors

Understanding risk factors can help target control efforts to where they will have most effect. ILRI scientists have explored risk factors for ASF in Uganda and Kenya (Dione *et al.*, 2015; Nantima *et al.*, 2015). Key drivers of outbreaks were panic sales of pigs and inadequate disposal of dead pigs. In an innovative study, ASF transmission paths and nodes were described using social network analysis (Lichoti *et al.*, 2016, 2017). This showed the importance of commerce in spreading ASFV between farms and across regions, implying that greater emphasis should be placed on post-farm nodes in the prevention and control of the disease (Dione *et al.*, 2016a).

Control

By combining knowledge and data from the various studies, it was possible to estimate disease transmission dynamics using geospatial mapping and mathematical modelling. This was used for *ex ante* assessment of the effectiveness of different ASF control strategies and to identify the optimum time for deployment of interventions in the field to minimize the losses following ASF outbreaks (Barongo *et al.*, 2015, 2016). This provided evidence to help national and international partners conduct targeted surveillance of pig diseases, including important zoonoses (Dione *et al.*, 2017). The evidence generated has informed the development of an ASF control strategy for Africa (FAO/AU-IBAR/ILRI, 2017).

In the absence of a vaccine, the most common recommendation for ASF control has been to implement biosecurity measures such as footbaths, fencing and quarantine. Such measures are usually promoted through training and public information campaigns. A randomized control trial was carried out to evaluate the effects of training farmers in biosecurity on the Kenya-Uganda border. The trial found that, although farmer knowledge improved after the trial, farmer practices did not (Nantima *et al.*, 2016). Another attempt in Bangladesh (with poultry) to promote biosecurity through training and public information also indicated that information was insufficient to change behaviour and that additional motivation was needed (Rimi *et al.*, 2016).

ILRI was a member of GASFRA. This organized four scientific conferences from 2013 to 2016 to conduct gap analyses of current knowledge and the available countermeasures to effectively control and mitigate the impact of a disease outbreak of ASF. Based on these analyses, a report was generated setting out the priority research needs (Seixas *et al.*, 2018).

ILRI, in partnership with FAO and the African Union, elaborated a strategy joined with an action plan to allow a progressive and coordinated control of ASF at the regional level. To achieve this objective, it prioritized the strengthening of capacities of technical services and the improvement of current production systems, creating optimal conditions for the modernization and development of the pig industry in a healthy context (FAO/AU-IBAR/ILRI, 2017).

Research impact: socio-economic studies

Scientists also explored the knowledge, attitudes, practices, capacities and incentives of pig value chain actors in relation to ASF and biosecurity (Chenais, 2016). This showed that respondents were well aware of the clinical signs of ASF, the routes for disease spread and the measures for disease control. However, awareness of the control measures did not guarantee their implementation. A majority of middlemen and butchers acknowledged having sold live pigs, carcasses or pork that they believed was infected with ASF. Factors that limit the adoption of biosecurity measures by farmers include cost and cultural factors such as the stigma related to the use of footbaths and the restriction of farm visits to neighbours or traders.

The results of an *ex ante* model projected that, although biosecurity measures would reduce ASF outbreaks, they would also lead to a 6.2% reduction in profit per year while giving a 7.8 % increase in profits accruing to butchers, traders, collectors and wholesalers (Ouma *et al.*, 2018). This could explain the low adoption of biosecurity practices by farmers and a need for other incentives for farmers (Nantima *et al.*, 2016).

Other studies assessed the gender dimensions of pig management and disease control. These found that, during disease outbreaks, especially of ASF, both men and women provided animal health care. Therefore, control information should explicitly target both men and women within the same household. This broader outreach would help spread knowledge of pig husbandry and ensure that action during outbreaks does not rely on a few individuals (Dione *et al.*, 2016b,c).

Mycoplasma Disease

Mycoplasmas are the smallest and simplest self-replicating bacteria. Several species of mycoplasma infect humans, causing pneumonia, urinary tract infections and sexually transmitted disease. Hundreds more species infect animals. CBPP is an infectious disease of cattle caused by the small-colony type of *Mycoplasma mycoides*; CCPP is a devastating disease of goats caused by *Mycoplasma capricolum*.

CBPP was introduced to Africa in the 1800s and is now one of the most important livestock

diseases in sub-Saharan Africa. It is now estimated to menace the livelihoods of nearly 25 million people in 19 African countries.

While eradication is the surest way to control CBPP, it is expensive and can only be tried during major outbreaks and on major trade routes. Eradication is generally infeasible in Africa because of animal movements and the limited resources of national veterinary services. The current control strategy relies on using a live vaccine. Unfortunately, this has limited efficacy, a short duration of immunity and causes severe side effects (including the loss of the animal's tail). The current diagnostic tests have limited sensitivity and are only useful at the herd level and are not practical at individual levels.

Research

An ILRI review of animal health and poverty issues identified CBPP and CCPP as major problems (Perry *et al.*, 2002), although CBPP research had not begun until the late 1990s. At this time, Ethiopia was experiencing major new outbreaks. ILRI initially supported a thesis on the cost of CBPP control in Ethiopia (Laval, 1999). Scientists subsequently estimated the presence and prevalence of CBPP in the Ethiopian highlands (Bonnet *et al.*, 2005), defined the basic epidemiological parameters of the disease in southern Sudan (Mariner *et al.*, 2006a) and promised a control model in East Africa (Mariner *et al.*, 2006b).

Careful analysis of the existing literature on CBPP suggested the key information and technologies needed to develop better control measures in an African environment (Jores *et al.*, 2013b). Research then focused on host-mycoplasma interactions, epidemiological models, improved diagnostics, elucidation of protective responses and identification of potential vaccine antigens.

Research impact: technologies

Diagnostics

In the absence of good vaccines, recurrent testing using improved diagnostic assays in combination with elimination of CBPP-positive animals or herds is a control option (Ssematimba *et al.*, 2015). ILRI research found that the inaccuracy of the official (OIE) prescribed assays (complement fixation test and competitive ELISA) make them suitable for use at the herd level only (Nkando *et al.*, 2012). This was confirmed by a comparison of four serological assays: one complement fixation assay developed in house and three OIE-recommended tests (Schubert *et al.*, 2011). None of the four tests detected all infected animals. ILRI scientists later contributed to the development of a novel, successfully validated, real-time PCR assay (Schnee *et al.*, 2011).

ILRI scientists next set out to develop an improved serological test, seeking to find novel mycoplasma antigens recognized by sera from infected cattle, thus having diagnostic potential to improve test sensitivity (Jores *et al.*, 2009; Naseem *et al.*, 2010). A systematic comparison of 17 selected *Mycoplasma mycoides* subsp. *mycoides* (*Mmm*) immunogens commenced, a standardized ELISA protocol was developed, and well-defined serum samples were used to compare individual proteins and protein combinations with respect to sensitivity and specificity (Heller *et al.*, 2016). The resulting assay, comprising the two best-performing immunogens, had an overall diagnostic accuracy comparable to the OIE-prescribed tests, and work to optimize the test further is under way.

The assay was further transferred to a lateral flow test format in collaboration with a commercial company, enabling rapid diagnosis (less than 30 min) of CBPP (Heller *et al.*, 2016). The test is currently undergoing final optimization and evaluation. A rapid and field-applicable recombinase polymerase amplification assay was also developed for a related pathogenic mycoplasma, *M. capricolum* subsp. *capripneumoniae* (*Mccp*) that could be further developed to make it commercial (Liljander *et al.*, 2015).

Vaccines

An early study suggested a minor role for CD4^{+} T-lymphocytes, which are involved in helping and regulating immune responses, in protection in a primary infection (Jores *et al.*, 2008), despite some earlier publications suggesting such a link. This was confirmed in a later study in cattle depleted for CD4^{+} T-lymphocytes (Sacchini *et al.*, 2011). Differences in disease severity are probably largely due to differences in cattle genotypes. Inflammatory cytokines, as expected, were found during infections in lung tissues (Sterner-Kock *et al.*,

2016) and in plasma (Sacchini *et al.*, 2012). Depletion of CD4^{+} T-cells did not significantly influence cytokine levels, again suggesting their minor role in control of a primary infection.

Several approaches were followed to identify protective antigens. Although antibody titres in a primary infection did not seem to correlate with a positive outcome for the animal (Schieck *et al.*, 2014), it was hypothesized that antibodies protect in a secondary infection or after vaccination. ILRI scientists and colleagues contributed towards the characterization of the *in vitro* core surface proteome of cultured mycoplasma, thus identifying candidate *Mmm* antigens for the development of improved control measures (Krasteva *et al.*, 2014). Another study characterized proteins expressed *in vivo* by mycoplasma obtained from pleural effusion (Weldearegay *et al.*, 2015).

Evidence was obtained by an ILRI student that whole, inactive mycoplasma were protective (Mwirigi *et al.*, 2016a). Immunizations were carried out with the live vaccine and with two formulations of inactivated *Mmm*. Heat-inactivated mycoplasma were found to be as protective as the live vaccine. This confirmed that live mycoplasma are not required for induction of immunity and suggested that protection can be induced by purified molecules, which are much preferable as vaccines.

Virulence factors are molecules produced by pathogens that allow them to infect hosts and evade the immune system and are currently the focus of intense research. If vaccines could be developed against virulence factors they could be helpful in preventing disease or reducing severity. For *Mmm*, no virulence factors have been confirmed *in vivo*. However, for the closely related goat mycoplasma, *Mycoplasma mycoides* subsp. *capri* (*Mmc*), biology tools such as genome transplantation can be employed to gain insight into the function of genes. The whole genome of *Mmc* is transferred into yeast cells, where it can be modified using molecular tools available for yeast, and the modified genome is then transplanted back into mycoplasma cells and the resulting mutant can be characterized. This approach was used to generate a mutant mycoplasma lacking the polysaccharide coating (an outer layer composed of carbohydrates), and *in vivo* experiments demonstrated that the polysaccharide coating is indeed a virulence factor (Schieck *et al.*, 2016;

Jores *et al.*, 2018). The polysaccharide molecules were purified, coupled to a protein and administered twice to cattle (Mwirigi *et al.*, 2016b). After challenge, the severity of disease in the immunized cattle was significantly reduced. It is interesting to know that carbohydrate can protect, and this is in agreement with the hypothesis that prevention of adhesion to lung cells is protective, but the polysaccharide coating would not be suitable for vaccine production, as it would be too expensive to produce.

Additional studies tested other potential pathogenic molecules for their capacity to protect against disease. Two promising protein candidates (Mulongo *et al.*, 2013, 2015) were investigated. Neither protein induced protection: in contrast, immunization with LppQ-N exacerbated pathogenesis as a result of the formation of immune complexes (Mulongo *et al.*, 2015). Immunization with the other candidate did induce good antibodies in cattle, but these antibodies did not inhibit the enzymatic function of the enzyme, which may have been necessary for the prevention of its pathogenicity (Mulongo *et al.*, 2013). These studies emphasize that care has to be taken when selecting candidate vaccine antigens, and that it is important to avoid including antigens that do not protect or that counterprotect in a subunit vaccine (Jores *et al.*, 2013b).

A successful approach in a comprehensive project was aimed at identifying candidate vaccine molecules using reverse vaccinology. As the genome of *Mmm* was available, a bioinformatics study selected 66 proteins that were likely to be present on the mycoplasma membrane or were secreted and were therefore accessible to the immune system. ILRI contributed synthetic genes for 38 of these *Mmm* proteins and the remaining were designed, and recombinant proteins produced. The potential antigens were ranked on their ability to elicit antibody responses, as tested in sera from immune animals (Perez-Casal *et al.*, 2015). After prioritization, the recombinant proteins were then pooled into groups of five antigens and administered to cattle. After challenge, three of the formulations induced protection (Nkando *et al.*, 2016). This suggests that more than one protein is protective, and further research suggested that a cocktail of four proteins mixed with an adjuvant formed a good vaccine. The Kenya Veterinary Vaccines Production Institute (KEVEVAPI) is currently acquiring the

capacity to produce and quality control the vaccine. Studies have been planned to determine its efficacy in the field and to determine how long immunity lasts.

Although in laboratory studies the efficacy of the subunit vaccine was the same as the live vaccine, it will still have a number of vital advantages: a lower price, no need for a cold chain (important to reach remote areas with little infrastructure) and the absence of serious side effects. This last condition is important to convince herders to vaccinate their animals. Another advantage of the subunit vaccine is that it may allow the development of a test to discriminate vaccinated from infected animals, which will greatly facilitate disease control.

Therapeutics

A study, initiated by the University of Nairobi and finalized at the BecA-ILRI Hub identified plants used by local herders to treat lung infections in their animals and tested extracts from these plants for their capacity to block *in vitro* mycoplasma growth (Kama-Kama *et al.*, 2016). Several had activity, and further research identified at least one chemical compound with bacteriostatic activity for *Mmm* (Kama-Kama *et al.*, 2017).

Research impact: molecular epidemiology

ILRI contributed to the isolation of new mycoplasma strains, as well as obtaining genome sequencing of several strains, including *Mmm* (Fischer *et al.*, 2015), *Mccp* (Falquet *et al.*, 2014) and *Mycoplasma feriruminatoris* sp. nov. (Fischer *et al.*, 2013; Jores *et al.*, 2013a). Additional important work was done by Gourgues and Barr (2016).

ILRI scientists improved our knowledge of the phylogenetic relationships and demographic history of mycoplasma of the 'mycoides cluster', a group of related mycoplasma that infect ruminants (Fischer *et al.*, 2012). They used multi-locus sequence typing on seven housekeeping genes from over 120 strains. Interestingly, the origin of *Mmm*, the cause of CBPP, dates back approximately 10,000 years, coinciding with the domestication of livestock. It is believed that the tradition of keeping goats and cattle in close proximity must have allowed a goat mycoplasma

(*Mmc*) to jump to cattle and differentiate into a pathogenic species.

Host-mycoplasma interactions

Because *Mmm* causes a severe infection in the lungs, one step in the disease process must be the interaction of mycoplasma with cells in the lungs. A study demonstrated strong attachment of cultured mycoplasma to *in vitro*-cultured bovine lung epithelial cells. While all cell types bound mycoplasma to some degree, very high binding was only observed with lung or bronchial epithelial cells from cattle (Aye *et al.*, 2015). However, when the epithelial cells were derived from fetal lungs, no such binding was observed. This would explain why newborn and very young calves do not develop lung disease, as they may lack a receptor for mycoplasma attachment. As expected if strong attachment is an essential step in the disease process, the mycoplasma also showed only strong specificity for bovine cells, and not for cells from other species including sheep and goat. Preventing this binding step may thus prevent disease. Monoclonal antibodies were created against *Mmm*, and a number that inhibited attachment were selected. In one further study on these monoclonal antibodies, a mycoplasma molecule was identified as being involved in the adhesion process (Aye *et al.*, 2018) and could be a target for vaccination. Further testing was not carried out, as, in the meantime, the reverse vaccinology approach had successfully identified protective antigens (described earlier).

Research impact: field epidemiology and control

Modelling control strategies

Treatment of affected cattle with antimicrobials has been officially discouraged on the basis that it may favour the creation of chronic carriers, which are believed to be responsible for disease spread. However, a simulation model developed by ILRI and collaborators based on field data from Ethiopia found that antibiotics were the most efficient strategy, suggesting that the use of antimicrobials by smallholder farmers should be reconsidered (Lesnoff *et al.*, 2004).

Jeffrey Mariner and colleagues also developed mathematical models assessing the impact

of alternative control measures on the transmission dynamics of CBPP, incorporating field parameters from pastoral systems. The results indicated that a control strategy based on the currently available vaccines alone would not be sufficient to eradicate CBPP unless the efficacy, safety and duration of immunity could be substantially improved. According to the models, the farmers would benefit from reduced disease prevalence and mortality through vaccination of healthy animals combined with antimicrobial treatment of clinical cases (Mariner *et al.*, 2006b). The models also suggested that, under the prevailing inter-herd contact patterns, CBPP can be maintained indefinitely, even in moderate-sized herds (Mariner *et al.*, 2006a,b). A recent model predicted that CBPP could be eliminated in approximately 2 years provided that 75% of the animals in an isolated herd are vaccinated annually (minimum vaccine protection required is 18 months) and recommended that recurrent testing be done using an improved diagnostic test and elimination of positive animals (Ssematimba *et al.*, 2015).

Epidemiological surveys

When CBPP increased in the Ethiopian highlands, ILRI and partners responded by researching the problem and solutions. At that time, there was little information reported in the literature on within-herd spread of CBPP during outbreaks. In collaboration with the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) and the National Animal Health Research Centre, a research programme was set up in a CBPP-infected zone in the Ethiopian highlands (Boji district in West Wellega Zone) to estimate the epidemiological parameters of the disease and to assess the effects of different disease-management strategies naturally implemented by the local farmers.

A longitudinal study was carried out, which found that 34% of cattle became seropositive over a 16-month observation period and 39% of these became clinically ill, while 13% died (Lessnoff *et al.*, 2004). There was no evidence that CBPP control measures used locally by farmers (including treatment) had any benefit. A subsequent study found that herd prevalence increased with herd size and that clinical signs observed in

the survey were not indicative of disease prevalence (Bonnet *et al.*, 2005). These studies brought to attention some of the complications in controlling CBPP.

Vaccine trial

The current CBPP control strategy in Africa is based on immunization with a live vaccine (mainly strain T1/44). The vaccine confers immunity only for 6 months to 1 year and has occasionally shown severe side effects at the inoculation site: 3.8% of animals showed side effects including loss of their tail (Kairu-Wanyoike *et al.*, 2014b). The vaccine needs a cold chain and must be applied within 1 h of reconstitution. These characteristics lead to low acceptance and willingness by the animal owners to present their animals for vaccination. In addition, the vaccine is not widely available as the veterinary services regulate its use.

ILRI and partners conducted a 3-year immunization trial using a modified vaccine formulation – the commercially available T1/44 vaccine – while concurrently evaluating vaccine delivery systems. The programme concluded that the modified vaccine did not result in improved protection when deployed under field conditions (Nkando *et al.*, 2012). While stating that properly delivered vaccination significantly reduced the impact of CBPP in affected areas, the study also highlighted the need for annual boosting for sustained protection.

Research impact: socio-economics

Demand for vaccines

ILRI scientists and partners used structured questionnaires to assess farmer practices and perceptions of CBPP control, the willingness of farmers to pay, their preferences regarding vaccination and an estimation of the impact of CBPP (Kairu-Wanyoike *et al.*, 2013, 2014a,b, 2017). Pastoral populations consider CBPP a threat to their cattle, but awareness of prevention control methods varied. Many farmers were reluctant to vaccinate their cattle due in part to adverse reactions. The need for a better vaccine was reflected in the low willingness of farmers to pay for the current vaccine and vaccination. The willingness to pay was higher for a hypothetical preferred vaccine

and vaccine attributes such as the inclusion of a pH indicator (Kairu-Wanyoike *et al.*, 2014a).

Vaccine delivery systems

CBPP control measures and disease perceptions were further studied from a gendered socio-economic perspective in north-eastern Kenya (Muindi *et al.*, 2015). It was concluded that poor road infrastructure represented the main obstacle for vaccine delivery in the study area and that women, being better at recognizing the early clinical signs of CBPP, could play an important role in preventing disease spread by alerting the community and thus averting herd and trade losses by swift implementation of quarantine and ring vaccinations (Waithanji *et al.*, 2015). Furthermore, the studies concluded that there is a market for the implementation and adoption of an improved CBPP vaccine by both men and women if it is thermostable, more efficacious and safer than the current vaccine. Women also found affordability an important attribute for a new vaccine (Muindi *et al.*, 2015). These types of study are well known to overestimate demand and willingness to pay and should be regarded as promising but inconclusive in this context.

Policy analysis

ILRI contributed to a policy analysis for the implementation of CBPP control strategies in pastoral regions of sub-Saharan Africa (Onono *et al.*, 2017). This found that current vaccination was low and suggested the adoption of signed contractual agreements between the public and private sectors to support the vaccination of susceptible herds raised in endemic regions.

Peste des Petits Ruminants

PPR, or 'goat plague', is a highly contagious disease of wild and domestic sheep and goats (Taylor, 1984; Robinson *et al.*, 2011). The disease is caused by peste des petits ruminants virus, genus *Morbillivirus*, which is closely related to rinderpest virus. PPR is a devastating disease in naïve small ruminants. Outbreaks have occasionally been observed in camels and some species of wild Asian ungulates, but no clinical disease has been reported in African wildlife. The disease was recognized as a 'rinderpest-like'

condition of goats in Nigeria in 1930 and was first characterized in Côte d'Ivoire in 1942. Until the 1980s, it was seen as a problem of West Africa: since then, it has spread rapidly to around 70 countries in Africa, the Middle East and Asia. The disease re-entered China in 2015 and spread to the borders with Korea and Vietnam. In 2016, Mongolia reported its first case in livestock and a subsequent mass mortality event in wildlife, especially the Saiga antelope. In 2018, the disease was reported in the European Union (Bulgaria). Kenya saw a series of epidemics in 2006–2008, killing almost 1.2 million small ruminants and causing a decline in milk production of 2.1 million litres (FAO, 2016). The mean annual global loss from PPR mortality has been estimated at US$1.5 billion, ranging from US$0.8 billion to US$2.7 billion (Mariner *et al.*, 2016).

Safe, effective and inexpensive live vaccines, based on the Nigeria 75/1 or Sungri strains, are available and widely used. The Nigeria 75/1 strain has been in use for decades without any adverse effects and has been shown to generate life-long immunity and to protect against all lineages of PPR. The availability of these vaccines combined with lessons learnt from the global eradication of rinderpest have inspired the international animal health community to target PPR for global eradication by 2030. ILRI aims to contribute to the global eradication effort while at the same time providing evidence to inform and guide it.

Research

ILRI has been involved in PPR research since 2010 with the aim of developing vaccination strategies for developing countries. ILRI hosted the second meeting of GPRA and its scientists contributed to the development of the first pan-African strategy for the progressive control of PPR (Elsawalhy *et al.*, 2010). Subsequently, ILRI scientists contributed to a business analysis for the global eradication of PPR (Jones *et al.*, 2016; Mariner *et al.*, 2016), and remain closely engaged with the FAO/OIE PPR Secretariat. ILRI scientists have been advocates for aggressive eradication of PPR through programmes that emphasize surveillance, epidemiological analysis and targeted vaccination.

Research impact: technologies

In southern Nigeria, ILCA developed and tested a package consisting of a tissue-culture rinderpest vaccine and a dipping programme to control mange. They reported that, as a result, kid survival had greatly increased, reproductive efficiency of does improved, and monthly mortality declined by 87% in goats and by 79% in sheep (Adeoye, 1985).

Research on PPR restarted in the 2000s (Balamurugan *et al.*, 2014). ILRI scientists demonstrated the feasibility of production of a thermostable vaccine for PPR, showing that effective PPR vaccines based on the attenuated Nigeria 75/1 strain could be thermostabilized using the protocol for the production of the thermostable rinderpest vaccine developed by Tufts University and the US Department of Agriculture (USDA) (Mariner *et al.*, 1990, 1991) and used in the Global Rinderpest Eradication Programme (GREP) (Mariner *et al.*, 2012). As the thermostable rinderpest manufacturing process is unencumbered by intellectual property constraints and could be used with the existing PPR vaccine produced in accordance with OIE norms, the vaccine was available for implementation in the field.

To identify the optimal process to achieve thermostability, two main approaches were compared, one based on the ThermoVax rinderpest vaccine developed by Tufts University and the USDA, which is free from intellectual property constraints, the other based on the patented Xerovac process. Thermostability was assessed in accelerated stability tests at a range of temperatures and using *in vitro* titration assays. The ThermoVax method used in rinderpest vaccine manufacture was found to provide the best long-term thermostability at 37°C. These batches consisted of existing PPR vaccine lyophilized in the same 72 h cycle that had been utilized in the production of thermostable rinderpest vaccine (Mariner *et al.*, 1991). Under OIE norms, changes to lyophilization procedures do not require revalidation of the immunogenicity of the vaccine. The ILRI team concluded that the efficiency of the lyophilization cycle, a key variable that impacts the efficacy of chemical stabilization, was the source of the enhanced stability, as this was the only variable changed in the batches found to have the highest levels of thermostability. Lyophilization is an activity that combines biological, chemical and physical sciences. Large-scale lyophilizers are purpose-built machines, and each has a different configuration of components that behaves uniquely. The lyophilization process has to be optimized for each machine. The result was a PPR vaccine that maintained the minimum required dose as a 25-dose presentation for over 5 months at 37°C and for over 10 days at 56°C. This level of thermostability is comparable to that achieved for the thermostable rinderpest vaccine used in the global eradication of rinderpest (Mariner *et al.*, 2017).

Current efforts focus on producing sufficient vaccine to enable pilot vaccination programmes. To this end, the Central Veterinary Laboratory in Mali and KEVEVAPI have started using the protocol with technical support from ILRI and Tufts University scientists. The performance of resulting batches will be assessed through the Pan African Veterinary Vaccine Centre (PANVAC) and its performance in the field and efficiency will be compared with conventional vaccine. Thus, this vaccine will be an important control tool for remote areas, providing essential support for global eradication efforts.

In addition, ILRI has supported the testing of novel DIVA (differentiation between infected and vaccinated animals) vaccines using African breeds, as ILRI is one of the few institutions where such tests can actually be done (Holzer *et al.*, 2016). DIVA vaccines differentiate between infected and vaccinated animals because the vaccines lack at least one antigenic protein that is present on the field virus. These vaccines are important for control because vaccination in poultry would have greater worldwide acceptance if naturally infected and vaccinated-only animals could be distinguished, and if culling were necessary then naturally infected animals could be targeted.

Research impact: field epidemiology and control

Vaccination strategies

ILRI has been active in advancing approaches using targeted vaccination as a more effective alternative to mass vaccination because it has higher effectiveness and lower cost. ILRI has also piloted more effective vaccination delivery systems based on public–private–community partnerships and quantity-based approaches to remuneration

for work done. One of the lessons of rinderpest eradication was that mass vaccination was not a successful approach for completing the eradication process. The success of eradication depended on the development of approaches that identified populations responsible for disease maintenance and then focused vaccination on those critical communities. This finding was applied to PPR as ILRI piloted vaccination activities in Karamoja, Uganda and Sudan. In Uganda, vaccination was implemented through community animal health workers with costs covered by the public sector. In Sudan, more conventional veterinary personnel were used, but the livestock owners covered the costs.

Global eradication

There are four components in the global eradication framework of PPR: (i) promoting an enabling environment and reinforcing veterinary capacities through public information, updating legal framework and preparing national and regional PPR plans; (ii) supporting diagnostic and surveillance systems, which includes assessment of the epidemiological situation and strengthening of regional epidemiology and laboratory networks; (iii) supporting PPR eradications and, if approximately 1.5 billion sheep and goats need to be vaccinated, controlling other small ruminant diseases in support of PPR eradication; and (iv) coordination at country, regional and global levels.

ILRI facilitated scientists who had played leadership roles in the global eradication of rinderpest to assess key lessons from rinderpest eradication and help lay the foundation for the global eradication of PPR (Mariner *et al.*, 2012). Social innovations in animal health institutions were identified as key to capturing the benefits of technological developments such as the thermostable rinderpest vaccine. This activity fitted well with ILRI's mandate in representing the interests of developing countries and improving our understanding of animal health institutions to mitigate the impact of disease.

Newcastle Disease

Newcastle disease (ND) is a highly contagious disease of poultry and other birds caused by the Newcastle disease virus in the family *Paramyxoviridae*. It is considered the most important TAD in village poultry. Periodic outbreaks result in high mortality among free-ranging flocks and serve as a disincentive for poultry keepers to invest time or resources in their birds. Because of the difficulty of attaining biosecurity in backyard poultry, vaccination is the preferred control strategy. Live vaccines have been widely used since the 1950s and have made great progress in preventing and controlling ND. Live lentogenic B1 and LaSota vaccine strains of low virulence are commonly used worldwide for protection.

Research

Poultry disease was not a focus of research during ILRI's first decades, and for a number of reasons, stakeholders did not prioritize poultry health. Moreover, in Africa, poultry did not make important contributions to the diet, although that has changed due to imports and the establishment of intensive production. Poultry disease first rose to prominence at ILRI because of the highly pathogenic avian influenza (HPAI) pandemic (see Chapter 8, this volume). Subsequently, a project investigated ND vaccine impact in East Africa, and further work studied a range of poultry diseases in Ethiopia.

Research impact: technologies

Live vaccines can show low efficacy due to administration challenges or failure of birds to mount a sufficient immune response. ILRI research in Ethiopia investigated the potential for improving vaccination success in village chicken. ILRI conducted a study to compare the antibody response to ND in intensively reared and backyard chicken. The latter mounted a much weaker response. A follow-on experiment found that veterinary treatment (especially worming) before vaccination could dramatically improve the antibody response and hence the protection offered by the vaccine (Abera *et al.*, 2017).

Research impact: field epidemiology and control

In the early 2000s, desk research developed background papers on ND in Ethiopia (Dessie and

Jobre, 2004) and southern Africa (McDermott *et al.*, 2001). ND was also addressed along with HPAI in South-east Asia as discussed in Chapter 5 (this volume).

The first major research into poultry health in Ethiopia was launched in 2011. Its aim was to identify infectious diseases of Ethiopian village poultry and to improve their control. ND was identified by farmers as the highest priority disease. A longitudinal study subsequently found that ND was responsible for the death of 843 chickens of the cohort of 1358 birds (Jarso, 2015).

Because of the lack of previous research, ILRI was also able to identify some diseases for the first time. The poultry farm at the Ethiopian Institute of Agricultural Research (EIAR), Debre Zeit, represents an important centre for research, farmer training in poultry production and distribution of birds among smallholders. As such, it has vital links with farmers, especially intensive and semi-intensive producers. In 2012, respiratory disease was a major cause of morbidity and mortality. ILRI used a combination of serological and molecular methods for the detection of pathogens, reporting for the first time variant infectious bronchitis virus (793B genotype), avian metapneumovirus subtype B and *Mycoplasma synoviae* in poultry. This information was used for planning vaccination programmes (Hutton *et al.*, 2017).

Research impact: socio-economic studies

ILRI conducted an economic analysis in Nigeria and found that ND caused an estimated 25.5 million poultry deaths each year nationwide, costing 8.9 billion naira. Control comprising vaccination, sanitary measures and surveillance was estimated to cost 1.8 billion naira per year (Fadiga *et al.*, 2011). Within this study, a related *ex post* analysis examined efforts to stop HPAI in Nigeria. A stochastic epidemiological model was used to parameterize counterfactuals of disease evolution with and without interventions. The results indicated that a programme of HPAI control versus a baseline of endemic, high-mortality HPAI gave a benefit:cost ratio of 1.75 over a 5-year period.

Vaccine adoption

ND vaccines are widely used in intensive poultry production and are effective and inexpensive. While ND vaccines are readily available, uptake by poor farmers has been very limited. A project conducted a study in 2011 to investigate vaccine adoption in Kenya and Tanzania in order to understand the barriers and bridges to adoption (Lindahl *et al.*, 2019). In this study, two areas in Kenya and Tanzania were studied, where all villages were eligible for government control programmes, but some villages had received additional support to get vaccination from a project (Tanzania) or non-governmental organization (Kenya). Where vaccination support had been given, 59% of households overall had used vaccines against ND, which was significantly ($p < 0.001$) more than the 17% of households that had used the ND vaccine in areas with no additional support. However, many farmers stopped using vaccines, and even those who did use them often used them suboptimally and continued to experience losses from ND. Despite this, there were significantly fewer reported poultry deaths in villages with support. This showed the importance of additional support if vaccines are to be taken up by poor farmers, and also the gap between theoretical performance of disease control and disease control in practice. Even with considerable external support, almost no farmers vaccinated their poultry in accordance with recommendations and losses from ND continued.

The Ethiopian work later evaluated vaccine uptake. A contingent valuation method was conducted to elicit farmers' willingness to pay for village poultry vaccine services. Two hypothetical vaccine programmes were designed for ND and Gumboro disease. The results showed that farmers recognized the benefits of the vaccine programme and that many would be willing to pay for it (Terfa *et al.*, 2015).

Other Livestock Transboundary Diseases

Rinderpest

Rinderpest is an infectious viral disease that has killed hundreds of millions of cattle over hundreds of years, often causing famine. Rinderpest was formally declared to have been eradicated in 2011, becoming only the second disease (after smallpox) to have been eradicated. This is widely

regarded as the greatest veterinary achievement of our time. It was the result of decades of effort by a wide range of research institutes, donors, intergovernmental organizations, national governments, non-governmental organizations and cattle-keepers. FAO had a key leadership role.

ILRI made a small but strategic contribution. First, economists developed and disseminated some of the first estimates of the very large benefits that could be obtained from control (Tambi *et al.*, 1999). ILRI economists also contributed to *post hoc* assessments of the socio-economic direct and indirect benefits of rinderpest eradication (Roeder and Rich, 2009). Rich *et al.* (2014) examined the *ex post* impact of rinderpest eradication in Chad and India. An important innovation of this study was methodological, in terms of identifying impact from the producer level to national and international levels. Farm impacts were examined through the use of a herd demographic model and macroeconomic impacts with a computable general equilibrium (CGE) model. Baseline benefit:cost ratios associated with eradication in Chad were 4.0 over 1963–2002 (ranging from −5.8 to 47.2). In India, the final stage of eradication yielded a benefit:cost ratio of over 64.

ILRI scientists also developed a mathematical model for disease dynamics (Mariner *et al.*, 2005). Estimates from simulations suggested populations of around 200,000 head of cattle were needed to sustain transmission. This meant that communities smaller than 200,000 head did not need to be prioritized in the final stages of eradication as the disease would naturally fade out in these populations. Furthermore, this supported the view that, if the disease was controlled in cattle, it would fade out in wildlife populations as the fragmented populations remaining in Africa are not large enough to sustain infection even if biologically competent to do so. More importantly, modelling was shown to be an effective communication tool to engage decision makers, illustrating concepts such as fade out of disease from small populations and how suboptimal vaccination could contribute to virus persistence (Roeder *et al.*, 2013).

Small contributions were made to field epidemiology. By the 1990s, Somalia was one of the few remaining reservoirs for rinderpest, but control there was hampered by political instability. ILRI contributed to developing a risk map based on social and network risk factors (Ortiz-Pelaez *et al.*, 2010), a method originally developed for mapping FMD in the UK. This identified areas in the central and southern regions of Somalia where veterinary authorities could concentrate surveillance activities.

Participatory surveillance evolved during the global eradication of rinderpest when the tools used for participatory rural appraisal were adapted to searching for rinderpest outbreaks. The approach proved its utility by identifying occult foci of disease and providing appropriate intelligence to guide the eradication strategy (Mariner and Roeder, 2003). ILRI conducted an evaluation of participatory surveillance to provide guidance for appropriate use (Hannah *et al.*, 2012). This found that participatory surveillance was a useful epidemiological tool, most appropriate for small-scale farmers and applied in complement to conventional surveillance.

Foot-and-mouth disease

Foot-and-mouth disease (FMD) is often considered the most economically important global animal disease (see Chapter 5, this volume). Notable achievements in FMD research were: (i) an impact for specific regions; and (ii) participation in GFRA. In 2010, GFRA performed a gap analysis to identify areas where FMD research could have the greatest impact and to guide and coordinate future research efforts. The 2014 gap analysis was updated to include work published in 2015 and was the subject of a special issue of *Transboundary and Emerging Diseases*. Most of the research syntheses involved ILRI scientists (Vosloo and Knight-Jones, 2016). An earlier case study of the Philippines showed benefits of ILRI work. In 1999, the National Foot and Mouth Disease Task Force of the Philippines requested ILRI's support for a national FMD control and eradication program. An ILRI team complied with the request and, in 2002, published the results of its epidemiological and economic assessment of the potential benefits of eradicating FMD from the Philippines. The results clearly indicated significant potential economic benefits, particularly for Filipino swine producers, who were threatened by a virus subtype highly specific to pigs that was causing high piglet mortality, widespread pig abortions, and infertility. The joint ILRI-Filipino

evidence clearly showed the proposed eradication program to be a worthwhile investment of public funds. This public-private partnership for control and eradication continued until 2011, when the Philippines was declared free of foot and mouth. This official disease-free status opened up markets for pork products from the Philippines and motivated the country's producers to upgrade their piggeries.

Classical swine fever

Classical swine fever (CSF) is a highly contagious, potentially fatal viral disease of swine. It is endemic in much of Africa and Asia. In India, pigs are most important in the north-eastern states, and ILRI started to work with the sector in the early 2000s. ILRI conducted epidemiological and economic studies on CSF in the Indian states of Assam, Nagaland and Mizoram in 2011. These found that pig farmers incurred huge losses, over 2 billion Indian rupees each year, from mortality, treatment and replacement costs. ILRI suggested interventions such as vaccine-based control to the government and private sector. As a result, the Government of India initiated a national swine fever control programme targeting north-east India. Moreover, policy changed to better facilitate the licensing of vaccine production by public and private institutes. A subsequent ILRI project trained community animal health workers and started vaccination against pigs. No cases of disease were reported after vaccination. The State Government of Nagaland then mainstreamed the approach (Bett *et al.*, 2014). Although at an early stage, there is some evidence for ILRI research leading to positive outcomes (Padmakumar *et al.*, 2017).

Porcine reproductive and respiratory syndrome

Porcine reproductive and respiratory syndrome (PRRS) is an important disease in pig production and is endemic in Vietnam. ILRI conducted the first nationwide studies of PRRS in Vietnam, identifying spatial and temporal patterns that are useful in planning control (Fig. 7.1) (Lee *et al.*, 2019).

Lumpy skin disease

Lumpy skin disease (LSD) is an economically important TAD of cattle caused by the lumpy skin disease virus in the genus *Capripoxvirus*. Although it is present in most African countries, the disease is mild and inapparent, so difficult to detect. Failure to report subclinical cases of LSD due to lack of good diagnostic tools is a major limitation in LSD control. ILRI included LSD in several field epidemiology surveys showing its importance in Ethiopia and Tanzania. An economic analysis of the hides and skins value chain in Somaliland found that LSD was a significant impediment to the export trade (Wanyoike *et al.*, 2018).

A major limitation to LSD control is the difficulty of detecting it. Despite the availability of molecular diagnostic methods that are appropriate for LSD diagnosis, there is no single rapid, sensitive and inexpensive method. The BecA-ILRI Hub tested a loop-mediated isothermal amplification (LAMP) assay (Lamprey and Reid, 2004) for LSD diagnosis; this is a gene amplification procedure that can amplify a few copies of DNA to a large amount in less than 1 h using simple equipment. The tests suggested that LAMP would be an accurate and useful diagnostic tool (Mwanandota *et al.*, 2018).

Infectious bursal disease

Infectious bursal disease is an acute, highly contagious, viral disease of young chickens. The disease causes small-scale poultry farmers huge economic losses, both from the many birds that die outright and from lost productivity among surviving birds. With collaborators, ILRI conducted the first molecular characterization of the infectious bursal disease in Kenya. The Directorate of Veterinary Services plans to use the findings to develop improved vaccination, surveillance and control strategies for infectious bursal disease, such as procedures for virus diagnosis (ILRI, 2018).

Transboundary Animal Diseases in Systems

Transboundary animal diseases (TADs) do not occur in isolation but as part of complex
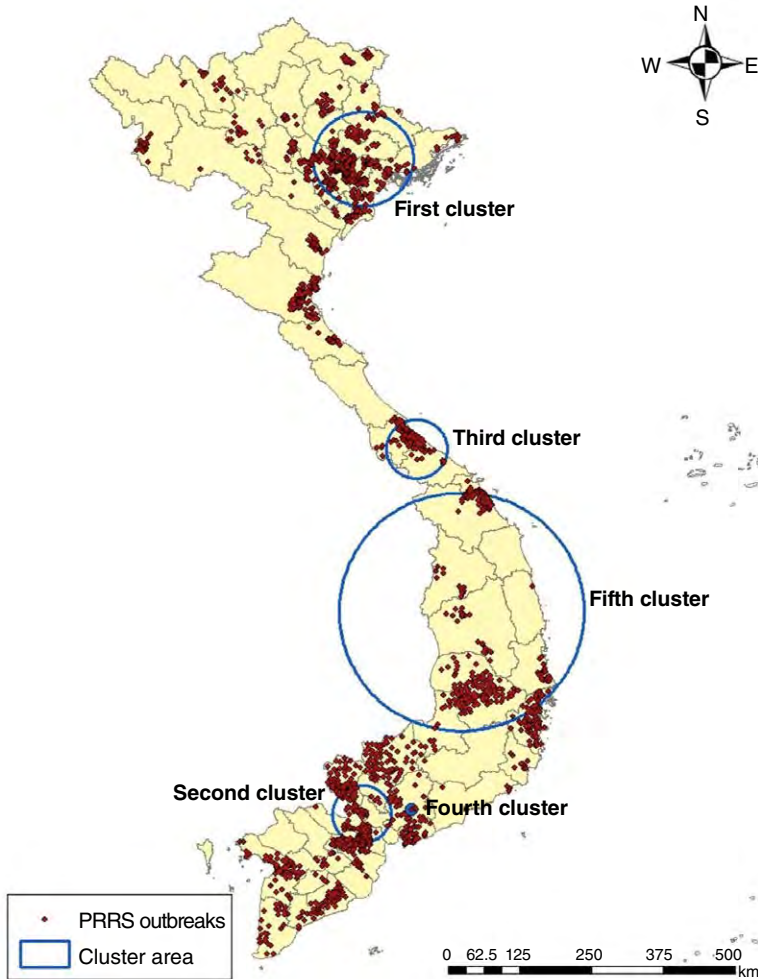
Fig. 7.1. Space-time cluster analysis of PRRS outbreaks from 2008 to 2016 in Vietnam. (from Lee *et al*., 2019).

ecosystems. Nearly all disease research focuses on a single disease or few closely related diseases, but in reality organisms are normally infected with a number of more or less pathogenic organisms at any one time. ILRI recruited a large cohort of calves in western Kenya to investigate a wide range of diseases (over 100) and to follow up each calf with monthly clinical examinations and laboratory testing for 51 weeks over a period of 3 years (Fig. 7.2) (Bronsvoort *et al.*, 2013). This enormous undertaking was the most ambitious veterinary epidemiological study to date carried out in a developing country. It was scientifically significant as the first attempt to describe the entire disease burden of

any naturally occurring animal population in the world. This study generated a wide range of scientific findings, published in high-impact journals. These included several 'firsts' in terms of pathogens, parameters and disease associations that had not been reported previously. Research tools were developed and validated. Although many of the findings have implications for disease control, their development impacts have not yet been evaluated.

Some of the more novel and important outputs and findings were as follows:

- The cohort experienced a high mortality rate of 16%, with at least 13% of this due to
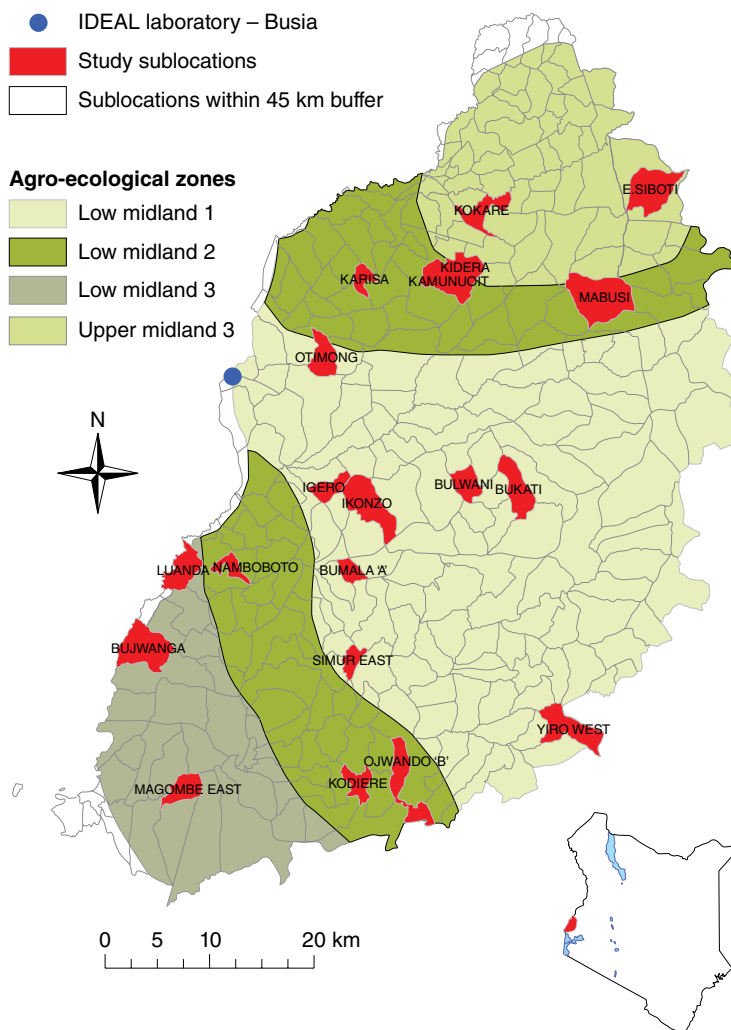
Fig. 7.2. Study area in western Kenya. (From de Clare Bronsvoort *et al.*, 2013.)

infectious diseases. Over 50 pathogens were detected in this population, with exposure to a further six viruses and bacteria. East Coast fever (ECF) was the main cause of death, accounting for 40% of all deaths, haemonchosis 12% and heartwater disease 7% (Thumbi *et al.*, 2013).

- Following a cohort of animals allowed investigation of coinfections. The study found that these were common and that the risk of ECF death was itself significantly increased by a high helminth burden and by coinfection with trypanosomiasis. Farmers that provided crop residues to their animals

as a feed supplement had significantly lower deaths from helminths. This study gave empirical evidence on simple actions that could greatly reduce calf mortality (Thumbi *et al.*, 2014).

- Heterologous reactivity is the influence of past or current infection on the outcome of infection with another: this may be positive or negative. Because calves were followed over time, researchers were able to obtain the first quantitative estimates of the effects of heterologous reactivity for any parasitic disease. The study provided three strands of evidence for heterologous protection against

ECF in a population of indigenous African cattle. A natural challenge analysis found that infection with less pathogenic *Theileria* spp. reduced mortality from ECF; the case–control study quantified the level of protection (43% reduction in mortality); and the mathematical model of heterologous protection successfully predicted key features of the epidemiology of ECF. This suggested that heterologous protection may determine the burden and distribution of many parasitic diseases in host populations, including humans (Woolhouse *et al.*, 2015).

- Many more farmers reported carrying out disease control measures such as tick control and worming than were actually observed. This suggests that farmers are answering what they think they should be doing or maybe have done, but a significant proportion actually then appeared to not carry out these measures over the course of our observations. This highlighted the need for caution in interpreting responses, especially from cross-sectional data (Bronsvoort *et al.*, 2013).

- Investigation of antibodies to four tick-borne haemoparasites found that 90% of dams were seropositive for at least one of the parasites, while 93% of calves had received colostrum. Surprisingly, there was no discernible difference in mortality or growth rate between calves that had taken colostrum and those that had not. These results are also important for interpretation of serosurveys of young calves following natural infection or vaccination (Toye *et al.*, 2013a).

- Bluetongue virus (BTV) and epizootic haemorrhagic disease virus (EHDV) are members of the genus *Orbivirus*, transmitted by biting midges. BTV spread from Africa to Europe, resulting in high economic losses. The study found that BTV and EHDV are highly prevalent, with cattle being infected from an early age. This was the first report of EHDV from East Africa (Toye *et al.*, 2013b).

- Calf respiratory disease is a major problem globally but is little researched in Africa. The study found that three viruses often implicated (infectious bovine rhinotracheitis virus, bovine parainfluenza virus type 3 and bovine viral diarrhoea virus) all have an estimated seroprevalence of around 20% (Callaby *et al.*, 2016).

- This study was the first to accurately describe the haematological parameters for any African breed of cattle. Unlike European cattle breeds that experience a fall in red blood cells following birth, the West African cattle showed a rise. This is useful in understanding what is normal, but also suggests a possible mechanism for disease resistance (van Wyk *et al.*, 2013). Data from the study were also used to develop and validate a girth band to predict live weight of East African Shorthorn Zebu (Lesosky *et al.*, 2012). This is useful for research but also appropriate for dosing of animals.

Conclusion and Future Directions

Because TADs can spread rapidly and cause catastrophic losses, they are of extreme concern to the intensive livestock sector in high-income countries. In these industries, many TADs have been eradicated, and hence they are vulnerable to reintroduction from developing countries. Because TADs were seen as having been well studied, they were not initially prioritized by ILRI. This has gradually changed as evidence has emerged that TADs can have deep impacts in poor countries.

A more pragmatic reason is that, because of their potential impact on high-income countries, there is often funding available for TAD control. This introduces a certain tension between the priorities of rich and poor countries, as non-epidemic animal diseases are almost certainly of greater burden than the epidemic TADs. However, TAD research offers a bridge between low- and middle-income countries and high-income countries research by providing a subject of common interest but differing relative advantage. Novel approaches, pioneered by ILRI and collaborators, to investigating multiple diseases in cohorts of animals can help us better understand the relative importance of endemic and epidemic disease and how they interact.

External drivers, including demographic growth, climate change, biodiversity loss, urbanization, globalization and dietary change, have potentially profound effects on TAD dynamics, which ILRI can influence, mitigate and take leverage of to fulfil its mission.

Laboratory-based work has produced some notable achievements including generating fundamental knowledge on genetics and phylogenetics, new and improved diagnostics, and promising vaccine candidates. Much of this research is upstream and, by its nature, development benefits will take several decades to be visible. However, there is well-documented frustration with the technologies available for TAD management and control, and much potential for improvement.

Some of the identified priorities, which inform future research, include: cheap, simple, robust field diagnostics; thermostable vaccines that do not require a cold chain; DIVA vaccines that allow vaccinated and infected animals to be distinguished; vaccines that are inexpensive and provide life-long immunity; vaccines that are free of side effects; multivalent vaccines so that one shot will immunize against many diseases; ways of telling whether a vaccine is authentic and functional; and vaccines that are more effective and do not 'break down' as the result of challenges in administration and because animals are immunocompromised. As this chapter has summarized, ILRI is working actively in all these areas with some success and the promise of more to come.

Developing innovative and impactful TAD control requires a good understanding of how both diseases and people behave. ILRI TAD research has had success in developing mathematical models and understanding transmission dynamics, i.e. how diseases move among hosts, vectors and the environment. This information has been central to important control successes in the past and will be in the future. However, good models require good data on disease parameters, and these are often not available or can only be gathered at costs that investors are unwilling to pay.

Students and graduate fellows have always been involved in ILRI health research, and this has been important for capacity development as well as establishing and expanding networks. To a lesser extent, training has been extended to decision makers, implementers and value chain actors. This is likely to be more important in the future.

As the research agenda has developed, ILRI and its investors have increasingly focused on impact today as well as tomorrow. Field studies have shown that, while vaccines are theoretically the best measure for disease control, poor farmers have very little propensity to buy them and the public sector has very little capacity to deliver them at scale, at least on a continuous as opposed to a campaign basis. This has opened new directions to explore.

The eradication of rinderpest raises hopes that progressive control may be the one best solution for those TADs that can be eradicated, notably PPR. At the same time, there has been more attention on influencing farmers' behaviour as a form of control. Research on several TADs makes it clear that 'training and information' are inadequate and that other incentives, whether social, financial or changes in choice architecture (nudges), are needed.

Finally, there is a shift from scientific papers to field products. This means relying on markets as well as public services, and public-private partnerships are an active area of research and engagement. Future research will continue to develop and improve diagnostics and vaccines with increasing focus on applications. This will be accompanied by efforts to create novel approaches to TAD control that use market and social forces. Understanding these needs a value chain and consumer focus, as well as an appreciation of equity issues.

Note

[1] The TickRisk project, led by Maxime Madder and Eva De Clerq and based largely in Benin, and the WecatiC project, led by Hassane Adakal, have provided the above data, mostly collected during 2012–2013.

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8 Zoonoses

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Contents

Executive Summary

The problem

Zoonoses are diseases that are transmissible between humans and animals through either direct contact or by way of food, water or the environment. Around 60% of all human diseases and around 75% of emerging human infectious diseases are zoonotic. Zoonoses have high impacts on human health, livelihoods, animals and ecosystems. The first global syntheses on the impacts of zoonotic diseases, led by the International Livestock Research Institute (ILRI), estimated that in the least-developed countries, 20% of human sickness and death was due to zoonoses or diseases that had recently jumped species from animals to people (Grace *et al.*, 2012a). Zoonoses sicken several billion people each year and kill millions, mostly in low- and middle-income countries. While estimates of the historical burden of zoonoses are lacking, the World Bank has estimated that emerging zoonoses cost around US$7 billion a year (World Bank, 2012).

Some zoonoses are considered neglected, classical or endemic, and others as new or emerging. Neglected zoonoses are mostly controlled or eradicated from high-income countries but impose a large burden on low- and middle-income countries. Emerging zoonoses are a global threat, but most of the economic burden falls on high-income countries. Disease categories are to some extent overlapping, and a disease may be endemic in one place and emerging in another. Many zoonoses, both neglected and emerging, are food-borne; these are discussed in Chapter 9 (this volume). This chapter focuses on zoonoses that are not transmitted primarily through food.

ILRI's role in the global context

ILRI has worked in joint partnerships with several universities and research institutes to develop research activities on zoonoses. This area of research commenced in the 1990s with small studies on neglected zoonoses. Initial work focused on bovine tuberculosis (TB), brucellosis, human African trypanosomiasis (commonly known as sleeping sickness) and rabies. From the 2000s, an agenda on the pig tapeworm that causes the parasitic tissue infection cysticercosis emerged, while research on specific neglected zoonoses continued, including work on anthrax; the acute bacterial swine disease known as erysipeloid ('diamond skin disease'); the bacterial diseases leptospirosis, Q fever and streptococcosis; and the parasitic (roundworm) disease trichinellosis, which humans can get when consuming undercooked or raw pork products.

Work on emerging zoonoses started in the 2000s as global attention heightened following the global pandemic of highly pathogenic avian influenza (HPAI, or avian influenza, caused by influenza A virus subtype H5N1) and the high-profile outbreaks of bovine spongiform encephalopathy (BSE or 'mad cow disease') and severe acute respiratory syndrome (SARS). ILRI research on emerging diseases focused on livestock-related antimicrobial resistance, avian influenza, Ebola virus disease, Middle Eastern respiratory syndrome coronavirus (MERS-CoV) and Rift Valley fever (RVF).

As the programme matured, ILRI zoonoses research moved from a predominantly veterinary public health paradigm to embrace one-health, which is predicated on the interdependence of human, animal and ecosystem health. As well as the research on high-priority zoonotic diseases, ILRI research initiatives addressed specific livestock systems, notably pastoral and urban.

In the last two decades, this work has extended from East Africa to India and South-east Asia, and in the last decade, ILRI's zoonotic research was aligned to the livestock value chains prioritized in the CGIAR Research Programmes (CRPs) on Livestock and Fish (2012–2016) and Livestock (2017–2021). Research on zoonoses has included estimating the prevalence and burden of zoonoses, identifying factors or drivers of emergence of zoonoses, understanding the risk factors of these infectious diseases, and strategies for reducing those risks and better managing these diseases.

Impacts of ILRI research

Because large-scale zoonoses research at ILRI is relatively new, ILRI's scientific impacts in this area are more notable than its impacts on development. The most-cited papers by any ILRI authors or co-authors are in the realm of climate change and human disease, emerging zoonoses and estimation of the human disease burden of zoonotic diseases. Research analytics show that ILRI research was especially dominant in MERS-CoV and RVF. There are also many important ILRI outputs on antimicrobial resistance, avian influenza, brucellosis, cysticercosis and sleeping sickness, but these diseases are the focus of considerable global research efforts, and ILRI has been a relatively minor player globally. Many syntheses chapters and papers on zoonoses have been authored or co-authored by ILRI scientists. An important scientific contribution has been development and deployment of tools as well as methodological advances. Most notable were mathematical modelling, systematic prioritization of zoonoses, use of geospatial data and participatory disease surveillance.

While many of ILRI's research activities helped to advance our basic understanding of disease, which can be anticipated to contribute to long-term improvements in human health, some had significant direct outcomes. In Uganda, ILRI scientists identified the first cases of swine erysipelas ('diamond skin disease'), established that swine brucellosis did not occur and established that trichinellosis (pork measles) might be transitioning from a wildlife to a livestock cycle. This kind of new and surprising information usefully alerted national medical services that some diseases they did not know were present actually were present and that other diseases they suspected to be present were in fact not present.

Similarly, a study in Uganda found substantial underdiagnosis of sleeping sickness, another in western Kenya found extensive misdiagnosis of human brucellosis, and yet another in northern Kenya found substantial overdiagnosis of malaria. ILRI brought these findings to the attention of local medical authorities. While the benefits of this work have not yet been well evaluated, this work is expected to lead to better treatment for tens of thousands of sick people.

Initial work on zoonoses logically focused mostly on improving our understanding of the presence, prevalence, burden and drivers of zoonotic disease. ILRI developed a prototype diagnostic for cysticercosis, but this did not go to scale because of lack of demand; tests for bovine tuberculosis diagnosis are ongoing at ILRI. A vaccine for RVF is under development by ILRI and has potential for widespread use. Vaccination (using a commercial vaccine) for avian influenza was piloted in Java, Indonesia, with ILRI support; an ILRI evaluation showed this was effective but unsustainable purely by the market. Another ILRI evaluation of vaccination for cysticercosis in Uganda came to the same conclusion. These findings helped identify more practical solutions, some of them potentially involving public-private partnerships.

Small pilots were conducted by ILRI to train farmers, extension agents, slaughterhouse workers and street vendors to improve food safety: most showed benefits, at least in the short term. ILRI has also conducted *ex ante* and model-based assessments to compare alternative response strategies for zoonotic disease, notably for RVF and sleeping sickness.

ILRI has been involved in policy support for better controlling zoonoses at local, national, regional and international scales (UNEP and ILRI, 2020). ILRI has partnered with the World Health Organization (WHO) and other international organizations on several initiatives to better control neglected zoonoses generally and cysticercosis specifically. It has also partnered with most of the major global one-health initiatives. ILRI supported regional initiatives on rabies and cysticercosis. At national levels, ILRI has supported contingency planning and groups

working in different countries on specific zoonoses, including MERS, brucellosis and RVF, as well as working groups and task forces focused more broadly on zoonoses and one-health. In cities and decentralized countries, ILRI has worked with local authorities and in some cases has documented beneficial shifts in policy and approaches. When engaging in these policy processes, ILRI provided evidence and advocated best practice, but ILRI's contributions to health policy and the impacts of policies influenced by ILRI have not been well documented.

Estimating development impacts is more difficult. Moreover, many of the benefits of better controlling zoonotic diseases come not from increasing incomes or improving nutrition of the poor but rather from averting their losses, which is difficult to measure in the absence of a counterfactual. Certainly, individual projects demonstrated far-reaching improvements in capacity linked to development impacts. For example, projects in South-east Asia piloted a village-based approach to community control of rabies that was subsequently extended to the entire island of Bali.

Millions of people have been reached by initiatives that aimed to protect human health and reduce economic burdens as the result of timely detection of emerging diseases and an appropriate response. For example, ILRI partnered several stakeholders in Kenya to develop a decision-support tool for better managing RVF. Together with risk maps, this tool was incorporated into the country's RVF contingency plan, which is the mainstay for mitigating the impacts of an outbreak of the disease. We estimate that hundreds of millions of people lived in areas where participatory disease surveillance was active. It is difficult to quantify the impact of these preparedness activities, but our best estimates suggest that timely surveillance can reduce the impacts of a disease outbreak by 90% (Grace, 2014). Several of these programmes were operational for many years during the HPAI pandemic, and national programmes for RVF are still active in Kenya.

In several cases, ILRI's scientific outputs have been taken up by other development actors with probable benefits. For example, ILRI's contributions to research on the burden and distribution of sleeping sickness in Uganda and on management options for better control of this disease influenced major donor investments that protected the health of hundreds of thousands of cattle (although the intervention did not prove sustainable). Zoonoses prioritizations conducted by ILRI have been directly connected to funding decisions by donors. ILRI has also led several evaluations of zoonoses control projects, most notably on avian influenza, which either endorsed national control programmes or led to improvements in how they were conducted.

Capacity development

Dozens of graduate fellows have been trained by ILRI and its partners as part of research into zoonoses. Many of these trained students have taken up important roles in ILRI and other organizations, including universities, ministries and health services. ILRI scientists also supervised and taught a novel epidemiological educational course for the Field Epidemiology and Laboratory Training Program within the Ministry of Health, Kenya, which has been evaluated positively. Veterinary staff members were trained by ILRI in several countries. ILRI also supported the establishment of one-health centres in Thailand and Indonesia and provided ongoing support to the development of similar centres in Côte d'Ivoire and Vietnam. These centres are all operational (as of 2020), providing training and conducting research in zoonoses. ILRI supported setting up and running a laboratory in the town of Busia, in western Kenya, which has helped improve understanding of livestock and human diseases and their links. In 2020, ILRI launched a major initiative, the One Health Research, Education, Outreach and Awareness Centre. Its aim is to improve the health of humans, animals and ecosystems through capacity building; strengthening local, regional and global networks; and evidence-based policy advice in the context of one-health by setting up a central facility for one-health in sub-Saharan Africa.

Introduction

This chapter considers ILRI research on zoonoses under two rubrics: (i) research on zoonoses occurring in systems; and (ii) research on high-priority emerging and neglected zoonotic diseases. Under the former, we prioritized diseases and conducted studies on disease emergence and participatory disease surveillance, investigated

multiple zoonoses occurring in systems, and collaborated in regional and international initiatives to control zoonoses. Under the latter, we conducted studies on antimicrobial resistance, avian influenza, Ebola virus disease, MERS-CoV and RVF, all of which are considered emerging disease problems, and on key neglected zoonoses including cysticercosis, brucellosis and sleeping sickness.

Zoonoses were not within the research mandate of the International Laboratory for Research on Animal Diseases (ILRAD), which, with the International Livestock Centre for Africa (ILCA), was a predecessor of ILRI. ILRAD focused on African animal trypanosomiasis and East Coast fever. ILCA did not conduct disease-specific research but frequently mentioned zoonotic diseases as key problems in Africa's livestock systems and judged them important due to the harm they cause the continent's livestock sector and public health.

When ILRI was constituted in 1994, neglected zoonoses were considered diseases well researched in high-income countries and therefore not high priorities for ILRI. However, opportunities for developing low-cost appropriate technologies for controlling neglected zoonoses in lower-income countries were not precluded from ILRI's research agenda. At that time (mid-1990s), emerging infectious diseases were not yet considered a global priority.

The first systematic approach to identify pro-poor animal health research priorities was conducted by ILRI in 2000 and identified several zoonoses as high priorities (Perry *et al.*, 2002). Following this, ILRI's new strategy identified impacts on the livestock livelihoods of the poor, including those caused by neglected zoonoses, as an important area of research. A programme on livestock impacts on human health was initiated in 2005, led by Tom Randolph. (In 2008, this programme was incorporated into a broader agenda on livestock markets research.)

Because ILRI had limited expertise dedicated to zoonoses (as distinct from veterinary public health), ILRI initiated a collaboration with the Danish Bilharziasis Laboratory and the Swiss Tropical Institute (STI) to develop a research agenda on zoonoses[1]. Over the next decade, work on neglected zoonoses continued. At the same time, emerging zoonoses climbed rapidly up the research agenda, driven by concern over high-profile outbreaks of avian influenza, RVF

and SARS. Several ILRI scientists were involved in emerging zoonoses research[2]. In 2011, following a research restructuring, zoonoses was once more the focus of a dedicated ILRI programme, namely, Animal Health, Food Safety and Zoonosis, led by Delia Grace.

In 2018, another restructuring saw this programme joined with three other units working on different aspects of health to constitute an Animal and Human Health programme, jointly led by veterinary epidemiologist Delia Grace and veterinary vaccine developer Vish Nene. Over the years, ILRI has invested substantially in several high-priority emerging and neglected zoonoses, including anthrax, avian influenza, brucellosis, COVID-19, cysticercosis, Ebola, MERS, RVF and sleeping sickness. The outputs, outcomes and impacts of this work are summarized in the next sections.

Prioritization

Priority setting is essential for directing finite resources to activities that maximize benefits. As discussed in Chapter 5 (this volume) on veterinary epidemiology, in 2002, ILRI was commissioned to conduct the first study aiming to determine the livestock diseases for which research investments were most likely to alleviate poverty. Zoonoses were considered as a separate category, and ranking was done by experts at regional workshops. The top three priorities were all neglected zoonoses: brucellosis, cysticercosis and leptospirosis. This landmark study influenced donor investment in research for development.

In 2005, WHO and the UK Department for International Development (DFID) convened the first meeting to tackle neglected zoonoses, and several ILRI experts participated (WHO, 2006). The meeting identified seven zoonoses – anthrax, bovine TB, brucellosis, cysticercosis, echinococcosis, rabies and zoonotic trypanosomiasis – as priorities. In 2012, ILRI developed the first global assessment of zoonoses and poor livestock keepers (Fig. 8.1) (Grace *et al.*, 2012b). This study combined updated maps of poor livestock keepers with a literature review on the prevalence and impacts of zoonoses. The study assessed 56 zoonoses, together responsible for around 2.5 billion cases of human illness and 2.7 million human deaths a year. The most important diseases in terms of burden and amenability to control
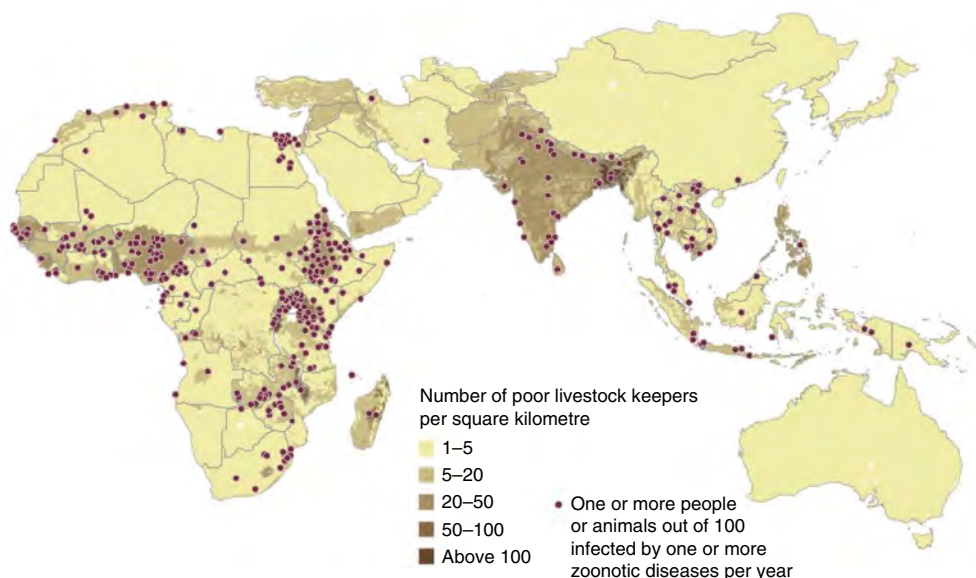
Fig. 8.1. Zoonoses and poor livestock keepers. (From Grace *et al.*, 2012b.)

were cysticercosis, leptospirosis and zoonotic gastrointestinal disease. This study was commissioned by DFID and was used to develop a major funding initiative by DFID on zoonoses.

From 2010, ILRI engaged with the Public Health Foundation of India and was a member of the Roadmap to Combat Zoonoses in India initiative. This used a systematic and validated method to prioritize a research agenda and identify priority zoonoses as well as vulnerable populations (Sekar *et al.*, 2011). Subsequently, ILRI organized a series of one-health dialogues in India with the Indian Council of Agricultural Research, the Public Health Foundation of India and other stakeholders (ILRI/ICAR, 2013; ILRI, 2014). ILRI has continued to support evidence-based one-health approaches and coordination through workshops and training in India, and one-health continues to be supported by the Bill & Melinda Gates Foundation as an important pathway to improving health care in India.

ILRI scientists also contributed to the first estimate of the global burden of food-borne disease (Havelaar *et al.*, 2015), which estimated not only the high burden of food-borne disease but also the importance of zoonoses and animal-source foods. More recently, ILRI is a partner in an initiative to develop a global assessment of

animal disease, which will include zoonoses (Global Burden of Animal Diseases initiative). While prioritization efforts have varied in their rigour and use of evidence, they have helped build a global consensus as to which of the many hundreds of zoonoses are most important to poor people, and this has also informed research globally on neglected and emerging zoonoses. There are clear links between evidence produced by ILRI and actions taken by donors in providing funding for zoonoses research for development.

In 2015, ILRI scientists participated in a systematic prioritization of zoonotic diseases for Kenya that was coordinated by the US Centers for Disease Control and Prevention (CDC) and Kenya's Zoonotic Disease Unit. The prioritization exercise identified the top five zoonotic diseases for the country: anthrax, brucellosis, rabies, RVF and trypanosomiasis (Munyua *et al.*, 2016a). The prioritization tool has been used by government researchers to allocate resources to specific surveillance, prevention and control campaigns. ILRI scientists have partnered with the Zoonotic Disease Unit to develop elimination plans for rabies and to target research on brucellosis and RVF. ILRI scientists also sit on the Zoonosis Technical Working Group, a panel of national experts in one-health.

Understanding drivers of disease emergence

ILRI conducted broad-based research to better understand the drivers of zoonoses emergence. A foundational research paper by Jones *et al.* (2008) had mapped all disease emergence events from the 1930s to the early 2000s. In collaboration with Jones, ILRI developed an updated disease emergence database focusing only on livestock (Grace *et al.*, 2012b). This reinforced the importance of livestock in disease emergence. It also found that disease emergence appeared to be shifting from the western seaboard of Europe and the western seaboard of North America to low- and middle-income countries.

Another ILRI review summarized work linking agricultural intensification to disease emergence (Jones *et al.*, 2013). The review found strong evidence that modern farming practices and intensified systems were linked to disease emergence. However, the evidence was not sufficient to judge whether the net effect of intensified agriculture was more or less propitious to disease emergence than if land was left unused. Subsequent fieldwork helped elucidate some of the relationships between land-use change and disease. Studies in Kenya found that degraded landscapes have more disease, but the relationship between biodiversity and disease is not straightforward. Additional research addressed the hypothesis that irrigation in dry areas would increase the zoonoses burden by creating habitats suitable for diseases; however, while irrigation was associated with increased risk of some zoonoses, adjacent pastoralist areas had increased risks of other zoonoses, suggesting a more complex interaction between ecosystems and economic development (Bett *et al.*, 2017a).

ILRI scientists were also active in understanding the links between climate change and disease emergence, often with a focus on zoonoses. They were commissioned by the CRP on Climate Change, Agriculture and Food Security to develop a paper on climate-sensitive livestock diseases that was incorporated into the planning processes of the United Nations Framework Convention on Climate Change (Grace *et al.*, 2015). ILRI scientists are also members of the very influential Lancet Commission on Health and Climate Change, which has produced some of the most-cited papers from CGIAR (Watts *et al.*, 2017, 2018a,b).

Participatory disease surveillance

Participatory epidemiology is the systematic use of approaches and methods that facilitate the empowerment of people to identify and solve their health needs. It should promote the direct agency of individuals, leading to a shared learning environment that improves the understanding of their risk perception, health risks, and options for surveillance, control and health evaluation in populations. Participatory disease surveillance is a form of active clinical surveillance. It involves the use of participatory approaches and is aimed at detecting clinical cases, which can then be confirmed by specific biological tests. Participatory epidemiology evolved in the 1990s as a new approach to working across cultures in animal health surveillance and epidemiological research (Jost *et al.*, 2007).

ILRI recruited scientists active in the development of participatory epidemiology from 2005, who proceeded to introduce the approach into the institute's research programmes. ILRI has been involved in researching and supporting participatory epidemiology and participatory disease surveillance for over a decade. Some examples include the following:

- Officials from 17 African countries received training in participatory epidemiology and disease surveillance.
- In 2008, a participatory surveillance programme was introduced in Egypt to improve animal health control activities through the use of participatory epidemiology. The programme eventually covered 53 districts (30% of Egypt's districts) in 15 governorates at risk of avian influenza (Verdugo *et al.*, 2016).
- A participatory disease surveillance programme in Indonesia began as a pilot in 12 districts with 48 staff. It was rapidly scaled up, resulting in more than 2000 practitioners in 31 provinces by March 2009 (Azhar *et al.*, 2010).
- Participatory disease surveillance was established in Pakistan as part of a rinderpest eradication campaign with support from the Food and Agriculture Organization of the United Nations (FAO).
- ILRI has supported participatory epidemiology and participatory disease surveillance in Kenya for many years, including its use in control of avian influenza and RVF.

An FAO review found that ILRI was the strongest contributor to participatory disease surveillance in terms of its projects and research outputs. Allepuz *et al.* (2017) found participatory epidemiology methods in 52 countries. Countries where ILRI efforts were concentrated (Egypt, Ethiopia, Indonesia, Kenya, Nigeria and Pakistan) had more activities of that work (Fig. 8.2).

The international community of participatory epidemiology practitioners recognized the utility of establishing a network to promote good practice and to act as a training resource (Mariner *et al.*, 2011). ILRI agreed to facilitate the process, and the Participatory Epidemiology Network for Animal and Public Health (PENAPH) was formed in 2008 with nine core partners, including international agencies, non-governmental organizations and universities with demonstrated commitment to participatory epidemiology. Initially, ILRI hosted the network and the secretariat with support from the Rockefeller Foundation for establishment and activities in two projects over 4 years. PENAPH continues to operate today as a self-sustaining network working across Africa and Asia. The secretariat is now hosted by Tufts University, Massachusetts, and ILRI continues to be a core partner. PENAPH hosted its second international conference in Thailand in 2018, at which several CGIAR scientists presented papers. ILRI's leadership thus facilitated development of a network subsequently sustained by its participants.

Through PENAPH, ILRI advocated one-health applications of participatory epidemiology; the techniques that emerged in animal health were extended and adapted to public health (Mariner *et al.*, 2014). PENAPH core partners include CDC and the African Field Epidemiology Network. Participatory approaches to surveillance for avian influenza were introduced in several countries in Africa, Egypt and Uganda in particular. The approach has had lasting impacts on epidemiological institutions in ILRI's partner countries.

Zoonoses in Systems

In 2006, ILRI started collaborating with STI (now the Swiss Tropical and Public Health Institute) to address the strategic methodological challenge of integrating veterinary and medical assessments of the impacts of zoonotic disease burden on the livelihoods of the poor. STI had found that, because zoonoses imposed costs in both the veterinary and health sectors and because these were not integrated, the benefits of zoonoses control were underestimated.
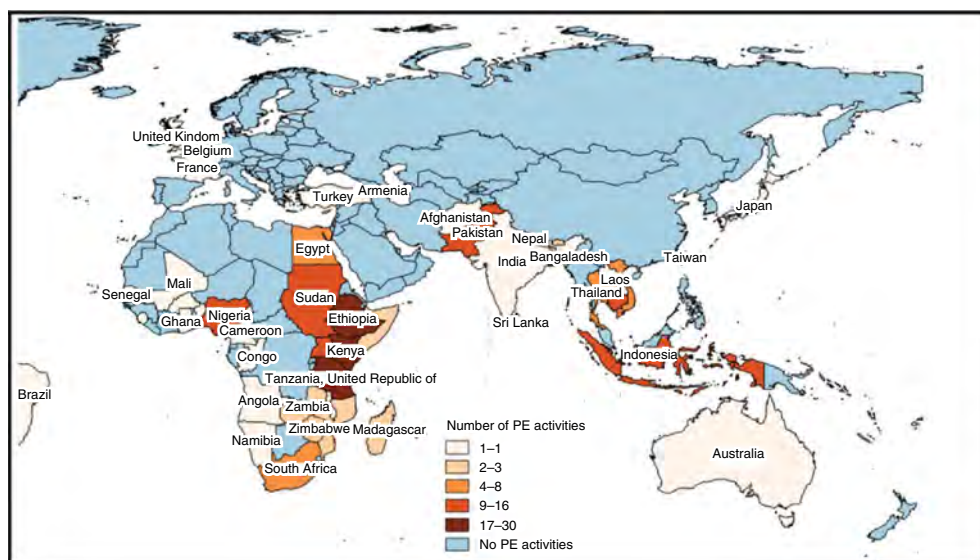

Fig. 8.2. Participatory epidemiology activities by country. (From Allepuz *et al.*, 2017.)

By integrating costs, they were able to show the 'double benefits' of brucellosis control in Mongolia (McDermott *et al.*, 2013). In collaboration with ILRI, this approach was extended to RVF in Kenya (Kimani *et al.*, 2016).

Africa is the least-irrigated continent, and it is predicted that more irrigated areas will be developed in the coming decades. However, there is long-standing concern about the health impacts of irrigation, especially in arid areas. A multi-year project in Kenya investigated links between irrigation and zoonoses. A key finding was that RVF virus (RVFV), West Nile virus and dengue virus were more prevalent in irrigated than in pastoral areas while *Leptospira* spp. and *Brucella* spp. bacteria were higher in pastoral than in irrigated areas (Bett *et al.*, 2017a). The same project investigated sociological aspects relevant to control. For example, the standard health advice was to bury animals that had died of disease, but studies in communities found that this was taboo, reporting, 'We do not bury dead livestock like human beings'; they preferred to eat them (Mutua *et al.*, 2017). This showed that the common approach to public health communication of telling people to bury dead animals was ineffective and other methods were needed to change behaviour.

In 2015, ILRI, along with the University of Edinburgh, UK, and other partners, established a field site in western Kenya for the study of zoonotic diseases. This allowed them to study neglected zoonoses in both livestock and the families that keep them, and to gather the essential baseline data about these infections and the populations affected by them that are so severely lacking. This research identified risk factors for zoonotic diseases in people and animals (Fèvre *et al.*, 2017). The diseases investigated included cysticercosis, leptospirosis, Q fever, RVF and taeniasis (tapeworm infection) (Wardrop *et al.*, 2016; Cook *et al.*, 2017).

The project identified slaughterhouse workers as high-risk groups for zoonotic diseases; this information is being used to explore interventions to reduce this occupational group's risk of exposure. The study demonstrated the existence of a socio-economic gradient within households in rural Kenya, determining individual infectious disease risk. The risk of infection with amoeba, hookworm and malaria was highest in poorer households and the risk of contracting TB was highest in better-off families (de Glanville *et al.*, 2017). This is relevant to understanding the specific health benefits of reducing poverty.

Research on urban zoonoses started in the early 2000s with support from a CGIAR system-wide initiative. As little was known about urban zoonoses, this work focused first on generating evidence. Some findings led to further research-for-development activities. For example, *Cryptosporidium*, a protozoan zoonotic parasite, was found to be unexpectedly high in urban dairies in Nairobi, which led to another project focusing on *Cryptosporidium*. While generating additional epidemiological evidence, the project staff also engaged with policy makers and developed a behavioural approach to extension, one based on encouraging farmers to implement good practices out of concern for their social status rather than out of fear about contracting an illness. This was evaluated as successful both in improving farmer practices (Kang'ethe *et al.*, 2012a,b) and in shifting policy in a pro-poor direction (Nyangaga *et al.*, 2012). Because cryptosporidiosis is a priority disease of immunosuppressed people, Kenyan medical authorities had been wary about promoting livestock keeping among people with human immunodeficiency virus/acquired immune deficiency syndrome (HIV/AIDs). An important finding was that cryptosporidiosis in Nairobi was transmitted more by person-to-person than by animal-to-human contact and that people with HIV/AIDs receiving antivirals did not have an elevated risk of cryptosporidiosis. These findings helped safeguard their access to livestock.

In Uganda, a policy-relevant finding from urban zoonoses research was that farmers who had experienced more harassment from authorities had fewer good practices (Grace *et al.*, 2008), and the project contributed to a better policy environment for urban farming (Cole *et al.*, 2008). Many of the results from this early work on urban zoonoses were summarized in a special edition of *Tropical Animal Health and Production* (Grace *et al.*, 2012c).

A more recent urbanization project focused on the emergence of zoonotic pathogens. This had several methodological innovations, including the use of a livestock value chain approach that allowed identification of the stakeholders, drivers and dynamics of urban livestock keeping, as well as the first-ever quantification of the

contribution that urban livestock keeping made to nutrition, economics and markets in the city (Alarcon *et al.*, 2017; Carron *et al.*, 2017). Another innovation in this work was the use of balloons with cameras attached to them, snapping images every second as the balloon handler walked through urban slums to map, for the first time, food kiosks, mobile street vendors and hazards such as rubbish dumps and open sewers.

At the same time, another large project focused on urban zoonoses in India and Vietnam. These projects have had scientific impacts in terms of generating both new findings and new ways of researching urban zoonoses and have helped to build local capacity in urban zoonoses issues (Bett *et al.*, 2019; Jakobsen *et al.*, 2019); it is too early to observe any development outcomes.

A large research programme in six countries of South-east Asia explicitly adopted an Eco-Health approach. Each country was supported to systematically identify priorities: for example, the Indonesian island of Bali identified rabies, the Laos team focused on pig zoonoses and the South Vietnam team identified leptospirosis. This was a strong departure from the usual mode of zoonoses research, in which donors funded projects according to their own priorities. Country teams bringing together researchers and implementers from animal health and social sciences were trained in research using EcoHealth principles, which require the involvement of the local target communities and relevant policy makers. Outcome mapping was used to identify the changes desired and to monitor success in achieving them. In all countries, there was evidence of capacity being built in these areas, and in most cases, teams were able to show community- and policy-level outcomes and impacts as well (Box 8.1). Assessment showed that this novel approach was appreciated and found useful, but its longer-term benefits and sustainability are less clear. However, the project generated actionable scientific findings such as an identification of the most common pig diseases in Laos (Holt *et al.*, 2019).

On a regional scale, ILRI played an important role in promoting the EcoHealth approach to better control zoonoses and emerging diseases in South-east Asia. A review in 2015 (Nguyen-Viet *et al.*, 2016) traced the history of EcoHealth in South-east Asia and showed the substantial role played by ILRI. It found that, in spite of barriers,

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Box 8.1. A successful intervention to control zoonoses in South-east Asia.

An ILRI-supported team in Indonesia built on an existing village cadres system to establish Village Rabies Working Groups for rabies control. These groups consisted of paraprofessionals equipped to raise awareness about rabies in schools, village meetings and small groups in their own homes. They also served as first responders to dog-bite cases, ensuring that victims received rapid post-exposure prophylaxis, which is most effective when given soon after the bite. General information on rabies and what it means to be a responsible dog owner encouraged communities to register and vaccinate their dogs, two evidence-based ways of controlling rabies. The model was recognized by provincial-level leaders as a promising community intervention. As a result, a legal decree was made to adopt the village rabies cadre system by officially appointing two persons to serve in this capacity in each of the 723 villages in Bali. In addition, the ILRI team partnered with the provincial-level leaders to provide technical training for the rollout of Village Rabies Working Groups in 30 villages that were hotspots for rabies (Gilbert *et al.*, 2014).

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the overall success of the use of the EcoHealth approach in the region was demonstrated by the scope and scale of activities collectively encompassed by the projects, programmes and initiatives reviewed. In a relatively short period of time, EcoHealth has been widely accepted and has gained a remarkable amount of exposure in South-east Asia. This, in turn, has led to more effective and efficient health delivery.

Zoonoses in smallholder pig systems

In 2012, the ILRI-led multicentre CRP on Livestock and Fish started and identified two smallholder pig value chains among the nine livestock value chains it considered most promising for research that would benefit poor farmers. This led to comprehensive initiatives to assess and manage pig-related zoonoses. Trichinellosis is a parasitic disease caused by nematodes in the genus *Trichinella*. This disease, commonly known as 'pork measles', historically caused outbreaks of severe illness in people, but the disease nearly disappeared when control measures were developed and adopted by many pork-producing

countries. Countries new to pork-keeping, however, had not investigated its potential risk. ILRI conducted the first study on *Trichinella* spp. in East Africa, which confirmed that trichinellosis was present and further suggested that trichinellosis might be shifting from a sylvatic transmission cycle, in which the pathogen cycles between wild animals and vectors, to a domestic cycle, in which it cycles between domestic animals and vectors, and thus might be in the process of spilling over from wildlife to establish itself in domestic pigs (Roesel *et al.*, 2016). Veterinary and medical authorities were not aware of the presence of trichinellosis or the risk that it was changing its epidemiology, so this was valuable information. In Vietnam, where pig keeping is long established, *Trichinella* spp. antibodies were detected at high levels (12%) in the serum of indigenous pigs kept in the central highlands (Unger *et al.*, 2016). Studies in Laos on trichinellosis revealed a seroprevalence in pigs of 14.4% (in Luang Prabang) and 9.3% (in Savannakhet) (Holt *et al.*, 2016).

Streptococcus suis is a leading cause of bacterial meningitis in Vietnamese adults. The major risk factors have been identified as consumption of raw pig blood in a Vietnamese dish of blood and cooked meat (*tiết canh*) and occupational exposure to pigs. ILRI conducted the first study in northern and central Vietnam and found *S. suis* type 2 in 1.4% of pig tonsils. Slaughterhouse workers were found habitually to consume raw pig blood to an even greater extent than consumers, and this was linked to excessive consumption of alcohol (Dang-Xuan *et al.*, 2015). Identifying groups at high risk allows targeted interventions. Studies in Vietnam investigated cysticercosis, dengue, leptospirosis, rabies and other zoonoses, often for the first time in a specific region (Lee *et al.*, 2020a,b). Models were also developed to inform control strategies (Bett *et al.*, 2019; Lee *et al.*, 2019). Information was shared with authorities, and high impact factor papers produced but the outcomes in terms of improvements in human health have not been evaluated.

A study on smallholder pig farmers in western Kenya was among the first to use tracer collars to understand the movement of pigs in free-ranging pig production systems. This study found that pigs move considerable distances each day (on average 4340 m) and spend almost 50% of the day outside the home environment (Thomas *et al.*, 2013). Pigs may interact with other livestock and wild animal species, which may expose them to infectious agents. Further research in the region demonstrated a high prevalence of non-typhoidal *Salmonella* spp. and *Leptospira* spp. in pigs at slaughter, which poses a risk to both slaughterhouse workers and consumers.

A large study in pigs in Uganda found that, contrary to expectations, swine brucellosis was not present. This meant that human health services could rule out swine brucellosis and remove a potential barrier to pig marketing and trade (Erume *et al.*, 2016). Another example from Uganda shows how taking a systems approach to zoonoses studies can lead to unexpected findings and eventually to development outcomes. Systems approaches do not start by choosing a specific zoonotic disease to target but instead explore all potential disease problems. During participatory rural appraisals conducted in 2013, farmers reported symptoms suggestive of diamond skin disease. This is caused by the bacterium *Erysipelothrix rhusiopathiae* and is an economically important disease of swine that had never been reported in Uganda. If transmitted to humans, it can cause erysipeloid, which manifests as skin lesions, and in more severe cases can have systemic effects and even lead to death. The farmer reports triggered an epidemiological study in pigs and pork. Overall, 67% of the pig sera carried antibodies against *E. rhusiopathiae* and 45% of the fresh pork samples were contaminated with *E. rhusiopathiae* (Musewa *et al.*, 2018). This, in turn, led to a study to determine the prevalence and factors associated with *E. rhusiopathiae* infection among raw pork handlers, which found a prevalence of around 10%. This was the first time that the disease had been reported in humans in East Africa. Because erysipeloid is an easily diagnosed and treated disease, alerting patients and health providers to its presence was necessary. ILRI paid for the treatment of all positive human cases and all findings were communicated to stakeholders. However, these treatment impacts were not formally assessed.

Collaboration in international initiatives

In September 2005, a memorandum of understanding was signed by ILRI and WHO to better

understand links between livestock keeping and the health and general well-being of poor people in poor countries. This engagement with WHO led to a major multi-stakeholder meeting in Nairobi in 2007 hosted by ILRI. The meeting appreciated that controlling, preventing and eventually eliminating neglected zoonotic diseases would be highly cost-effective from a societal point of view, taking into account both the health and agricultural aspects. A plan of action for implementing integrated control of neglected zoonotic diseases in Africa was recommended. ILRI scientists also made major contributions, including developing a methodology for prioritizing diseases, to a WHO report on human infectious diseases of poverty (WHO, 2013).

ILRI was a lead organization in developing one-health approaches in low- and middle-income countries. As such, it engaged with international organizations promulgating one-health and Eco-Health and contributed to many of the global initiatives around one-health, including international meetings on avian influenza, the Stone Mountain Dialogue, the International One Health Congresses and meetings at Bellagio, Italy, and Chatham House, UK (Galaz et al., 2015). One-health has clearly emerged as a powerful and dominant approach for managing zoonotic diseases, with most evaluations of this approach citing positive impacts, although there are some concerns about gaps between theory and implementation. Figure 8.3 shows how ILRI is embedded within one-health research groups.

In Asia, ILRI is one of the active institutional members of the Vietnamese Government's One Health Partnership for Zoonoses and a member of Gestion des Risques Emergents en Asie du Sud-Est (GREASE, Management of Emerging Risks in Southeast Asia), initiated by the Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD). ILRI is also working with the Southeast Asia One Health University Network, based in Chang Mai, Thailand, to develop the capacity of partners in one-health work.

Emerging Infectious Diseases

Emerging infectious diseases are those that have newly appeared in a population or have existed previously but are increasing in incidence or geographical range (Morens et al., 2004). These diseases are caused by: (i) newly evolved pathogens; (ii) pathogens that have spread to new areas or populations; and (iii) re-emerging pathogens such as those associated with demographic, environmental or other societal changes. Emerging diseases are more likely than not to be zoonotic in origin (Woolhouse and Gowtage-Sequeria, 2005), i.e. acquired by humans from animal reservoirs, including livestock (Cleaveland et al., 2001). Emerging infectious diseases are largely associated with ecological changes that destabilize existing equilibria among pathogens, hosts and vectors. These ecological changes are often the result of human intervention, such as hunting, land clearing for crops or for livestock, urbanization and irrigation.

Rift Valley fever

One new zoonotic disease is now emerging every 4 months. While many are trivial, a minority have devastating health and economic impacts (e.g. avian influenza, COVID-19, HIV/AIDS and Spanish flu). Agricultural expansion and intensification as well as climate change are driving an accelerated emergence of these new diseases. Yet without proper assessment, undue emphasis on emerging infectious diseases may deflect interest from diseases of more importance to the poor. RVF is a model emerging infectious disease because it causes severe disease in people but is not yet readily transmitted between people, it is sensitive to change in land use, and it has implications for trade and for the most poor and vulnerable populations. ILRI's geographical location also means that it has a comparative advantage in studying this important disease.

RVF is a mosquito-borne viral zoonosis that mainly affects sheep, goats, cattle, buffaloes and camels. Humans become infected following a bite from an infected mosquito or after close contact with acutely infected animals or their infected tissues. In people, the disease manifests as a mild influenza-like syndrome in most cases (over 80%) or as a severe disease with haemorrhagic fever, encephalitis or retinitis in a few cases (Njenga et al., 2009). In livestock, the disease manifests as extensive abortions and perinatal mortality.
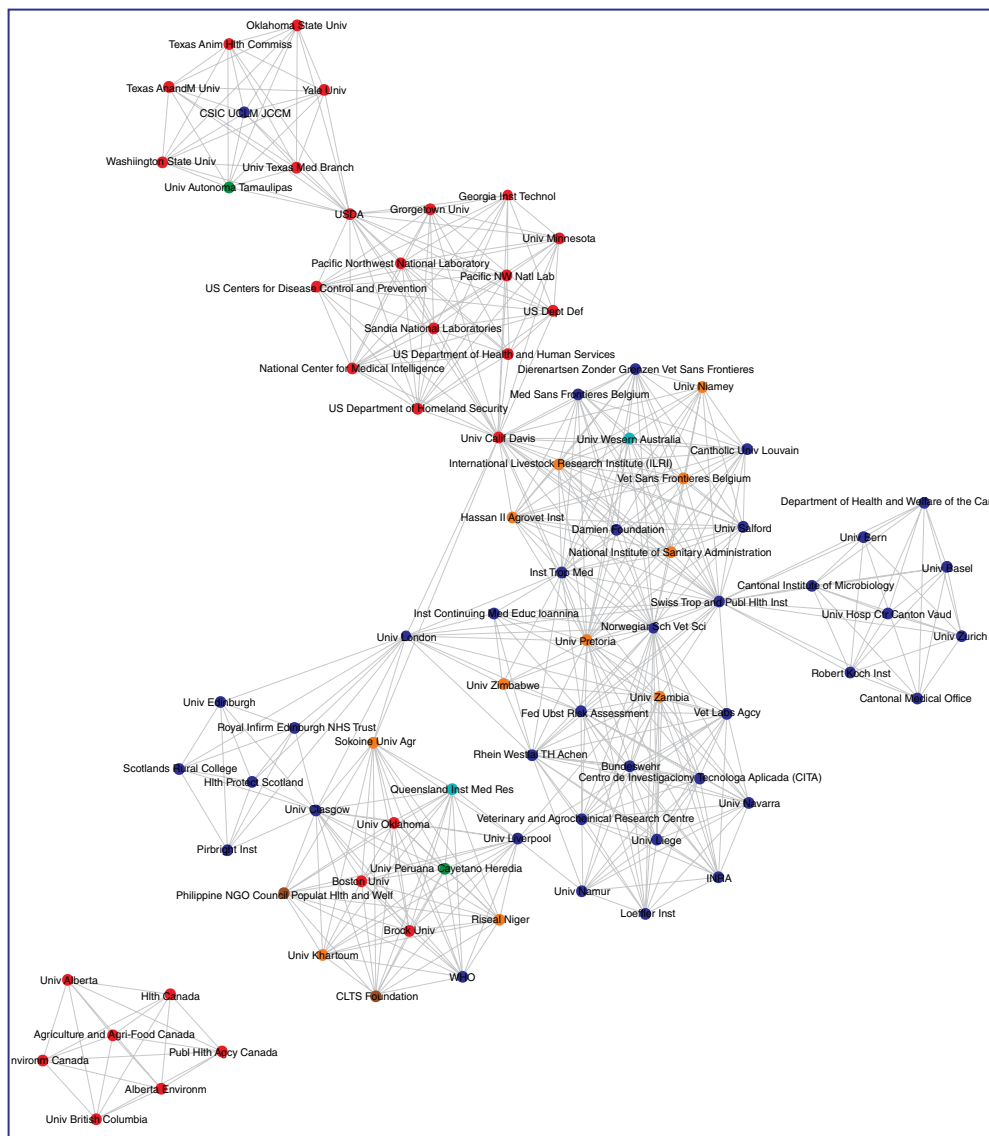
Fig. 8.3. Network digram of co-publishing patterns among organizations having six or more co-authorship relationships (ILRI in blue). (Adapted from Galaz *et al.*, 2015.)

RVF outbreaks occur after periods of above-normal precipitation associated with the warm phase of the El Niño/Southern Oscillation phenomenon (Bett *et al.*, 2017b). Outbreaks have occurred previously in Egypt, Kenya, Madagascar, Mauritania, Mayotte (French archipelago in the Indian Ocean), Saudi Arabia, Senegal, South Africa, Sudan, Zimbabwe and Yemen (Nanyingi *et al.*, 2015). In South Africa, RVF outbreaks

observed from 2008 to 2011 were associated with relentless and widespread seasonal rainfall and high soil saturation (Williams *et al.*, 2016). In Mauritania, an outbreak was associated with a fourfold increase in rainfall in a desert region in 2009–2010 and affected small ruminants, camels and people (Faye *et al.*, 2014). Similar outbreaks occurred in Senegal from 2013 to 2014, where the situation was exacerbated by

livestock movements that aided dissemination of the virus (Sow *et al.*, 2016).

Understanding transmission and burden in Kenya

Data from studies identifying rainfall patterns associated with increased risk of RVF provided the basis for development of dynamic models by ILRI and partners for evaluating the transmission dynamics of this disease (Gachohi *et al.*, 2017). The model allowed researchers to determine alternative vaccination strategies for RVF. ILRI led a related study, which revealed a positive association between flood irrigation and endemic transmission of the virus in an arid and semi-arid area of Kenya (Sang *et al.*, 2016; Bett *et al.*, 2017a; Mbotha *et al.*, 2017). The Kenya study demonstrated that standing water enhanced mosquito development, including the primary vectors of RVFV, which included *Aedes mcintoshi*, *Aedes ochraceous*, *Culex univittatus* and *Culex pipiens*.

The effects of flood irrigation on RVFV endemicity had not been explored previously. Earlier environmental impact studies of irrigation mainly considered malaria and schistosomiasis as case studies of irrigation and vector-borne diseases (Ijumba and Lindsay, 2001; Keiser *et al.*, 2005a,b). We estimated that RVF induced losses of more than US$32 million (2.1 billion Kenyan shillings) on the Kenyan economy, based on its negative impacts on agriculture and other sectors (e.g. transport, services) alike (Rich and Wanyoike, 2010).

ILRI also made the first-ever assessment of the impact of RVF on human health in Kenya using a disability-adjusted life year (DALY) approach. (This is a standard human health metric: one DALY corresponds to 1 year of lost healthy life.) This was used to model the cost-effectiveness of livestock-based control of RVF from a public health perspective in Kenya. This ILRI assessment found that improving livestock vaccination coverage before a hypothetical outbreak could avert close to 1200 DALYs. Improved vaccinations showed cost-effectiveness values of US$43–53 per DALY averted (Kimani *et al.*, 2016). These findings on the economic and human health impacts of RVF helped raise awareness of its importance and were cited in subsequent national policy documents and successful research proposals.

Developing a more effective vaccine

No licensed vaccines are currently available to protect humans against RVF and those widely used in livestock have major safety concerns. A one-health vaccine co-developed for multiple susceptible species is an attractive strategy for RVFV. In partnership with the Jenner Institute, UK, and the Kenya Agricultural and Livestock Research Organization (KALRO), ILRI is developing an adenovirus-vectored vaccine called ChAdOx1-GnGc to protect both livestock and humans from RVF.

The vaccine has passed critical safety and challenge studies. A single-dose immunization elicited high-titre neutralizing antibodies and provided solid protection against the disease in the most susceptible natural target species of the virus – sheep, goats and cattle (Warimwe *et al.*, 2016). The vector being used is a replication-deficient chimpanzee adenovirus (ChAd), with a high capacity to insert genomic clones and plasmids that encode desired antigens. The clone used in this case had a genetic sequence encoding the RVFV Gn and Gc envelope glycoproteins. The methods used to identify the most appropriate vector and to develop the clone are given by Warimwe *et al.* (2013). Clinical trials are still required to evaluate the vaccine before it is approved for use. Results to date suggest that the vaccine has great potential given its safety characteristics and ability to generate good levels of neutralizing antibodies. The new vaccine is likely to achieve higher levels of uptake due to its safety margin being higher than the existing livestock vaccines, which may cause abortions.

Studies on RVF vaccines have focused on the production processes, safety and efficacy standards, but those on uptake and adoption levels are rare. ILRI conducted a study that identified barriers faced by men and women farmers in the uptake of livestock vaccines (Mutua *et al.*, 2019).

Supporting response in East Africa

Studies conducted by ILRI in Kenya and Tanzania following a 2006/2007 RVF outbreak in these nations indicated that the impact of the outbreak was exacerbated by delays in recognizing the risk and in implementing prevention and

control measures (Jost *et al.*, 2010). Many stakeholders later identified the need to develop a framework to promote timely decision making and to improve targeting of prevention and control measures while encouraging closer collaboration among research and disease control institutions. In partnership with the African Union–Interafrican Bureau for Animal Resources (AU-IBAR), CDC, FAO and the Kenya Department of Veterinary Services, ILRI has developed a RVF risk map (Munyua *et al.*, 2016b), contingency plans and a decision model (Consultative Group for RVF Decision Support, 2010) to be used jointly to determine optimal interventions during an outbreak of RVF. The decision model breaks down the epidemic cycle into phases and identifies actions to manage the disease in both animals and humans. ILRI has also been a member of a RVF task force in Kenya, which coordinates surveillance and response, especially during periods of heightened risk.

A search for 'Rift Valley fever' in the Altmetric database (www.altmetric.com/; accessed 18 February 2020) shows that ILRI's RVF projects have generated 91 outputs of the 632 outputs in this field overall, with the ILRI outputs being mentioned 291 out of 1986 times and being quoted in nine policy documents.

Highly pathogenic avian influenza

Highly pathogenic avian influenza (HPAI) threatens poultry industries and livelihoods worldwide as well as human health. The HPAI Asian subtype H5N1 is especially deadly for poultry. The virus was first detected in 1996 in geese in China, and human cases were first detected in 1997. Because of its ability to cause human cases and the possibility that it could evolve to cause a human pandemic, the emergence of this disease in 2003 was of great concern.

Supporting surveillance in Africa

As HPAI threatened to become a pandemic, there was concern that countries in Africa were unprepared to cope. An early ILRI activity was providing training in relevant laboratory techniques. A project on Early Detection, Reporting and Surveillance for Avian Influenza in Africa (EDRSAIA) ran from 2007 to 2012 with a main objective of increasing the capacity of veterinary services in practical, community-focused, active surveillance in 11 countries in West and East Africa. This project developed risk maps, which were used to develop risk-targeted surveillance, and conducted risk factor analyses to inform vulnerability and control work.

There was a large capacity-building component. The training covered participatory epidemiology, data management, risk mapping using geographic information systems (GIS) software and use of risk maps. A subsequent independent assessment of the impacts of the project's capacity building in participatory epidemiology and participatory disease surveillance on national infectious disease surveillance was generally positive. These capacity building materials were integrated into regional field epidemiology and laboratory training programmes supported by the CDC and used for additional surveillance and disease investigations. A participatory surveillance team diagnosed peste des petits ruminants in Nigeria, which led to an effective emergency disease control programme. In 2010, Nigeria chose to use participatory epidemiology practitioners trained by the EDRSAIA project to investigate animal diseases in five regions (Mariner *et al.*, 2014).

Response models in Egypt and Indonesia

Indonesia saw a major HPAI outbreak in 2004. By the end of 2005, it had spread to more than 23 provinces and more than 10 million birds had died. In January 2006, working with FAO, the government of Indonesia began a programme in Participatory Disease Surveillance and Response (PDSR) for HPAI in poultry. This project was partly driven by ILRI research on participatory epidemiology.

By 2009, the FAO/Indonesia programme was operating in 27 out of 33 provinces of Indonesia. About 20,000 villages (30% of all villages in Indonesia) and 2.5 million backyard poultry producers were covered by surveillance, control and prevention activities, indicating the ability of PDSR to deliver animal health cover at scale.

A subsequent external evaluation found that PDSR did not appear to have had a significant impact on the prevalence of HPAI, partly because it focused on the backyard sector while much of the disease was driven by commercial firms. However, the PDSR programme did introduce two valuable

approaches: (i) information, education and communication activities were well planned, supported and executed, and most targeted people had good knowledge of HPAI; and (ii) participatory and pro-poor animal health services were strengthened.

Egypt has some of the highest poultry densities on the African continent, with most birds concentrated along the River Nile. After the first Egyptian outbreaks of HPAI H5N1 in poultry in February 2006, there was widespread culling of both commercial and household poultry. In 2008, a participatory disease surveillance programme was introduced in Egypt, with technical support from ILRI. By 2014, it was covering 30% of Egyptian districts, again demonstrating the potential to deliver impact at scale. In 2011, when the overall HPAI surveillance had slowed, the PDSR programme proved resilient, contributing over 50% of the HPAI confirmed cases in 2012.

While cover and resilience of the initiative were high, accuracy was moderate (Verdugo *et al.*, 2016). Therefore, the results suggested that the PDSR programme might best suit epidemic situations or those where a high rate of false positives is acceptable, given a high need to detect true positives.

Identifying and supporting pro-poor interventions for disease control

An initial response to controlling HPAI worldwide was the culling of infected birds, an effective approach in high-income countries. However, if smallholders in poor countries are not compensated for the loss of their culled birds, they may be reluctant to report HPAI outbreaks and thus help spread the disease. In partnership with the International Food Policy Research Institute (IFPRI), ILRI undertook research into pro-poor interventions in Africa and South-east Asia. These interventions explicitly used a risk-based approach and built in capacity development work in the use of risk analysis. The research contributed to a better understanding of how HPAI is spread, what the critical control points for HPAI risk mitigation are, and what would be cost-effective, pro-poor risk-reduction strategies. For example, in the Mekong Delta, this information led countries to coordinate HPAI control efforts and to revise their culling strategies from 'radical' to 'targeted', substantially reducing the negative impacts of disease control on the poultry livelihoods of poor people.

Evaluation of control in Indonesia and Nigeria

When HPAI H5N1 hit Nigeria, the first African country it occurred in, in early 2006, the federal government of Nigeria requested a World Bank/International Development Association credit of US$50 million, provided under the Global Program for Avian Influenza and Human Pandemic Preparedness and Response, to fight its ongoing outbreak. ILRI was asked to conduct an independent evaluation of Nigeria's response to avian influenza. A broad-reaching multidisciplinary evaluation found overall positive impacts but drew attention to areas that needed to be addressed to ensure that the benefits were sustainable.

In Indonesia, an FAO-coordinated response addressed the HPAI pandemic. However, as of 2007, efforts to control the disease in small-scale commercial and backyard flocks had not proven effective. ILRI was asked to evaluate intervention strategies against HPAI in backyard and small-scale commercial farms by assessing the feasibility of implementing the interventions. ILRI's evaluation consisted of a longitudinal study on intervention options and specific studies targeted to epidemiological studies. The longitudinal study found vaccination in the backyard sector was effective in backyard poultry (Bett *et al.*, 2015). The incidence of HPAI declined by 12% in the HPAI-vaccinated group and by 24% in the HPAI-plus-Newcastle disease-vaccinated group.

However, vaccination appeared to be unfeasible as an open-ended programme because the cost of avoiding one poultry death was far greater than the value of a bird (Lapar *et al.*, 2012). However, it was found that vaccination might have a role as a short-term targeted response. This information was crucial for planning public-sector control of HPAI. The targeted epidemiological studies also had useful results; for example, a study of village chicken found that vaccination was needed every 4 months due to high chicken population turnover; such information is, of course, essential for planning effective vaccination campaigns (Unger *et al.*, 2014).

Middle Eastern respiratory syndrome

Middle Eastern respiratory syndrome-coronavirus (MERS-CoV) is an emerging virus first identified in 2012 in Saudi Arabia. The case fatality rate for infected humans with overt respiratory symptoms is in the region of 30%. As with many coronaviruses, MERS-CoV is thought to have originated in bats, although camels appear to play a significant role in maintaining the virus and transmitting it to humans. While the virus appears to be poorly transmissible to humans, it can lead to human-to-human infections. Indeed, the largest outbreak of the disease was in South Korea in 2015, when human-to-human transmission resulted in hundreds of infections.

Understanding disease reservoirs and transmission

ILRI and partners have explored the role of camels in the epidemiology and transmission of MERS-CoV, with a focus on Kenya. The first important work was to mine biobanks of historical camel samples as far back as the early 1990s, which confirmed extensive exposure of camels to MERS or MERS-like viruses (Corman *et al.*, 2014; Muller *et al.*, 2014). High seroprevalences (up to 50%) were identified in herds in central Kenya (Deem *et al.*, 2015) and in herds from locations around the whole country. Liljander *et al.* (2016) identified one seropositive human in Kenya, which was the first reported human case in Africa.

The Kenya studies were important in elucidating MERS epidemiology historically and in the present. A working hypothesis is that MERS is a geographically widespread coronavirus that acquired an ability to infect humans in the Middle East, but that this zoonotic trait has not spread throughout the range of the virus. ILRI researchers have been collaborating with the government of Kenya and the Emerging Pandemic Threats-2 programmes of the US Agency for International Development (USAID) to isolate the MERS virus itself (a challenge given its transient nature in the camel host) and to carry out virus sequencing. This will allow placement of the East African virus in a global phylogeny and identification of its full host range.

Improving the national response

ILRI researchers have been members of the government of Kenya's MERS Working Group, a reflection of the importance of ILRI's role in studies in the region. ILRI scientists have been involved in establishing MERS serodiagnostics at the Biosciences eastern and central Africa (BecA)-ILRI Hub laboratories and hosted a regional FAO training programme for government veterinary staff to learn about MERS diagnostics.

A search of the Altmetrics database for 'MERS-CoV' indicated that ILRI generated three out of 325 outputs on this subject. The ILRI outputs have been cited in four policy documents, including FAO's *EMPRES360 Animal Health* bulletin (Issue No. 46, 2016) and the UK government's *Infectious Disease Surveillance and Monitoring System for Animal and Human Health* (Summary, March 2016).

In early 2020, ILRI started to plan a research agenda around COVID-19, caused by SARS-CoV-2 (severe acute respiratory syndrome coronavirus 2), a virus related to SARS-CoV, which causes MERS. ILRI has contributed to evaluation of a diagnostic (Hoffman *et al.*, 2020) and is undertaking studies to understand the impact of COVID-19 on farmers, value-chain actors and consumers, their responses to the pandemic, and their knowledge, attitude and practices related to COVID-19.

Ebola

Ebola was first described in 1976 with two simultaneous outbreaks in the Democratic Republic of Congo (Zaire at the time) and South Sudan. It has since been responsible for several deadly outbreaks, most recently from 2013 to 2016 in West and Central Africa and more recently (2019–2020) in two outbreaks in eastern and north-western regions of the Democratic Republic of the Congo. Many aspects of Ebola epidemiology remain unknown, such as the virus reservoir and the role of wildlife and domestic animals in its transmission. However, there has been long-standing concern that domestic livestock, in particular swine, might have a role in its disease epidemiology (Atherstone *et al.*, 2015). Pigs in the Philippines were shown to be infected with Reston virus, one of six known viruses within the genus *Ebolavirus* and related to the Ebola virus found in Africa but that does not affect people (Marsh *et al.*, 2011). Moreover, pigs have been experimentally infected with Zaire

Ebola virus (Kobinger *et al.*, 2011) and antibodies to Ebola viruses have been found in pigs in Africa.

First risk assessment in livestock systems

Uganda has experienced four Ebola outbreaks since the disease was first identified, accounting for 606 cases (probable and confirmed) and 283 deaths (CDC, 2020). In Uganda, motivated by interest to improve risk management, ILRI has conducted *ex ante* assessments of the potential health risks associated with the pig value chain in the country (Atherstone *et al.*, 2014, 2015). This pioneering work is not only informing development of healthy and risk-free pig production and pork value chains in the country but also providing an important basis for understanding missing links in the complex epidemiology of Ebola disease.

ILRI's research has produced a policy brief that summarizes Ebola dynamics, including the role of bats (the main suspected reservoir of the Ebola virus) and a demonstration of how an integrated one-health approach is being used to address the main research gaps (Smith *et al.*, 2015). Findings from ILRI's research on Ebola in Uganda will help protect the health of the more than 1.1 million Ugandan households engaged in swine production. This research will help policy makers develop recommendations to support safe systems for pork production and supply with an emphasis on identifying suitable disease management interventions for smallholder farmers, who make up a large proportion of Uganda's pig farmers. New collaborations with Australian, Canadian and German institutions have been started to bring together expertise in developing new diagnostics for surveillance of Ebola viruses in livestock species.

Ongoing research will provide evidence on the role of pigs in Ebola transmission in Uganda and in contexts with similar agroecologies, will identify places along the pork value chain that may increase Ebola transmission to humans and will evaluate areas in the country at high risk of Ebola. This work is the first to systematically characterize and describe Ebola viruses in pigs in Africa. This information will inform policies around pork value chain development, may help to predict and prevent the spread of emerging zoonotic disease to humans, and will provide the evidence needed to understand and manage Ebola outbreaks.

Antimicrobial resistance

Antimicrobial drugs are indispensable in managing infectious diseases in humans and animals. If these drugs stop working, millions of human lives and livelihoods are at risk because of treatment failure. Drug resistence in the microbes infecting animals could lead to economic loss and reduced yield of animal-source foods, fuelling global food insecurity. Drug-resistant pathogens – viruses, bacteria, fungi and parasites – are considered as emerging infections given that the genetic transformations that potentiate their emergence distinguish them from their parent generations. They also have the potential to spread between humans and animals and internationally through travel and trade, causing higher numbers of infections globally. Resistance to antimicrobials – here defined as substances of natural or synthetic origin that kill or inhibit the growth of microorganisms – is not a new phenomenon; it has been a concern since the discovery of antimicrobials. However, the recent increases in microorganisms developing resistance to antimicrobials and the resulting increasing threat to public health (O'Neill, 2015) warrant focused attention on the problem in both medical and agricultural sectors. ILRI research suggested that around twice as many antimicrobials are used in agriculture as in treatment of humans (Grace, 2015).

Discovery of anti-parasitic drugs

ILRI's antimicrobial resistance research aims to intensify livestock productivity while reducing its negative externalities for human health. ILRI assumes that the world's poor farmers should have access to antimicrobial drugs to safeguard the health of their livestock, upon which so many depend. These principles have guided work related to antimicrobials since the 1990s. ILRI's initial focus was on anti-parasitic drugs and problems of emerging drug resistance in parasites given the importance of parasites to smallholder livestock production. In addition to research on drug use, ILRI scientists contributed

to the development and testing of new anti-parasitic compounds, such as plant compounds for the control of helminths. For example, Githiori *et al.* (2002) evaluated the effectiveness of a widely used natural compound derived from Cape myrtle (*Myrsine africana*) and Cape beech (*Rapanea melonophloeos*) against the helminth *Haemonchus contortus*, a pathogen of sheep, and showed that the effect on parasite egg count was negligible. Another study of the anthelmintic effect of *Albizia anthelmintica* showed that it, too, was not efficacious against *H. contortus* in sheep (Githiori *et al.*, 2003). This led to a widely consulted review of plants used in ethnoveterinary sources and highlighted the need for *in vivo* studies to take into account anthelmintic properties and overall effects of these plants on the performance of the parasitized hosts through potential anti-nutritional effects (Githiori *et al.*, 2006).

Understanding and improving the use of antibiotics

Initial antimicrobial work by ILRI focused on understanding the knowledge, attitudes and practices of antimicrobial use among farmers and animal health service providers. Starting in the 1990s, significant ILRI research on trypanocides had provided crucial evidence for improving control of African animal trypanosomiasis and drew attention to trypanocide resistance (Mulugeta *et al.*, 1997). Research to understand the use of trypanocides and the occurrence of resistance prompted more work on managing trypanosomiasis by evaluating different control strategies (McDermott *et al.*, 2001; Clausen *et al.*, 2010) (see also Chapters 2 and 3, this volume, on trypanosomiasis). Methodologies to evaluate use of veterinary dugs, especially participatory approaches, remain of use and are being developed further (Grace *et al.*, 2009). Further developing the capacity of farmers to better use veterinary drugs was considered promising (Grace *et al.*, 2008) but as a stand-alone intervention was found insufficient to fundamentally change farmer behaviour. As these findings are relevant to antibiotic use, this line of research has shifted over the years to antibacterial drugs.

An ILRI review highlighting a dearth of data on antimicrobial use in livestock production systems in developing countries (Grace, 2015) led to increases in ILRI research on the use of antibiotics in these systems. ILRI scientists have closely collaborated with others to review global antimicrobial use in livestock production systems (van Boeckel *et al.*, 2015) and have led discussions highlighting the need for one-health approaches to controlling and preventing antimicrobial resistance (Robinson *et al.*, 2016). These publications have been heavily cited and have helped shape the evolving research agenda on antimicrobial use in developing countries. Documentation of antimicrobial resistance in the food value chains has become key to understand risks to public health. In Ethiopia, a study in a slaughterhouse isolated multidrug-resistant *Escherichia coli* O157 from goats, identifying the need for surveillance of antimicrobial resistance (Dulo *et al.*, 2015). In general, ILRI has called for taking more integrated and one-health approaches to work on antimicrobial resistance and use at the interface of people, animals and the environment (Nguyen-Viet *et al.*, 2016, 2019). ILRI was the first research organization to draw attention to the worrying phenomenon of farmers in Uganda sharing their antiretroviral treatments with their livestock in the belief that it would make them gain weight and is currently researching this practice.

Understanding drug resistance emergence and transmission

More recently, research on antimicrobial use is being complemented by a growing bioscience research portfolio. For example, scientists at the BecA-ILRI Hub collaborated in genetic research on resistance mechanisms in *Salmonella* isolates for quinolones and β-lactam antimicrobials (Eguale *et al.*, 2017). To understand what is driving the emergence of antimicrobial resistance at the human–livestock–environment interface, ILRI in collaboration with academic partners has set up studies in urban settings to track antimicrobial resistance genes between species and to investigate the role of the environment in the transmission of these genes.

The CGIAR Antimicrobial Resistance Hub

ILRI's research on antimicrobial resistance focuses on developing, testing and evaluating interventions that can mitigate livestock-associated antimicrobial resistance in livestock value

chains. ILRI is increasingly involved in policy work to stem the rise of antimicrobial resistance, such as supporting the development and implementation of national action plans and supporting capacity development in various stakeholder groups. An increasing importance of livestock-associated antimicrobial resistance is reflected at the CGIAR level with two CRPs having taken up antimicrobial resistance research: Agriculture for Nutrition and Health focuses on reducing risks to public health resulting from antimicrobial resistance arising in livestock systems, while Livestock Agri-Food Systems promotes rational and effective use of antimicrobials in smallholder livestock systems to prevent future failure to treat disease in livestock and humans alike.

In both of these CRPs, ILRI scientists have assumed leading roles in antimicrobial use-related research. In early 2019, a CGIAR Antimicrobial Resistance Hub was launched at ILRI, Nairobi. It is convening stakeholders with various interests in antimicrobial resistance. It will work to influence a pro-poor antimicrobial use agenda, provide an environment fostering collaboration and new research partnerships, and streamline communications around agriculturally associated antimicrobial resistance to support evidence-based discussions.

ILRI has produced 20 out of 7967 antimicrobial resistance outputs in the Altmetrics database; one of them has been quoted in a policy document.

Neglected Zoonoses

Neglected zoonoses persist in communities with complex and interrelated development problems such as poverty, isolation, poor access to services, insecurity, political marginalization, low literacy rates, gender inequality, lack of sanitation, degraded natural resources and high dependence on livestock. In these regions, ILRI research has focused on high-priority neglected zoonoses, including bovine TB, brucellosis, cysticercosis and trypanosomiasis.

Bovine tuberculosis

Bovine tuberculosis (bovine TB) is a chronic disease of animals caused by *Mycobacterium bovis*, which is closely related to the bacteria that cause human and avian TB. This disease can affect most mammals, causing a general state of illness and eventual death. Bovine TB is a zoonotic disease transmitted to humans mainly by their consumption of contaminated milk. Zoonotic TB makes up only a small proportion of the overall human TB disease burden but ending the TB epidemic will not be possible without combating zoonotic bovine TB.

One of ILRI's first research activities dedicated to bovine TB was evaluation of a new test for TB (interferon (IFN)-γ) in Ethiopia. The cornerstone of bovine TB control is a rapid and accurate identification of infected animals and their removal from the herd. Conventional testing for bovine TB involved injecting cattle in the neck with antigens to *M. bovis* and checking after several days to see whether the animals had a swelling on their skin, indicating they were positive for bovine TB. This test requires specialist personnel and is expensive and time consuming. The newer IFN-γ test uses blood samples, which are relatively easy and cheap to collect. Developed in Australia in the 1980s, the IFN-γ test was approved by European Union legislation for use in cattle in 2002. Comparing the conventional and new IFN-γ bovine TB tests, the ILRI study found that both tests performed similarly well and concluded that the choice of which to use depended on their relative cost and simplicity of use, as well as on livestock management and time factors (Ameni *et al.*, 2000). This finding led to further evaluation of bovine TB diagnostics in Ethiopia (Ameni *et al.*, 2006).

ILRI participated in a consortium investigating bovine TB in developing countries. ILRI's role was to determine cattle breed differences in immune responses to vaccination with BCG (bacille Calmette–Guérin vaccine, an attenuated strain of *M. bovis*) followed by infection with *M. bovis*. Previous studies and epidemiological surveys had shown a difference in susceptibility to, and disease severity in, bovine TB in Zebu and Holstein cattle (Ameni *et al.*, 2006). The BCG vaccination experiments confirmed that native African Zebu cattle were more resistant to bovine TB than exotic Holstein animals (Vordermeier *et al.*, 2012).

ILRI studies of the kinetics of IFN-γ released in the peripheral blood of calves vaccinated with the BCG vaccine showed a strong positive reaction in the calves to tuberculin inoculation 15 weeks post-vaccination, demonstrating BCG's ability to induce the release of IFN-γ in the peripheral

blood and its role in protecting calves against infection with *M. bovis* (Ameni and Tibbo, 2002).

Another area of ILRI research was surveys conducted to understand the presence, level and risk factors associated with TB. These included the following:

- A study in Narok, which vindicated a long-held official position that bovine TB was absent in Kenya (Koech, 2001).
- A study of dairy farms in central Ethiopia, which found that 45% of cattle and 13% of milk samples were positive for bovine TB, with a much higher prevalence in Holsteins than in local breeds (Ameni *et al.*, 2003). This represented a very high risk to public health. In contrast, a survey in northeastern Ethiopia found that the prevalence of bovine TB seemed low, but there was little awareness of TB and a public health risk was present (Hadush, 2015), while a study in Gondar found a moderate but concerning prevalence of 8% (Shewatatek, 2015).
- A meta-analysis of studies in Tanzania found a prevalence of 1.8%, which was less than that of brucellosis (8.2%) or trypanosomiasis (10.2%) (Alonso *et al.*, 2016).
- A more recent project is investigating bovine TB in six cities in India, but the results are not yet available.

ILRI collaborated in a study describing best practices for diagnosing and assessing livestock productivity losses due to bovine TB and summarized the methodology of assessment for this particular disease (Tschopp *et al.*, 2009).

Cysticercosis

Cysticercosis, a parasitic tissue infection caused by larval cysts of a tapeworm (*Taenia solium*) that infect brain, muscle and other tissue, is a major cause of adult-onset seizures in most low-income countries. The adult tapeworm lives in the human gut and the larval stages develop in pig muscle. However, if humans ingest the egg of the adult tapeworm, then cysts may develop in the human skin, eye, brain and other tissues resulting in serious illness. Endemic areas are located predominately across Latin America, sub-Saharan Africa and South-east Asia where pigs are raised under 'traditional' extensive systems

and where latrine coverage and meat hygiene capacity may be low.

T. solium cysticercosis is often ranked among the top priorities of neglected zoonoses and was an early focus for ILRI research. Initial priorities, formulated and led by Lee Willingham, were on better defining the health and economic burden of cysticercosis and supporting an important regional collaboration to better control it. When Phil Toye joined ILRI, a multi-year effort focused on developing lateral-flow diagnostics for this disease, as well as testing simpler approaches to its diagnosis. Meanwhile, extensive epidemiological surveys were conducted in Kenya, Mozambique, Tanzania and Uganda in Africa, and in India, Laos and Vietnam in Asia. The participation of Lee Willingham and subsequently of Eric Fèvre in WHO-led initiatives has given ILRI an influential position in the global one-health phalanx of efforts to control cysticercosis.

A collaboration with the University of Guelph in Canada included a component on training local extension officials, farmers and pork butchers on cysticercosis control, as well as ways to improve pig productivity. Engaging stakeholders in workshops and one-on-one training sessions at the farm level was associated with improved knowledge about cysticercosis (Wohlgemut *et al.*, 2010). Three PhD students were trained under the collaboration, and several undergraduate students were exposed to relevant research activities in western Kenya.

Cysticercosis causes illness and productivity losses in both people and livestock. Estimates of the burden of this disease provide essential, evidence-based data for conducting cost–benefit and cost–utility analyses that should help secure political will and financial and technical resources. ILRI led work on developing frameworks for assessing and combining health and economic information (Carabin *et al.*, 2005). Several of the scientists involved went on to participate in landmark assessments of the global burden of diseases. The methods were also used to estimate disease burdens in proof-of-concept studies. For example, an estimate of the impact in the Eastern Cape Province of South Africa found that there were an estimated 34,662 cases of epilepsy due to cysticercosis in 2004. The overall monetary cost was estimated to vary between US$18.6 million and US$34.2 million in a population of about 7 million people, depending on the method used to estimate productivity losses. The agricultural

sector contributed an average of US$5 million (Carabin *et al.*, 2006).

Epidemiological studies on prevalence and risk factors were conducted in several countries generating evidence, often for the first time, on the presence and prevalence of cysticercosis. These findings led to further research and stimulated efforts to improve control. Among the highlights were the following:

- In Tanzania, the prevalence of swine cysticercosis was found to be 7.6%, 8.4% and 16.9% for Chunya District, Iringa Rural District and Ruvuma Region, respectively. Risk factors were free-ranging of pigs, home slaughtering of pigs, pork not being inspected before consumed, lack of latrines and barbecuing pork (Boa *et al.*, 2006).
- A study of 1051 epileptics in western Kenya found that one-third had observed nodules in pork meat and one-half had observed tapeworm segments in their own faeces, suggesting a possible role of cysticercosis (Grace and Downie, 2011). Another study in Homa Bay confirmed that cysticercosis was endemic (Eshitera *et al.*, 2012).
- A study in western Kenya found that 34.4–37.6% of pigs at slaughter were positive for *Taenia* spp. using an HP10 antigen enzyme-linked immunosorbent assay (Ag-ELISA). All pigs, however, were reported to have passed routine meat inspection, raising considerable concern over the effectiveness of current public health measures (Thomas *et al.*, 2016). In contrast, an earlier study found that only 4% of pigs were positive using a B158/B60 Ag-ELISA and no slaughtered pigs were positive (Kagira *et al.*, 2010). A study in slaughterhouse workers found a low but concerning prevalence for both *Taenia* spp. and cysticercosis (Cook, 2014).
- While an abattoir study in Nairobi found the prevalence of *Taenia* spp. was 8.5%, all the carcasses were passed for human consumption. Furthermore, the abattoir had no facilities for handling *T. solium*-infected carcasses (Akoko *et al.*, 2016).
- A study in south-east Uganda found that 8.6% of pigs screened were seropositive for cysticercosis. In addition, 26% of homes did not have pit latrines, indicating a high probability of pigs having access to human faeces and thus *T. solium* eggs (Waiswa *et al.*, 2009).
- A later study in Uganda found a prevalence of 14% in the Lake Kyoga Basin (Nsadha *et al.*, 2014). Subsequently, one of the largest and most rigorous and representative studies found a high prevalence of *T. solium* in rural production settings (10.8%) and an even higher prevalence in urban settings (17.1%) (Kungu *et al.*, 2017).
- A review suggested that cysticercosis was problematic in Mozambique. Human serological studies found that 15–21% of apparently healthy adults were positive for cysticercosis antibodies or antigen, while in neuropsychiatric patients, seroprevalence was as high as 51%. Slaughterhouse records indicated a countrywide occurrence of porcine cysticercosis, while studies have shown that 10–35% of pigs tested were seropositive for cysticercosis antibodies or antigen (Afonso *et al.*, 2011).
- A study in the state of Nagaland, in northeast India, found an alarmingly high prevalence of cysticercosis in marketed pork (Fahrion *et al.*, 2014).
- A study in Laos found a low but concerning prevalence of cysticercosis in people and pigs that was associated with poor hygiene (Holt *et al.*, 2016).

Field studies in Uganda identified additional risk factors for cysticercosis. Much pork is consumed in 'pork joints', typically with alcohol. Because pork fat is thought to absorb alcohol, some customers prefer undercooked pork, believing that when pork is fully cooked, the fat drips off and therefore will not fully 'neutralize' the alcohol. This undercooked pork can expose customers to several zoonotic pathogens, including *T. solium* (Thomas *et al.*, 2017).

The Cysticercosis Working Group of Eastern and Southern Africa was founded in 2001 by scientists from Kenya, Mozambique, South Africa, Tanzania, Uganda, Zambia and Zimbabwe with the purpose of collaborating against cysticercosis. This cysticercosis working group had considerable success in organizing workshops, obtaining funding, conducting studies, agreeing on a regional action plan and developing a widely used standard questionnaire about the

disease (Gabriël *et al.*, 2017). The group has been described as one of the notable successes of Danish aid (Johansen and Mukaratirwa, 2013) and is now recognized internationally, serving as a model for other similar networks.

A promising avenue for control of cysticercosis is the development of rapid and cheap diagnostics for the disease in live pigs, which could be made readily available to farmers and meat inspectors. This would allow infected animals to be identified and rejected either before transport to slaughter or at slaughter. Infected pigs could then be treated (e.g. with the anthelmintic oxfendazole) and re-presented for slaughter when its cysts had become non-viable. This would safeguard public health while allowing pig farmers to retain an important source of their income. ILRI undertook development and validation of a pen-side lateral-flow assay to detect porcine cysticercosis, which showed that the assay performs acceptably well compared with standard laboratory-based assays.

A second round of funding was obtained for further development of the assay, in particular to convert to a format that would allow whole blood to be tested instead of serum. The lateral-flow assay is now undergoing further developments; with an initial sensitivity of 73.84% and specificity of 66.7%, and a κ index of 0.38, it has clear potential to be developed and used for diagnosis of cysticercosis in the field (Kivali *et al.*, 2013). ILRI scientists are now establishing a 'gold standard' sera bank collected from known cysticercosis-positive and -negative pigs, achieved through fine dissection of carcasses after slaughter to identify cysts. This sera bank will be used for the validation of current and future diagnostics for cysticercosis.

Cysticercosis has traditionally been diagnosed by lingual palpation, a technique the utility of which was confirmed in an early study by ILRI (Mutua *et al.*, 2007). A subsequent meta-analysis found that all areas with more than 10% of pigs having cysts in their tongues had at least 30% seroprevalence of cysticercosis, and assessing the prevalence of tongue cyst-positive pigs is a potentially rapid epidemiological tool for identifying areas at high risk of cysticercosis, although further refinement and validation is required using standardized data sets (Guyatt and Fèvre, 2016).

In resource-constrained developing countries, it is often difficult to obtain the funding needed to support public health campaigns. This has led to interest in public–private or market-based solutions to controlling diseases. These are most likely to be effective for diseases such as cysticercosis that inflict costs on farmers and traders. ILRI collaborated with the Global Alliance for Livestock Veterinary Medicines (GALVmed) to evaluate an approach to cysticercosis control based on marketing pig vaccines and wormers to farmers in Uganda. A series of surveys, auctions and economic studies showed that farmers were unwilling to pay for cysticercosis prevention (vaccine and wormer), suggesting that these vaccines would have to be highly subsidized to make them attractive to pig keepers (Dione *et al.*, 2019).

Given the failure to achieve the WHO goal for a validated strategy for *T. solium* control and elimination by 2015, ILRI continued to work with international partners to develop alternative frameworks for the development of realistic control goals for endemic areas (Braae *et al.*, 2019).

Human African trypanosomiasis

Human African trypanosomiasis, known commonly as sleeping sickness, is caused by a protozoan parasitic infection of public health importance. In East Africa, sleeping sickness presents as an acute syndrome caused by the *Trypanosoma brucei rhodesiense* parasite, which is maintained in an animal reservoir. Where wildlife is not abundant, domestic livestock species, particularly cattle, are the main reservoir. West African sleeping sickness is caused *by T. b. gambiense* and is transmitted in a human–tsetse–human cycle. The role of an animal reservoir still needs to be clarified. ILRI work focused on East African sleeping sickness and global control.

Uganda and the Congo experienced a massive sleeping sickness outbreak from 1900 to 1920 and a more recent outbreak from 1976 to 1989. Building on its long history of trypanosomiasis research, ILRI has collaborated with local partners, the University of Edinburgh, UK, and FAO to better understand the potential role of veterinary interventions in controlling sleeping sickness in Uganda.

An early desk study produced the first-ever one-health assessment of the burden of tsetse-transmitted trypanosomiasis by combining

economic losses in livestock with impacts on human health measured in DALYs (Odiit *et al.*, 2000). This led to studies of the risk factors for transmission of *T. b. rhodesiense* sleeping sickness in endemic regions and to identification of new endemic areas (2004). Importantly, closeness to a reporting health unit was a major determinant for detecting early rather than advanced cases (Odiit *et al.*, 2004). A related study investigated late diagnosis of sleeping sickness, which typically results in a worse outcome for patients. This found long delays in diagnosis (and therefore in treatment), much of it due to the service provider failing to diagnose sleeping sickness among symptomatic individuals (Odiit *et al.*, 2004). Following this work, a model was developed to quantify underdetection of sleeping sickness in Uganda during a 1988–1990 epidemic. This showed that, of 73 undetected deaths, 62 entered the healthcare system but were not diagnosed and 11 died without seeking healthcare from a recognized health unit (Odiit *et al.*, 2005). This evidence of under detection stimulated an initiative to upgrade 12 facilities to perform confirmatory testing for sleeping sickness, resulting in a substantial reduction in the distance necessary to travel to get a diagnosis for sleeping sickness (Wamboga *et al.*, 2017). The work was also used by the WHO to support the argument that zoonoses were neglected.

Further work helped to identify the distribution of villages at risk of sleeping sickness using GIS and remote sensing (Odiit *et al.*, 2006). Distribution maps based on archival and contemporary data showed that the disease focus had moved from lakeshore Buganda (1905–1920) to the Busoga and south-east districts (Berrang-Ford *et al.*, 2006). This information was used by medical services to better understand risk.

A model of *T. b. rhodesiense* infections transmitted by a single tsetse species between cattle and humans was developed at ILRI using empirical data (Coleman *et al.*, 1999) to assess the relative impact of mass treatment of cattle versus treatment of human cases on the prevalence of *T. b. rhodesiense* sleeping sickness in south-eastern Uganda. Mass treatment of cattle with a coverage of 80% was predicted to break the transmission to humans. This evidence contributed to a major public–private partnership campaign called 'Stamp out Sleeping Sickness' that aimed to slow the spread of sleeping sickness, which itself was driven by cattle movements.

The campaign helped private-sector animal health providers to treat cattle with preventive drugs and insecticides. Between 2006 and 2010, nearly 200,000 cattle were treated, and the intervention was shown to reduce sleeping sickness in people and to halt its expansion. However, both the human and animal forms significantly increased after the intervention, and uptake by farmers was low. These disappointing results were attributed to a lack of community concern about sleeping sickness, the cost of treating cattle, insufficient incentives for private-sector disease control, a lack of control infrastructure, the seasonality of the disease and poor targeting, among other factors (Bardosh, 2018).

While the development impacts of this large-scale, low-technology, private sector-based intervention were disappointing, ILRI's evidence on the burden, distribution, under-reporting and potential of managing sleeping sickness through treatment of the livestock form of the disease helped to draw attention to the importance of sleeping sickness and to increase efforts to control it, which were globally spearheaded by WHO.

ILRI scientists contributed to the WHO Expert Committee Report on Human African Trypanosomiasis and the WHO stakeholder meetings on *T. b. rhodesiense* human African trypanosomiasis. Work continued with the first geographically delimited estimation of the burden of sleeping sickness disease at the subcounty scale in Uganda (Hackett *et al.*, 2014). Importantly, this work found that, whereas the relative burden of sleeping sickness was low at the national level, in some districts it was a high-priority disease. Human sleeping sickness was also considered in economic analyses of the control of African animal trypanosomiasis in East Africa (Shaw *et al.*, 2015). More recently, ILRI has been involved in evaluating diagnostic tools for sleeping sickness (Lejon *et al.*, 2017).

Brucellosis

Brucella spp. infect many animals, including cattle, small ruminants, camels, water buffaloes,

yaks and pigs. Different *Brucella* spp. infect different animal species, but most have the potential to infect humans, with some species causing more disease than others. *Brucella* spp. infection rates in some developing countries can reach more than 10% of the human population, making it a serious public health disease. In livestock, *Brucella* spp. cause diseases that reduce animal production and cause abortions in females and reduced fertility in males. The most common method by which humans are infected is through ingestion of unprocessed milk products from infected animals, but direct contact with infected animals and meat can also be a source of infection.

Initial work at ILRAD and ILCA identified brucellosis as one of many constraints to livestock production in Africa and Asia. Surveys on brucellosis in livestock and marketed milk were conducted in the late 1990s in Ethiopia and Kenya (Asfaw *et al.*, 1998; Kang'ethe *et al.*, 2000). These surveys confirmed the presence and importance of the *Brucella* pathogen and also revealed problems with the commonly used diagnostics for this disease. In Kenya, *Brucella abortus* antibodies were not detected in raw milk sold in urban areas but were found at low levels (2–5%) in milk sampled from consumers in rural areas, and at higher levels (25%) in pasteurized milk (Omore *et al.*, 2000). This finding added to the body of evidence being developed by ILRI that formal milk is not always safe and informal milk is not always risky. These results were instrumental in a radical, pro-poor shift in Kenyan dairy policy (Leksmono *et al.*, 2006).

ILRI produced important syntheses of research on brucellosis in developing countries. The first assessment of brucellosis in Africa found that the incidence of the disease was highest in pastoral production systems, that this incidence decreased with decreases in herd size and size of landholding, that little was known of brucellosis in other species and that control of brucellosis was largely inadequate (McDermott and Arimi, 2002). A systematic review of the economics of brucellosis control found that the benefits of control always exceeded its costs (McDermott *et al.*, 2013). Interestingly, *ex post* assessments had relatively higher benefits than *ex ante* assessments, and control in lower-income countries had relatively higher benefits than control in higher-income countries.

A workshop held by ILRI and USAID in 2013 brought together participants from 16 countries to identify gaps in brucellosis epidemiology, diagnosis, surveillance and control (USDA/USAID/ILRI, 2013). The workshop provided information to help design brucellosis research programmes and intervention strategies at national and regional levels.

A landmark study of brucellosis tested 825 patients for the disease at the Busia County Referral Hospital and the KEMRI Alupe Research Centre, located in the same area (de Glanville *et al.*, 2017). The team used the regular government febrile antigen *Brucella* agglutination test and a second called the rose Bengal test, while another two kits were used to confirm the results. Of the 825 cases, 196 patients (19.6%) were found positive for brucellosis from the regular tests. However, when the positive cases were tested with the second and other confirmatory tests, only eight people (1%) of the total were found to have been infected with *Brucella* spp. In this case, if not for the secondary and confirmatory tests, 188 people would have unnecessarily been put on the rigorous treatment to cure brucellosis. This high-profile study drew widespread attention and led to the formulation of improved guidelines for diagnosing brucellosis. In addition, ILRI scientists have worked on evaluating improved tests (Falzon *et al.*, 2019).

Brucellosis is especially problematic to manage in countries where the culling of cattle is not acceptable, such as in India. ILRI work commenced with a systematic review to clarify the contradictory evidence on prevalence. This has been reported to be as low as 1% and as high as 60% by different researchers. The ILRI review concluded that the disease's overall prevalence in the country was probably 12% or less (Deka *et al.*, 2018), which is still high. This was followed by a number of prevalence studies to better understand the true picture of this disease (Lindahl *et al.*, 2018), which confirmed that the disease was highly heterogeneous. This information is essential for targeting control efforts to where they are needed most.

China's Yunnan Province is at particular risk of brucellosis because ruminants are increasingly introduced to the province from other parts of the country in response to increasing demand for milk. ILRI developed an EcoHealth approach to control brucellosis.

ILRI conducted studies on brucellosis in a range of species, products, and countries:

- A study in camel-rearing areas of Ethiopia found that around 6% of camels were sero-positive for *Brucella* spp. As camel milk here is rarely boiled before being consumed, this represents a significant public health risk (Teshome *et al.*, 2003).
- Brucellosis was detected in just under half of the cows' milk samples tested in Tanga, Tanzania (Shija, 2013).
- An anthropological study in Mali provided a key insight – that brucellosis was common but that pastoralists believed milk to be in-trinsically 'pure' and hence incapable of being a source of disease (Fokou *et al.*, 2010).
- Brucellosis was not found in goats in west-ern Kenya (Akoko *et al.*, 2013).

Other neglected zoonoses

Neglected zoonotic diseases are commonly asso-ciated with poverty and greatly impact in particu-lar the lives and livelihoods of millions of poor livestock keepers, processors and consumers of livestock products. WHO has identified a sub-group of eight 'neglected zoonotic diseases': an-thrax, bovine TB, brucellosis, cysticercosis, hydatidosis, leishmaniasis, rabies and sleeping sickness. ILRI research has focused mostly on bovine TB, brucellosis, cysticercosis, rabies and sleeping sickness. (ILRI's work on rabies is noted in Chapter 5, this volume.) Limited ILRI research has been conducted on other zoonoses on the WHO list, as well as other zoonoses that fit a broader definition of neglected.

Anthrax is a bacterial zoonosis, caused by *Bacillus anthracis*. It primarily affects herbivores and is highly lethal to them. Humans contract the disease from contact with infected or dead animals, and infections can result in a high mor-tality rate for people as well, if not diagnosed and treated promptly. Anthrax is also of interest as a 'dreaded disease', a climate-sensitive disease and a possible 'bioterrorist' agent. When alarming outbreaks of anthrax occurred in Nakuru, Kenya, ILRI was part of the team sent to investigate. Participatory epidemiology was used to map current and previous outbreaks, with the results suggesting a long history of outbreaks (Muturi

et al., 2018). ILRI is currently (2020) developing an anthrax risk map for the country for use in developing prevention and control measures aimed at reducing the public health and economic impact of anthrax.

In many low- and middle-income countries, it is a common practice to consume animals that have died of an illness because they are a valu-able and scarce source of protein. An assess-ment in Zambia found that the risk to humans of contracting illness due to consuming meat from animals that have died of disease was rather low and could be reduced by taking precautions, in-cluding careful butchery and ensuring that meat is cooked properly (Simpson, 2015). This example illustrates the complexity of work aim-ing to change behaviour, especially when people do not have sufficient incentives to change their behaviour.

Human cystic echinococcosis is a neglected zoonotic parasitic disease caused by the larval stage of the dog tapeworm, *Echinococcus granulo-sus*. Ungulates are intermediate hosts, but if a human consumes tapeworm eggs, they may develop into fluid-filled cysts in organs and tis-sues. The infection is most common in pastoral communities, where it causes considerable socio-economic impact. A systematic literature review showed its widespread occurrence in small ruminants in Ethiopia (Asmare *et al.*, 2016). A study in abattoirs in Narok, Kenya, found that 16% of sheep had cysts, which was considered a high level of infection constituting a public health risk (Odongo *et al.*, 2018).

Q fever, caused by *Coxiella burnetii*, is an old zoonotic disease believed to be widely present in ruminant populations worldwide. It is a com-mon cause of abortion in ruminants, and in people can cause flu-like illness. There is little de-tailed knowledge of its presence in livestock sys-tems in low- and middle-income countries. ILRI conducted or supported surveys of Q fever in Kenya and Tanzania. These showed a high prevalence (20%) in camels in Laikipia, Kenya (Browne *et al.*, 2017), and in livestock (13%) and people (27%) in Tana River, Kenya (Mwolo-lo, 2016). A moderate prevalence was found in cattle (10%) and humans (2.5% in slaughter-house workers) in western Kenya (Cook, 2014; Wardrop *et al.*, 2016) and in cattle reported as sick (15%) by farmers in northern Tanzania (Alonso *et al.*, 2015).

A study of hospital patients in Kenya found acute Q fever in 16% of patients, a finding unsuspected by the treating clinicians. A diagnostic tool was developed based on symptoms and was shown to be reasonably accurate (sensitivity 93.1%, specificity 76.1%) (Njeru *et al.*, 2016). This tool has obvious potential to improve diagnosis and hence healthcare, but its impact has not been evaluated. Other studies have looked at farmer awareness of Q fever, finding it low (Nyokabi *et al.*, 2017), while studies looking at the disease risk and economic impacts found they were high (Oboge, 2016).

Conclusions and the Future

ILRI research has contributed to an emerging consensus about neglected and emerging zoonotic diseases. It is clear that zoonotic diseases associated with livestock and livestock production are constraints to human health, well-being and economic development. Many of these diseases pose risks to wildlife and to the ability of ecosystems to provide services. However, for many of these diseases, basic epidemiological data are unavailable. ILRI research has often overturned conventional wisdom by finding zoonoses absent where they were believed to be common and to be major problems when their existence was unsuspected.

Establishing systematic data collection is the first step to manage zoonoses. Management is complicated by heterogeneity: zoonoses may have a significant and debilitating effect on some communities but not on others. Understanding the spatial distribution of the burden of zoonoses is important to better focus control efforts. A significant constraint is the lack of collaboration between medical and veterinary authorities: institutionally speaking, zoonoses typically find themselves homeless and ignored. There is a need for one-health thinking and research to overcome inter-sectoral barriers to effective control of zoonoses.

We can suggest some future directions. A first step is to develop cheap and efficient diagnostics in human and animal hosts to assist in understanding zoonoses and in managing them. Another important step is to develop metrics that capture the societal burden of zoonoses,

recognizing the high dependence of the poor on livestock. DALYs and economic costs of livestock and human disease are important metrics, but good information is expensive and difficult to collect, and even when available, we lack agreed ways of combining epidemiological and economic metrics. Moreover, other aspects of the zoonoses burden, such as the cost of a high-impact, low-probability and civilization-altering pandemic, are difficult to capture. ILRI is involved in new and ongoing initiatives to measure the multiple burdens of zoonotic diseases.

It is generally accepted that zoonoses are best tackled in their livestock rather than human hosts. This avoids human suffering, has been shown to be more cost-effective in studied cases (e.g. rabies) and historically was the main means of eliminating many neglected zoonoses from high-income countries. However, most developing countries still lack comprehensive programmes to tackle zoonoses in their livestock reservoirs. To generate additional investment, more information is needed on the costs, benefits, acceptability and scalability of interventions, including those targeting animals. Malaria and water research show how credible, comparable information on control options can underpin action.

The majority of emerging human diseases are zoonotic, often following amplification in a farmed animal host. The current (as of 2020) COVID-19 pandemic is just one of a series of emerging zoonoses over the last decades that has resulted in enormous impacts, both health and economic. ILRI long-standing research into the drivers of disease emergence and into more timely and effective surveillance and response can contribute to a new urgency around the need to prevent and manage pandemics.

Zoonotic diseases are particularly complex disorders involving the environmental sciences, agriculture and public health. Policy frameworks for managing zoonoses are sometimes weak, and there are often gaps between policy and implementation. Successful control of zoonoses requires a judicious legal and policy framework, well-functioning institutions, adequate financing, rapid detection and an intervention implementation plan. The failure of the public sector to manage neglected zoonoses in developing countries has led to interest in public–private partnerships and market-based solutions. Although harnessing market or social forces has

great potential in improving human health in resource-scarce environments, they have not yet been shown to be sustainable or scalable, and further innovation is required. The role of behavioural sciences is therefore an active area of ILRI.

Notes

[1] This work was led by Arve Lee Willingham and Esther Schelling, respectively, both of whom shared joint appointments at their home institutions and ILRI.

[2] These included Silvia Alonso (Spain), Bernard Bett (Kenya), Delia Grace (Ireland), Joerg Jores (Germany), Lucy Lapar (Philippines), Anne Liljander (Germany), Johanna Lindahl (Sweden), Jeff Mariner (USA), Karl Rich (USA), Fred Unger (Germany) and Francis Wanyoike (Kenya). A later collaboration involved the University of Edinburgh, and later the University of Liverpool, led by Eric Fèvre (UK).

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9 Food Safety and Nutrition

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Contents

Executive Summary

The problem

'Is our food safe?' is a fundamental concern of consumers. Moreover, as populations urbanize and food systems develop, concerns about food safety grow. The emergence of food safety science responds to those concerns.

Food safety science – drawing on health, agriculture, technology, marketing and psychology – emerged as a separate discipline in the latter half

of the last century. Food safety is relevant to domestic and international markets and involves private and public sectors as well as civil society. Recent evidence suggests that the health burden of food-borne disease (FBD) is comparable to that of three major diseases – malaria, human immunodeficiency virus/acquired immune deficiency syndrome (HIV/AIDS) and tuberculosis. Most of the unsafe food health burden is due to contaminated fresh foods purchased from informal markets. Livestock products – milk, meat, offal and eggs – are especially risky. As our understanding of the importance of FBD, and its complicated links with livestock development, has increased, so too has research conducted by the International Livestock Research Institute (ILRI) and other research organizations in this area.

ILRI's role in the global context

Food safety was historically a minor part of CGIAR research. This was partly due to a lack of awareness that FBD was a major development issue but also because FBD was conceptualized as an aggregation of specific diseases rather than as a systems problem. Donor investments in food safety were small compared with the scale of the problem, with investments in comparable diseases and with the potential return on investments (GFSP, 2019). Most investments have focused on trade rather than on ensuring the health of consumers in low- and middle-income countries. In the early 2000s, ILRI conducted some work on the health aspects of trade in livestock but did not have a major programme in food safety.

Rather, food safety was seen mainly as a potential barrier to market access by poor livestock keepers. It was addressed to some extent in dairy projects and initiatives such as the Debre Zeit Dairy Technology Centre. As such, ILRI and its predecessors, the International Livestock Centre for Africa (ILCA) and the International Laboratory for Research on Animal Diseases (ILRAD), were one of many research and development institutes seeking to increase the quality of agricultural products through research, training and capacity building. An evolving focus on food value chains in these institutions, however, helped shift the research agenda towards the food attributes desired by consumers, which often included food

safety, and towards consumer willingness to pay for food attributes, including safety.

In the early 2000s, ILRI began a programme on improving human health through livestock research in three areas: (i) animal-source foods for nutrition; (ii) zoonoses (diseases transmitted between animals and people); and (iii) FBD. This was the first CGIAR group with an explicit food safety mandate (rather than focusing on specific hazards) and with expertise in using research methods for food safety rather than diseases in general. ILRI was also one of the first groups to focus on food safety in the 'informal markets' of developing countries, and by the 2010s, had become the lead research institute globally in this emerging area.

Impacts of ILRI's research

Scientific impacts

ILRI developed, contributed to, adapted and tested tools, methods and metrics, including participatory risk assessment, systematic literature reviews of food safety in informal markets, systems dynamics and food safety system performance assessment. Technology development and testing was a growing area with a focus on appropriate technologies such as disinfectants and pest control. Many publications were produced, often regarding tools and technologies. In addition, publications covered other aspects of evidence generation including reviews, reports of surveys, risk factor analyses, and interaction between food safety and other development issues, such as gender equity.

Development impacts

ILRI's initial work on food safety focused on adapting methodologies for developing countries, assessing the extent, nature and drivers of FBD, and piloting potential solutions. Only with the advent of the CGIAR Research Programmes (CRPs) (2012–2016) did the focus shift to achieving wide-scale development impacts. However, some development potential and realized impacts can be discerned. In summary, pilot projects identified various promising technologies. Moving to the intermediate scale, food safety research has been embedded in high-potential livestock value chains identified by the CRP on Livestock. These CRP initiatives reached hundreds of value chain

agents, thousands of farmers and tens of thousands of consumers, although the impact on food safety outcomes is more difficult to estimate. In Kenya and the Indian state of Assam, there is some evidence that food safety interventions went to scale and were sustained after the end of projects. We estimate that 6.5 million people benefited.

Policy impacts

The first assessment of the global health burden of FBD found that the burden was unexpectedly high and borne mostly by low- and middle-income countries (Havelaar *et al.*, 2015). ILRI was one of the few research institutes with a substantial track record and publications in this area. As such, it was requested or commissioned to produce evidence syntheses for several intergovernmental organizations and donor agencies, substantially influencing their policies and activities. At a national level, ILRI has had a major impact on food safety policies in Kenya and Vietnam, as well as in India's Assam state, and has had a moderate impact in several other countries, including Cambodia, Uganda, Tanzania and Ethiopia.

Capacity building

Given the previous neglect of food safety in the domestic markets of low- and middle-income countries, ILRI research had a strong emphasis on capacity building. Most food safety research projects included students at undergraduate, MSc and PhD levels. In several countries, such as Tanzania and Vietnam, all qualified risk analysis professionals have been trained by ILRI. In addition, ILRI developed and delivered a range of 1–2-week trainings aimed at policy makers and implementers. Many thousands of value chain agents were trained in individual projects. This was done to develop appropriate training and to test approaches because the role of CGIAR was seen to be that of developing material, approaches, delivery systems and incentives that could support the training of value chain agents rather than to conduct the training itself.

Introduction

What is the role of international agriculture research in food safety? This chapter looks at ILRI's work on food safety to draw conclusions about its actual and potential impacts. Unlike other aspects of agricultural research, food safety is a relatively new area for CGIAR, and we can easily trace the emergence and growth of its research agenda. The research agenda represents a departure from traditional CGIAR research in two main ways: (i) food consumers rather than food producers are the focus of food safety research; and (ii) the prime motivator of food safety research is improving human health rather than improving farm productivity, food security or natural resource management.

Why food safety matters

Food-borne disease (FBD) includes any illness caused by ingesting contaminated or naturally hazardous food or drink. Food produced in developing countries often contains high levels of biological and chemical hazards and is prone to adulteration (Grace, 2015a,b), therefore creating conditions in which FDB thrives.

Only recently has good evidence on the burdens of FBD in developing countries started to emerge. The best assessment was published by the World Health Organization (WHO) in 2015, the culmination of nearly 10 years of work by dozens of experts (Havelaar *et al.*, 2015; Gibb *et al.*, 2015). A conservative estimate found that the health burden of unsafe foods (a combination of morbidity and mortality) was comparable to that of malaria, HIV/AIDS or tuberculosis, making FBD a major public health priority. The first part of the study, focusing on 31 hazards for which there was enough information to generate global estimates, found that around 98% of the FBD burden fell on developing countries, and 97% was due to microbes, parasites or viruses, with the remainder due to chemical hazards. FBD from these hazards caused 600 million illnesses and 420,000 deaths in 2010. The second part of the study, using a less conservative methodology, found four heavy metals resulted in an additional 1 million illnesses and 56,000 deaths in 2015. FBDs are estimated to cost the USA US$15–80 billion a year (Scharff, 2012; Hoffmann *et al.*, 2015), which would be as high as 0.4% of estimated 2020 US gross domestic product (GDP). A recent World Bank/ILRI study estimated that FBD costs developing countries at least US$100 billion a year (Jaffee *et al.*, 2019).

The WHO study on FBD identified the hazards responsible for most illness and death. In developed countries, most of the FBD burden is attributable to microbes, especially those of zoonotic origin; in developing countries, macroparasites are relatively important in addition to the microbes controlled in developed countries (such as those responsible for cholera and brucellosis) (Havelaar *et al.*, 2015). It is more difficult to ascertain which food is responsible. In developed countries, most of the burden is due to animal-source food and fresh produce, and this seems to be the case in developing countries (Hoffmann *et al.*, 2017; Grace, 2015a).

Aside from its health burden and associated economic costs, FBD is important as a barrier to market access. Food export markets, formal markets and provisioning programmes already require food to meet certain sanitary and phytosanitary standards and, as a result, tend to exclude smallholder, women, less educated and more remote farmers, who have less ability than others to meet these standards (Unnevehr and Ronchi, 2014). As concern over FBD increases, meeting food safety standards is likely to become an ever more important constraint to smallholder production. These health, economic and equity concerns show how relevant food safety issues are to pro-poor agricultural research for development.

This chapter first summarizes the history of food safety research at ILRI and CGIAR, describing how the discipline grew, became a research agenda and evolved from an ad hoc and hazard-based agenda to one that was more systematic and risk based. The next section sets out the theory of change linking food safety research to economic and health benefits. It identifies two main pathways: evidence that counts and impact that scales. The following sections summarize ILRI progress along both pathways, and we end with conclusions and recommendations for new food safety research.

The History of Food Safety Research at ILRI and in CGIAR

ILCA was established in 1974, and by 1977 had developed a research programme on smallholder production in the eastern African highlands. An ILCA Dairy Technology Unit was founded in 1986 at Debre Zeit, about 65 km south-east of Addis Ababa (ILCA, 1987), which aimed to develop milk-processing methods adapted for smallholders. This unit produced manuals that covered hygienic milk handling but did not focus on milk safety. The episodic production of dairy manuals and training material continued over the next decades: a major achievement was seen in 2006 when dairy boards in Kenya, Rwanda, Tanzania and Uganda endorsed generic training material for informal milk traders in the eastern and central Africa region. During this time, dairy research for development work continued in Botswana, Burundi, Ethiopia, Ghana, Kenya, Malawi, Mali, Nigeria, Senegal and Zimbabwe, among others; in the early 2000s, this was extended to Latin America and India.

Food safety, as opposed to food technology, research started at ILRI after the institute widened the focus of its predecessors to cover a broader range of livestock issues following the merger of ILRAD and ILCA in 1995. The first food safety research started in the late 1990s. It was conducted within a veterinary public health framework and focused on milk safety in Kenya (Aboge *et al.*, 2000; Kang'ethe *et al.*, 2000, Mwangi *et al.*, 2000; Omore *et al.*, 2000). This work was extended to Ghana, Tanzania and Uganda in the early 2000s. Food-borne zoonoses were specifically considered among other zoonotic diseases in a landmark ILRI volume prioritizing the livestock diseases whose control would most significantly reduce poverty (Perry *et al.*, 2002). Around the same time, another strand of research started on economic aspects of food safety, especially the trade-offs between safe food and other development objectives (Omore *et al.*, 2001). This led to the development of an ILRI programme on Animal Health and Food Safety for Trade, which had the objective of addressing food safety as a barrier to smallholder market access rather than as a constraint to human health. Congruent with the economic perspective, there was research on consumer demand for safety and quality. Ten studies from seven countries in Asia and Africa were brought together in an influential report (Jabbar *et al.*, 2010)

In 2003, for the first time, ILRI initiated a programme – Livestock Keeping and Human Health Impacts – with an explicit focus on improving human health through livestock. This marked the start of ILRI research employing a risk

analysis framework and focusing on improving food safety outcomes rather than subsuming food safety under market issues or veterinary public health. Following an external review (Science Council/CGIAR, 2008), food safety was again placed in an economic programme: in hindsight, this was a retrograde move given the broad trends of agricultural research towards greater emphasis on human health. Subsequently, the ILRI programme on Animal Health and Food Safety for Trade became Animal Health, Food Safety and Zoonoses, and finally Food Safety and Zoonoses, as it became clear that world export markets were less important to poor people and that FBD was more important than had been realized. In 2017, the wheel came full circle when research groups working on different aspects of human and animal health in four separate ILRI programmes across ILRI's two directorates (biosciences and integrated sciences) were brought together in a new Animal and Human Health Programme. Food safety was one of four major areas in this programme (the others were zoonoses and emerging infectious disease, herd health, and vaccines and diagnostics).

The ILRI food safety research agenda focuses its attention on traditional 'informal markets', where most smallholder and poor farmers sell their livestock products. Traditional processing, products and prices predominate in these informal or 'wet' markets, which tend to escape effective health and safety regulation, go untaxed and unlicensed, and sell food at lower prices than formal markets. Informal markets are also closer to and more accessible for poor consumers than formal markets.

An ILRI review of food safety and informal markets largely categorized the attitude of officials and donors towards informal markets as one of either neglect or unhelpful attention (Roesel and Grace, 2014). Much attention has been paid to the role of informal markets in maintaining and transmitting diseases but little to their role in supporting livelihoods (especially for women) and nutrition. Informal markets are often seen as outdated and unsafe, destined to be replaced by industrial production and modern retail. The ongoing COVID-19 pandemic has accentuated this belief among many stakeholders, especially those not familiar with wet markets.

Nevertheless, informal outlets are much more common and widely distributed than formal

sector alternatives and often offer services (such as immediate payment to farmers and provision of credit to consumers) that the formal sector does not provide. Food is perceived by consumers to be fresh, healthy, natural, convenient and less expensive (Roesel and Grace, 2014; Zhong *et al.*, 2020). With these advantages, it is not surprising that the formal sector share of animal-source food markets is less than 10% in most of sub-Saharan Africa and South Asia (Gomez and Ricketts, 2013). In southern and East Africa, informal markets currently supply 85–95% of market demand and are predicted to still supply 50–70% of market demand in 2040 (Tschirley *et al.*, 2015). In South Asia, traditional food retail occupies 95% of the market, in South-east Asia 71% and in South America 54% of the food retailed. In this context, informal markets are likely to remain important for at least several more decades.

The relative neglect of informal markets compared with other CGIAR research areas implies greater marginal utility of research investments. ILRI is almost unique in having a large research programme focused on food safety in informal markets, with a strong focus on generating actionable, high-quality evidence. As such, the group is responsible for much of the research information in this area. Importantly, the group produced the first book on food safety in informal markets (Roesel and Grace, 2014), in addition to dozens of journal papers, theses, posters, conference papers, research briefs, policy briefs, videos, infographics and blogs. ILRI also conducted numerous training courses for policy makers, researchers and value chain agents. The results of the various research and training activities are all available in open-access formats from the ILRI document repository (CGSpace: https://cgspace.cgiar.org/; accessed 19 February 2020) and other sites.

In parallel with the evolution of food safety at ILRI, there have been developments in the role of food safety in CGIAR, in which ILRI has been a major player. Food safety was not an initial focus of CGIAR research, with the first official mention of food safety in 2000 (Technical Advisory Committee, 2000). However, eight CGIAR centres had started small-scale research related to food safety in the following areas: breeding staple crops resistant to pests (so farmers can reduce pesticide use), breeding staple crops resistant

to aflatoxins, controlling aflatoxins using other organisms (biocontrol), breeding ergot (fungus) resistance in sorghum, reducing cyanide levels in cassava, and improving milk quality and safety (Kassam and Barat, 2003). Only research in the last area assessed health outcomes. In 2011, another survey of CGIAR food safety research was conducted, with more centres reporting food safety research. Aflatoxin research dominated, but there was an expansion of risk assessment and prioritization activities and substantial programmes on the safety of perishables (vegetables and animal-source foods), on zoonotic diseases, on occupational hazards and on water-associated diseases. As this list suggests, food safety research was almost entirely supply led, with centres looking at problems in the commodities they specialized in and with no overall alignment to health outcomes. The research effort and budget were very small compared with the overall CGIAR research portfolio.

Food safety research became more prominent with the development of the CRP on Agriculture for Nutrition and Health (A4NH), one of 15 CGIAR multicentre research programmes (Box 9.1). The Nutrition and Health programme was originally conceived as a joint venture between ILRI and the International Food Policy Research Institute (IFPRI). However, the CGIAR Consortium (now the CGIAR System Office) refused a jointly led CGIAR research programme, and, because most of the research in this programme focused on nutrition, it was agreed that IFPRI should lead the programme. A4NH had four main themes, or flagships, three focused on nutrition and one on the diseases associated with agriculture, including FBD. A4NH brought together portfolios on aflatoxin research led by the International Institute of Tropical Agriculture (IITA), the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), IFPRI and ILRI, and a portfolio of research on animal-source foods led by ILRI (A4NH, 2011). After two successful external evaluations (Sridharan *et al.*, 2015; Compton *et al.*, 2015), in which the research was deemed to be highly relevant, to have generated important evidence and to have generally met expectations, it was decided to make food safety a new, stand-alone flagship in the second phase of A4NH, starting in 2017.

> **Box 9.1.** Justification for incorporation of food safety research at ILRI.
>
> Food safety research is a relatively new area for CGIAR and ILRI. It can be seen as a response to changing agri-food systems and as evidence of the ability of CGIAR to take on new challenges. Like most organizations, ILRI periodically revisits its priorities and strategies, but this is typically done based on donor interest, popular wisdom, consultation and expertise rather than by using a systematic framework. Important exceptions at ILRI were: (i) an institutional prioritization in 1998 based on *ex ante* returns to research, which tightened ILRI's focus but led to a reduction of work in Latin America and with pastoralists; (ii) a geographic information system (GIS)-based mapping of poor livestock keepers, suggesting that Asian poor livestock keepers were neglected clients (Thornton *et al.*, 2002); (iii) an accompanying identification of research priorities based on expert opinion of pro-poor impacts, which showed the importance of zoonoses (Perry *et al.*, 2002); (iv) a non-systematic identification of priority countries for CRPs, which for the first time focused on consumers as well as producers; and (v) a mapping of zoonoses and poverty, which suggested that FBDs were among the most important zoonoses (Grace *et al.*, 2012c). These exercises in general provided justification for increased focus on FBD. In particular, compared with other animal health issues, FBD is relatively important, neglected and tractable, characteristics suggesting that it is a relatively promising area for research investment.

Food safety pathways to impact

The 2017–2021 strategy for food safety research in A4NH identified two impact paths: evidence that counts and impact that scales (A4NH, 2016). The first pathway, evidence that counts, posits that ILRI evidence, published in peer-reviewed journals and actively communicated to users in ways that are clear, compelling and actionable, will lead to better decisions and these will lead to positive impacts. The second pathway, impact that scales, is based on ILRI discovering, developing or contributing to novel technologies or institutions that improve food safety for millions of people. Our big-idea impact pathway is the triple path to improving food safety in mass domestic markets by working with informal traders through a combination of

increasing their capacity to sell safe food through training and technologies, providing motivation for behaviour change (e.g. by improving business and marketing skills) and providing a more enabling operating environment, so that authorities, instead of ignoring or punishing informal traders, encourage them to professionalize their work.

Empirical evidence

The first pathway – evidence that counts – is well within the traditional research sphere. Our theory of change is that, for 'evidence to count', the right information must be conveyed to the relevant people through appropriate channels. Research efforts can also build capacity of the relevant people so that they can make good use of the evidence generated and better align their incentives with action to improve food safety.

Recent decades have seen an increasingly systematic and systemic approach to using evidence across a broad range of fields; ILRI seeks to apply this to the issue of food safety in informal markets. Much of the interest can be traced back to the evidence-based medicine movement, which started in the 1990s in Canada. Evidence-based medicine was defined as 'a systemic approach to analyse published research as the basis of clinical decision making' (Claridge and Fabian, 2005). The approach quickly spread to allied health fields, such as dentistry, and then to areas such as education and housing.

Evidence-based approaches explicitly weight different types of evidence. In the evidence hierarchy, scientific evidence trumps anecdote or opinion, and scientific evidence itself is considered weaker or stronger depending on defined characteristics. For example, evidence from a multi-centre randomized controlled trial is stronger than evidence from a cohort study, which in turn is stronger than evidence from a cross-sectional study. While the best research evidence is intended to be the major factor in medical decisions, it is acknowledged that research evidence is only one factor, often a minor one, in development decision making. However, there is a consensus in the literature that, especially in developing countries, a more evidence-based, or at least evidence-informed, approach to policy

and practice is desirable, and that research can also tackle the process problem of insufficient reliance on evidence in decision making. As a result, important research-for-development donors rely increasingly on evidence. The food safety work at ILRI, which strongly drew on epidemiology, was and is well placed to meet this demand.

CGIAR is an important generator of agricultural research evidence in developing countries. Surveys have found that CGIAR science outputs compare well with advanced research institutes in production of evidence (Elsevier, 2014). However, there is less information on how this evidence is used or linked to development impact. In general, the implementation of research evidence is not straightforward. A review of the use of public health evidence in developed countries found that there was no reliable evidence on the extent of its use and that its impact was often indirect, competing with other influences (Orton *et al.*, 2011). The same review suggested that barriers to the use of research evidence included: decision makers' perceptions of research evidence, the gulf between researchers and decision makers, the culture of decision making, competing influences on decision making and practical constraints.

Food safety research is more likely to have an impact if the following are true:

- *The research is of objectively high quality.* Our food safety research seeks to drive up quality by publication in high-impact-factor journals, shifting from less to more rigorous protocols and following best practice guidelines for conducting and reporting studies.
- *Stakeholders are involved.* For example, they may take part in the design of the research, serve as advisory members or visit research sites. ILRI's food safety research has often involved national 'champions' who were identified as key promoters and disseminators of the research findings.
- *The research is produced by scientists in whom decisions makers have confidence.* For example, Kenyan policy makers want to see studies on aflatoxins in feed from Kenya, even if studies from Tanzania are likely to be almost as relevant. ILRI's food safety research has taken place in 27 countries as of 2020.

- *The research is important but non-obvious.* For example, our finding in Vietnam that pork in supermarkets was less safe than pork sold in wet markets contradicted policy makers' preconceptions. They initially resisted the information, but when they saw the reasons for this finding, it made more of an impression on them than research findings that matched their preconceptions.
- *The evidence is timely, coming when decision makers need to do something.* For example, research on training dairy traders in north-east India provided a solution for decision makers dealing with public concern over milk safety.

We have found that food safety evidence leading to impacts generally occurs as one of three kinds: (i) developing the methods and tools needed to generate evidence of food safety in informal markets; (ii) developing and testing innovations with potential for widespread use; and (iii) influencing policy.

Developing research methods and tools

Faced with the challenge of informal food hazards but little understanding of their risks to human health, ILRI identified the need for new tools and methods for conducting food safety research in a development context. The overarching framework for food safety work was an approach that ILRI called 'Participatory Risk Analysis'. Over the past several decades, risk analysis has been accepted as the 'gold standard' for assuring food safety. It has been adopted by the international community and underpins trade in foods and livestock. However, risk analysis has not had much success in the informal markets of developing countries, where most of the poor buy and sell their food. Conventional risk analysis is often expensive and time consuming, requires considerable amounts of data and quantitative analysis, and is typically led by technocrats. By taking the core concepts of risk analysis and combining them with proven development analytic methods such as participatory rural appraisal and gender analysis, an approach emerged that could be applied successfully to the food safety challenges in developing countries. Applying this food safety approach was an important innovation of the programme (Grace *et al.*, 2008, 2010, 2011, 2012a,b; Grace and Randolph, 2009). The approach was subsequently used in Tanzania, Uganda, Vietnam and elsewhere, and its strengths and weaknesses, as well as the recommendations generated, were captured in peer-reviewed publications (Häsler *et al.*, 2018; Nguyen-Viet *et al.*, 2019; Roesel *et al.*, 2019).

Within this risk analysis framework, other methods and innovations were developed, including a global mapping of zoonotic diseases and poverty. This involved an updating of the global maps of poor livestock keepers, a systematic prioritization of zoonotic diseases likely to be relevant to the poor, a systematic literature review of the prevalence of these zoonoses in people, livestock and food products, and combining these in global maps (Grace *et al.*, 2012c). This was subsequently used to inform a major call for research on zoonotic diseases funded by the UK Department for International Development (DFID) and British research councils, which subsequently generated important research findings across a range of projects.

Economic assessment is another key tool to improving food safety. Collaborative research by ILRI over a number of years on the demand for livestock products in Ethiopia, Kenya and Tunisia in Africa, in Bangladesh and India in South Asia, and in Cambodia and Vietnam in South-east Asia provided strong empirical evidence on food safety (Jabbar *et al.*, 2010). The study identified 'wet markets' as the typical point of purchase of animal products. The quality and safety of livestock food products were mostly defined according to how these attributes were perceived by consumers: by their taste, colour, flavour and smell. Developing-country consumers also judge quality and safety by what they perceive to be the nutritional attributes of the foods, such as freshness, absence of adulteration, fat content (milk) and fat cover (meat), and various aspects of appearance, packaging, geographic origins, indicators of expired shelf life, a government inspection stamp and the cleanliness of the premises selling the products. The same consumers are aware of microbial, chemical and physical hazards in animal-source foods. In general, quality and safety issues were not always clearly demarcated: consumers tended to

associate some attributes with both while in other cases the differences were clearer.

One ILRI innovation was an adaptation of system dynamics – a model that maps resource flows and management processes within a complex system – to informal food systems (see Chapter 6, this volume, for an adaptation to East Coast fever). This was used to investigate interventions in the pork chain in Vietnam. Desk studies have combined information on the health burden of FBD, the foods responsible and macro-economic models to predict future trends in FBD in terms of health burden and economic cost (Kristkova *et al.*, 2017). In India, the number of FBD cases is expected to rise from 100 million to 150–177 million in 2030 compared with 2011, and an economy-wide model predicted that this would incur costs equivalent to 0.5% of the GDP.

CGIAR identified gender as a cross-cutting issue that should be mainstreamed in research. However, most food safety research does not have a gender perspective. We adapted and applied gender analysis tools to understanding food safety and documented this in several papers (Kimani *et al.*, 2012; Grace *et al.*, 2015d; Kiama *et al.*, 2016).

Similarly, although food safety and nutrition are biologically coupled, they are not often well integrated in agricultural development. This can be problematic because interventions intended to improve food safety can work against nutrition and vice versa. We developed a framework for a rapid assessment of food safety and nutrition and applied it to several of the livestock value chains where the CRP on Livestock and Fish was working (Eltholth *et al.*, 2014; Hoa *et al.*, 2014; Häsler *et al.*, 2019) and, along with the lead UK think tank at Chatham House, developed a widely disseminated evidence synthesis on animal-source foods in the first 1000 days of life, covering nutrition and food safety (Grace *et al.*, 2018a).

What cannot be measured cannot be managed. When ILRI started work on food safety, there was little understanding of suitable metrics and indicators for food safety in low- and middle-income countries. ILRI led a working group with broad expert inclusion to develop the first synthesis and analysis of food safety metrics for these countries (Grace *et al.*, 2018b). It also developed a tool to measure 'food safety system performance', inspired by a similar tool developed

and applied to the countries belonging to the Organization for Economic Cooperation and Development (OECD). Currently, ILRI is providing technical support to develop the world's first 'Food Safety Index', which the African Union intends to include in the Malabo Declaration process. This means that all African Union countries will have an obligation to report on food safety and be mutually accountable, driving up food safety in Africa. ILRI is also a partner in the international Global Burden of Animal Diseases initiative.

Developing and testing innovations for application

Another suite of ILRI research focuses on generating outputs or products intended for use by value chain agents and implementers, including technologies, approaches and surveillance.

- *Technologies*. Food safety technologies are technical approaches to improving food safety. Nearly all of the technologies researched by ILRI food safety scientists are adaptations of products developed by others. For example, we adapted the insecticide-treated bed nets widely used in the control of malaria to reduce flies in informal markets. In other cases, ILRI had no role in the development of the technology but tested it in order to assess its suitability and/or to suggest improvements to make it more useful (e.g. use of ozone in disinfection). None of the technologies developed, tested or adapted is being delivered at scale but several are considered to have potential for widespread use.
- *Approaches*. These comprise processes or different ways of doing things. Many are oriented around capacity building in new practices or providing information. We can consider that one approach is having impact at scale: this is the triple-path approach to informal traders comprising capacity building, enabling environment and motivation.
- *Surveillance*. The third category of innovations is concerned with disease detection, reporting and response, such as the use of information technology for reporting from slaughterhouses.

Table 9.1. Food safety product lines. Green shading indicates that the development is on track, yellow indicates that there are some delays or problems, orange indicates that there are significant delays or problems, and red indicates that it has been cancelled. (Constructed by authors).

Category	Product	Stages of development			
		Research	Proof of concept	Evaluate to development	Delivery
Technologies	Aflatoxin binders for animal feed	green	green	green	
	Aflatoxin probiotics for food and feed	green	green	green	
	Insecticide-treated netting for food safety in wet markets	green	green		
	Ozone disinfection for wet markets				
	Chlorine disinfection for wet markets	red	red	red	red
	Filter paper tests for bacterial load in food	red			
	Mazzican for less mastitis and safer milk	green	green	green	green
	Boiling milk to improve safety	green	green	green	green
	Fermenting milk to improve safety	green	green	green	green
	Off-ground slaughter using a metal grid	yellow	yellow	yellow	yellow
Approaches	Training slaughterhouse workers	green	green	green	green
	Training and certification of traders	green	green	green	green
	GAP light – simplified Good Agricultural Practice	green	green	green	green
	SMS messages for changing farmer behaviour	green	green	green	green
	Biosecurity	yellow	yellow	yellow	yellow
Surveillance	Bidirectional e-surveillance system for slaughterhouses	green	green	green	green
	Participatory epidemiology for outbreak investigation	yellow	yellow	yellow	
	e-Surveillance for disease reporting	green	green	green	green
	Participatory disease surveillance for managing large-scale outbreaks	green	green	green	green

The most important ILRI food safety products in these categories are summarized in Table 9.1. This summary of product lines gives an overview of ILRI evidence generation. More insight into potential impact can be gained by looking at specific research projects and topics. To give a concrete example, we analysed research outputs on aflatoxins posted on the CGSpace document repository. Over a period of 6 years and with the input of one or two full-time-equivalent ILRI scientists per year working with students and partners, we produced 29 journal articles accompanied by 50 science outreach items (conference presentations, reports), 14 policy outreach items (briefs, technical packages) and 50 public outreach items (videos, infographics, press conference, blog articles). In addition, we communicated the research results to all the farmers and value chain agents participating in this research. This suggests that these projects are indeed producing outputs that go beyond research papers and that plausibly will help to ensure that 'evidence counts'.

Outcome and impact assessments carried out by specific projects can also illustrate the potential use and benefits of evidence generated on food safety projects (Box 9.2).

Capacity building activities by ILRI

Capacity building was integral to all of ILRI's food safety research and is an important dimension of CGIAR research. Between 2012 and 2015, the following training activities were carried out by ILRI's food safety research programme (Table 9.2): (i) training of value chain agents for the purpose of developing and testing models and approaches; (ii) training

Box 9.2. Evaluation of a multi-country food safety project.

Safe Food, Fair Food was the first major ILRI research project to focus on food safety. It conducted a peer-to-peer project assessment whereby teams from participating countries visited another country to conduct a structured evaluation. This was generally positive. For example, the project had five major components, the first being a situational analysis of food safety. The main impacts of this situational analysis work were: (i) raised awareness on food safety in informal markets among food safety stakeholders; and (ii) a coming together of different sectors (especially medical and veterinary) to discuss the common issue of food safety. A semi-quantitative analysis of the situational analysis identified four success criteria, and a peer evaluation was conducted when each of the seven country teams evaluated another country against these criteria (maximum score of 5). The average across seven countries was 16.4 out of 20, equivalent to 82 out of 100, suggesting good overall impact.

Assessment points (maximum score of 5 for each category)	Average score
1. Did the participants of situational analysis represent stakeholders of food safety in the country well?	4.7
2. What information does the situational analysis provide?	4.1
3. Was there any delay in conducting situational analysis?	3.6
4. Were there measurable impacts from the situational analysis?	4.0
Subtotal	16.4
Percentage	82.1

Table 9.2. ILRI capacity development in food safety, 2012–2015. (Compiled by authors from ILRI archives). (unpublished data, ILRI).

Year	Value chain agents	Officials and policy makers	Researchers and students	Graduate fellows
2012	70	110	52	26
2013	524	77	42	69
2014	304	146	161	101
2015	1460	37	192	42

government officials and policy makers to increase their capacity to understand and make good decisions, creating an enabling policy environment; and (iii) training researchers to build their capacity but also to influence future implementers and decision makers. Although we do not have denominator data, we believe this represents a majority of the food safety graduate fellows and researchers in the countries in which ILRI worked, a substantial proportion (around half) of relevant government officials and policy makers, and a much smaller proportion (much less than 1%) of value chain agents.

The benefits of training have been documented to some extent by projects that conducted outcome studies, including Safe Food, Fair Food (Box 9.2), which worked in multiple countries in sub-Saharan Africa, and PigRisk, a project working in Vietnam.

Influence on international, regional and national policies

International and regional agriculture and health organizations are considered crucial to development and this implies that ILRI engagement with them can have far-reaching impacts. Some ILRI inputs were specific to food safety high-level processes (e.g. its participation in WHO, 2013), while others incorporated food safety dimensions into broader livestock or development initiatives (e.g. food safety as an aspect of sustainable livestock development). Another distinction is between initiatives led by ILRI and initiatives where ILRI scientists were part of a broad range of scientists. Some of the most notable contributions are shown in Tables 9.3 and 9.4.

The following summary gives examples of where ILRI food safety research has contributed

Table 9.3. Food safety research led by ILRI.

Commissioner	Food safety aspect	Outcomes from the report	Source
DFID	FBD in low- and middle-income countries	Contributed to a funding call on food safety	Grace (2015b)
OIE	FBD as neglected livestock diseases	OIE communiqué issued	Grace *et al.* (2015a)
UNEP	Aflatoxins	Featured in UNEP annual report	Harvey *et al.* (2016)
EAC	Aflatoxins in feed and livestock products	Developed technical briefs used for setting policy at East African Community level	Grace *et al.* (2015b,c)
World Bank	Food safety in Vietnam	Contributed to a major funding initiative and to national policy	World Bank (2017)
USAID	Food safety in developing countries	Contributed to initiation of first food safety Innovation Laboratory	Grace (2017)
LCIRAH	Food safety metrics	Contributed to food safety tracking by African Union	Grace *et al.* (2018a)
DFID/BMGF	Food safety	Investment report influenced major funding call	Grace *et al.* (2018b)

OIE, Office International des Epizooties (World Organisation for Animal Health); UNEP, United Nations Environment Programme; EAC, East African Community; USAID, US Agency for International Development; LCIRAH, Leverhulme Centre for Integrative Research on Agriculture and Health; BMGF, Bill & Melinda Gates Foundation.

Table 9.4. Food safety initiatives to which ILRI contributed.

Commissioner	Food safety aspect	Outcomes from the report	Source
IFPRI	Aflatoxins	2020 briefs – an influential series of communications	Unnevehr and Grace (2013)
WHO	Food safety burden	Co-author on the FERG report	Havelaar *et al.* (2015)
WHO	Trade and human health	Chapter in WHO book	Hawkes *et al.* (2015)
IFPRI	Emerging economies	Paper in Global Food Policy Report	Grace and McDermott (2015)
HLPE	Food safety as an element of sustainable livestock systems	Co-author in 'Sustainable Livestock' report	HLPE (2016)
FAO	Food safety as an element of a healthy food environment	Included in International Conference of Nutrition agenda	Grace (2017)
World Bank	Food safety	Contributions to two major reports	Jaffee *et al.* (2019); GFSP (2019)
FAO/WHO	Food safety	First FAO/WHO/AU conference on food safety issued a communiqué	http://www.fao.org/3/CA3225EN/ca3225en.pdf
WTO	Food safety economics	Speaker at pre-panel event	https://www.wto.org/english/tratop_e/sps_e/faowhowtoapril19prog_e.htm

HLPE, High-Level Panel of Experts; FAO, Food and Agriculture Organization of the United Nations; FERG, Foodborne Disease Burden Epidemiology Reference Group.

to policy. A more detailed explication can help illustrate the specific contributions.

WHO undertook the first global assessment of FBDs through its Foodborne Disease Burden Epidemiology Reference Group (FERG). This showed the high burden of FBD and is likely to lead to increased funding in this neglected area. The WHO's burden of disease studies were highly influential in determining the global health agenda and especially in directing billions of dollars in funding to the 'big three' diseases (Maudlin *et al.*, 2009). It is therefore plausible that the FERG study will also have widespread impacts.

A High-Level Panel of Experts (HLPE) is the science–policy interface of the Committee on World Food Security (CFS), the foremost international platform for food security. In October 2014, the CFS requested the HLPE to prepare a report on sustainable agricultural development for food security and nutrition, including the role of livestock (HLPE, 2016). An important planning meeting was held at ILRI, where ILRI's Delia Grace served as one of ten members of the HLPE livestock project team. HLPE reports are widely used as reference documents within and beyond CFS and the United Nations system, by the scientific community as well as by political decision makers and stakeholders, and at international, regional and national levels.

A World Bank-supported task force on risk assessment for food safety comprising researchers and policy makers was formed in 2013 to build capacity for food safety management in Vietnam. ILRI scientists were involved in the task force and A4NH provided funding (Nguyen-Viet, 2012). The task force consisted of researchers in Vietnam working on risk assessment and food safety with representatives of the Vietnamese Ministry of Health and Ministry of Agriculture and Rural Development. The task force first analysed the situation of food safety policy in Vietnam. Key constraints and areas where research and development interventions could assist policy were identified. Stakeholder workshops were conducted to determine the scope of activities and to prioritize food safety issues. Training sessions with a focus on case studies of risk assessment for food safety were organized to strengthen the risk assessment capacity of task force members and of policy makers. Case studies were conducted to: (i) assess the health risks of vegetables and fish grown/caught in wastewater; (ii) assess the health risks related to antibiotic residues in pork; and (iii) disseminate research results and advocate for risk assessment as a tool for food safety management. The health risks from these case studies were assessed quantitatively, and risk communication and management strategies were developed. Achievements of the task force included the training of policy makers, managers and researchers; the publication of case studies of risk assessment in a special edition of a Vietnamese journal; and the publication of policy briefs. The task force was also requested to run training courses for veterinary professionals of ministries. The process, outcomes, challenges and potential impacts of the task force have been documented by Nguyen-Viet *et al.* (2018).

IITA coordinated the development of technical packages for the East African Community comprising technical papers on aflatoxin situational analysis, the scientific basis for aflatoxin control and policy recommendations for aflatoxin control. These technical packages aimed to assemble the best scientific thinking on the topic as the basis for policy recommendations. Through A4NH, ILRI scientists drafted two of these packages, which were submitted to the East African Community (Grace *et al.*, 2015b,c) and officially launched in 2018.

ILRI was commissioned by the US Agency for International Development (USAID) to develop a white paper on the potential need and role of a new Feed the Future Innovation Lab on Food Safety (Grace, 2017). The report recommended this, which contributed to the initiation of the laboratory in 2019.

ILRI was asked by the Global Food Safety Partnership (GFSP; a World Bank hosted public–private initiative for supporting food safety capacity building) to participate in a study on previous food safety investment in Africa and to make recommendations for future directions (GFSP, 2019). This led to engagement with the East African Community (EAC) and three-way collaboration between the EAC, GFSP and ILRI to support EAC in developing food safety strategy.

ILRI was asked by the World Bank to be a partner and co-author of the Eat Safe Initiative, which sets out global strategy for improving food safety and developed the first estimate of the cost of foodborne disease in low- and middle-income countries (Jaffee *et al.*, 2019).

In 2015, the African Union (AU) launched the Comprehensive Africa Agriculture Development Programme (CAADP) Biannual Review (BR) to monitor progress on agricultural development in the continent. The CAADP BR encompassed 43 indicators, seven of which tracked nutrition, but none captured food safety. In discussion with the AU, ILRI partnered to help develop the first African Food Safety Index (AFSI). The AFSI was launched as part of the 2019 CAADP BR, and 50 out of 55 AU Member States reported in at least one of its three elements.

Impact that scales

International agricultural research has always aimed for widespread impact, first by improving food production in developing countries and later by widening its focus on livelihoods and on the health and environmental externalities of agriculture. Impact assessments show large and well-documented benefits to CGIAR research on crop genetic improvement, most notably rice, maize and wheat, and especially in Asia. There is much less evidence, however, for large-scale benefits from global agricultural research in the fields of policy, natural resource management and livestock (Renkow and Byerlee, 2010; Jutzi and Rich, 2016).

There are different models for understanding how innovations in agri-food systems, whether technologies or institutions, could have widespread, sustained impact. In developing countries, agricultural extension services and development initiatives are important but often have limited reach. In recent years, interest has grown in other dissemination actors, especially the private sector and collective action and in novel dissemination pathways such as social media. The food safety research agenda explores the potential of different partnerships to achieve impact at scale.

ILRI food safety research partnered with four broad categories of individuals or organizations: researchers, agents in value chains, development programme implementers and enablers. The relative level of involvement of these groups varies – it will grow, reduce or stay the same – based on the particular stage of given research.

Specifically, ILRI's food safety research partners include the following:

- *Researchers.* Important research partners in ILRI food safety are the veterinary, agriculture and, to a lesser extent, medical universities, national agriculture and medical research systems and centres of excellence in the countries in which we work. Advanced research institutes are important partners, especially Free University Berlin, Liverpool University, Uppsala Agricultural University, the University of Florida and the University of Sydney. The CGIAR centres IFPRI, IITA and World Fish have been major partners.
- *Value chain agents.* Most of ILRI's food safety research engagements have been with small-scale value chain agents, often via intermediaries such as trader associations, but there has been increased interest in medium-sized formal businesses. We have also worked with public–private partnerships such as the Global Alliance for Livestock Veterinary Medicines (GALVmed).
- *Development programme implementers.* Development-implementing partners of ILRI include non-governmental organizations such as Veterinarians without Borders and large-scale development projects funded by the World Bank, USAID and others.
- *Enablers.* The international and regional enablers include: the Africa Union–Interafrican Bureau for Animal Resources(AU-IBAR), Association of Southeast Asian Nations (ASEAN), EAC, Economic Community of West African States, Food and Agriculture Organization of the United Nations (FAO), Intergovernmental Authority on Development, United Nations Environment Programme (UNEP), World Bank, WHO and the Office International des Epizooties (OIE, World Organisation for Animal Health). We also work with policy makers and implementers at the country level, including national ministries, state veterinary services and municipal authorities.

Training and enabling informal sector agents

Demand for fresh foods is growing rapidly in developing countries and most of this demand

must be met by markets. A study in southern and East Africa found that most food is already obtained from markets (54% in 2010, predicted to reach 70% in 2040) and that the informal sector currently supplies 85–95% of market demand and 51–57% of total demand (Tschirley *et al.*, 2015).

ILRI pioneered a 'triple-pathway' approach to improving food safety in informal markets by professionalizing rather than penalizing the informal sector, with the aims of supporting smallholder market access, safeguarding the supply of cheap nutritious food to the poor and reducing the burden of FBD. In the early 2000s, a training and certification scheme was designed and launched in Kenya to improve the quality and safety of informal dairy markets by improving the practices of traders, while also supporting the livelihoods of the dairy value chain agents. The scheme was taken up by a large proportion of eligible traders (with project support).

The traders were trained in hygienic milk handling and business practices and at the end of their training could apply for a certificate from the Kenya Dairy Board that entitled them to legally sell milk (Box 9.3).

Participant tests before and after the training showed that trader knowledge and practices improved, and microbiological tests showed that there was a substantial and significant decrease in unsafe milk. A later economic evaluation found an important reduction in transaction costs attributable to less harassment by authorities, less confiscated equipment and fewer bribes paid but also fewer losses of milk to spoilage. There was anecdotal evidence of improved business performance. A more recent evaluation found that, although the scheme had encountered some challenges, it was still operational. Eight years after the project officially ended, many traders have continued in the scheme; we estimated that up to 5 million consumers are benefiting from

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Box 9.3. Smallholder dairy training and certification initiative.

In Kenya, dairy products are a significant expenditure in poor households. The informal, small-scale milk sector dominates the milk marketing chain, with some 60 - 70 % of the raw milk market. Milk sold informally from door to door or in milk bars reaches poor consumers who pay a lower price for it than for factory-packaged milk; it also generally provides farmers with higher prices than they can get in the formal sector.

However, prior to policy change in 2004, informal vendors, including mobile milk traders and bar vendors, milk transporters and small-scale milk producers (many of them women), were not officially recognized. They were unable to obtain a licence and were frequently harassed by powerful dairy market players, who sought to protect their own interests while professing concern over the safety and quality of milk sold in the informal sector.

Efforts to revise the dairy policy were spearheaded by ILRI's Smallholder Dairy Project. Implemented along with the Kenya Agricultural Research Institute (KARI) and the Kenya Ministry of Livestock and Fisheries Development, the project generated research-based evidence to reveal the economic significance of the informal milk sector and highlight the potential for improved handling and hygiene practices to ensure milk quality.

As part of the ongoing development of pro-poor strategies for small-scale milk market development, the Dairy Traders Association of Kenya was officially launched in September 2009. Its aims and activities include self-regulation based on the training and certification concept originally developed by the Smallholder Dairy Project and further scaled up by other projects. Around 4000 milk traders, offering employment to over 10,000 people, have been trained and certified by the Kenya Dairy Board through the association. Field regulators also ensure that licensed outlets and premises operated by milk traders meet conditions for milk hygiene, testing requirements and sanitation, and that operators know how to comply with these conditions.

A key supporting aspect of the Smallholder Dairy Project was the development of modules for training (milk handling, processing and marketing) and certification of vendors to improve milk quality. This training, along with simple innovations such as wide-necked milk cans, were shown to improve the safety of milk significantly. The proportion of milk with high levels of contamination fell from 71% to 55% among traders using plastic containers and from 48% to 42% among those using metal containers. Without the intervention, policy change would have been unlikely (WRENmedia, 2010).

milk provided by trained traders and tens of thousands of dairy farmers from market access through trained traders.

An evaluation of the Kenya-ILRI collaborative Smallholder Dairy Project was conducted in 2008 (Kaitibie *et al.*, 2010a,b; see Chapter 17, this volume). This showed significant economic benefits derived from changes in dairy policy resulting in lower transaction costs. Some 73% of national benefits accrued to producers and consumers with the balance going to traders and input suppliers. Related evidence showed improvements in milk quality (Omore and Baker, 2011), although it was not possible to link such improvements to changes in market prices.

Key lessons from the Smallholder Dairy Project were as follows:

- The scheme was successful in improving the quality and safety of milk, at least in the short term, and the focus on quality seems to have improved business performance.
- The scheme reduced milk marketing costs and was appreciated by both traders and consumers.
- The traders provided information to consumers and can be a practical node for dissemination of nutritional change and promotion of milk consumption to consumers as part of a marketing intervention.
- Training in business skills, including a greater consumer orientation, can improve business performance.

Key policy lessons were the following:

- Policies seeking to exclude the informal sector are unlikely to improve food safety or nutritional quality and may paradoxically decrease food safety and reduce the accessibility of food.
- Food safety and nutrition programmes should also help to reform anti-informal sector policies. Merely reducing inappropriate regulatory pressure on small businesses has the potential to increase small business capacities and to create incentives for them to improve the quality of their product.
- 'Light-touch' interventions centred around training can deliver substantial improvements in product quality, even in the absence of major technological or infrastructure upgrades.

There was, however, a lack of systematic support to this initially successful project. The original assumption that vendors would pay private business development services to provide training was not valid. However, other development actors did use the modules to provide one-off trainings. More critically, changes in the institutional and political context were not favourable to the informal sector and a subsequent follow up found that, while traders expressed a very favourable opinion to training, there was no systematic training programme in place and moreover milk sold by trained traders was no safer (Alonso *et al.*, 2018).

Moreover, the approach used in the Smallholder Dairy Project was never evaluated to see whether health benefits were obtained from safer milk. Although marketing skills were taught, there was no emphasis on teaching vendors how to promote the nutritional benefits of milk. The capacity-building initiative did not benefit from a gender perspective in design or implementation, notwithstanding the importance of women as milk producers, traders and consumers. Sustainability and scalability challenges had not been fully overcome. These deficits are being addressed in a project under way in 2020 (www.ilri.org/research/projects/moremilk-making-most-milk); accessed 1 August 2020.

The trader intervention is a model for improving food safety when approaches based on regulation do not work (Johnson *et al.*, 2015). The model has been adapted and tested in other contexts, including dairy (India and Tanzania) and meat (Ethiopia, Nigeria and Senegal). In two of the three cases, evaluations documented that participating value chain agents increased their knowledge and skills and improved their food-handling practices. In some cases, better milk quality and higher incomes were found (Lapar *et al.*, 2014) and significant economic benefits were generated (Kaitibie *et al.*, 2010a,b). In the case of Nigeria, the intervention could plausibly be linked with a reduction in diarrhoea and savings in reduced healthcare expenditure worth many times the cost of training butchers (Grace *et al.*, 2012a). However, follow-up research 9 years later revealed a marked deterioration in meat quality as the result of lack of follow-on training and, more importantly, a shift from enabling to disabling environment (Grace *et al.*, 2019).

Based on results from early studies, a formal theory of change was developed by Johnson *et al.* (2015). This identified three components that they considered essential for success. The so-called 'triple-path' model included the following:

- *Training and technologies.* Informal sector agents needed tools to deliver safe food. This usually meant training, awareness raising and simple technologies such as disinfectants. Training in business skills was often included.
- *Enabling environment.* Regulatory authorities had to be on board with the intervention and there had to be some mechanism for institutionalization (e.g. a locally or nationally recognized certificate) and a means of quality assurance.
- *Motivation and incentives.* Incentives were essential for behaviour change but were very context specific. In one case, certificates protected traders against harassment from authorities; in another, the training enabled traders to improve their bargaining power with the public sector. It was originally hypothesized that trained traders would be able to charge a premium for safer food, but in no project were they able to charge more for food, although some may have increased their market share.

This triple-path approach is sometimes called 'Training, Certification and Marketing', or TCM, where 'training' refers to the capacity building aspect, 'certification' to the enabling environment and 'marketing' to the provision of incentives for behaviour change.

Table 9.5 presents evidence for the outcomes and impacts of food safety interventions, based on five relatively well-evaluated projects.

Human Nutrition Research at ILRI

Many rural poor people worldwide subsist on substandard diets consisting largely of the same cheap cereal and tuber staples day in and day out. When they move to cities, their intake of cheap, highly processed foods high in sugar, salt and fats increases. Nutritional deficiencies in such diets are common and are associated with a range of poor health and development outcomes. The first 1000 days of life, from conception to around 2 years of age, are considered an especially crucial nutritional period: setbacks during this period are hard to recover from by later attempts to 'catch up'. Undernutrition, while declining, remains at high levels in vulnerable communities, while diseases associated with too much food consumption trend upwards.

An initiative in 1984 brought together 12 CGIAR centres at ILCA, in Ethiopia, to discuss how the centres were addressing human nutrition. At that time, ILCA was including nutritional status in its field research, while ILRAD viewed its contribution to better nutrition as an indirect one made by tackling serious livestock diseases (Doyle, 1984).

During the 1960s and 1970s, insufficient energy was thought to be the most serious dietary constraint to improved human nutrition. As a result of research during the 1980s and 1990s and improving levels of energy consumption, attention shifted to micronutrient deficiencies in the diets of the poor. Because milk, eggs and meat are among the richest dietary sources of vitamins and minerals, in addition to protein, this created a new appreciation for the contribution that livestock products can make to ensuring nutritious and diverse diets.

In the late 1990s, ILRI conducted its first empirical studies investigating links between livestock keeping and human nutrition. A study from Ethiopia (using data from 1989 to 1998) found that introducing cross-bred cows could improve human health and nutritional status (Thornton and Odero, 1998); similar findings were reported from coastal Kenya (Nicholson *et al.*, 1999). Another Ethiopian study, in 1997 and 1999, indicated that market-oriented livestock activities moderately reduced poverty and improved food security and nutrition of smallholder households (Ahmed *et al.*, 2003). Econometric models applied to data from coastal and highland Kenya in the late 1990s found positive impacts of dairy cattle ownership on chronic malnutrition in coastal Kenya (Nicholson *et al.*, 2003).

A major event to bring together nutrition researchers and stimulate nutrition research in CGIAR was held in 2000 in the Philippines (Pinstrup-Andersen, 2000). Discussions at this meeting explicitly addressed the role of highly nutritious foods, including livestock products. The meeting concluded that ILRI efforts to increase the supply of livestock products to the poor could

Table 9.5. ILRI food safety interventions in informal markets.

Particulars	Kenya	Senegal	Ibadan, Nigeria	Assam state, India	Kampala, Uganda
Value chain	Informal milk sector	Goat restaurants	Butchers	Informal milk sector	Butchers
Year range	1997–2006	2010–2011	2009–2011	2009–2013	
Number of traders	25,000–30,000	Several hundred in three slaughterhouses	Around 900 in the market	Around 300 traders and 600 producers in the main milkshed	
Number of market agents trained	In 2010, 4200 traders registered nationally; in pilot areas, 85% of traders had been trained	Around 100 trained	80 directly by the project and around 420 by peer-to-peer training	265 traders and 480 producers have been trained	50% of butchers
Consumers reached	Around 0.5–5 million	Nearly 1 million	Around 360,000	Around 1.5 million	Around 0.5 million
Gender aspects	Not explicit; women made up about one-third of the traders	Not included: all workers were men	Targets for women participation and gender dimensions researched	Not explicit; nearly all traders and farmers were men	
Intervention	Training in hygiene and business practices, provision of hygienic dairy cans, with a certificate given to successful trainees, reducing their harassment by officials	Training in hygiene, raising awareness on food safety	Peer-to-peer training on basic hygiene; provision of equipment, banners and promotional material; use of butchers' associations to monitor performance and ensure compliance	In-depth training needs analysis; training of trainers; training covering hygiene and business skills; traders motivated by better relations with officials and positive publicity and farmers by visible reduction in mastitis	Training in hygiene, equipment, posters, certificates
Documented impact	Improved KAP after training; improved milk safety after training with reduction in unacceptable coliforms from 71% to 42%; This project gave training and certification programs for informal milk traders, enabling thousands to be licensed and resulting in national economic benefits having a net present value of US$230 million.	No change in KAP after training; management provided no soap or other necessities and were rather indifferent to practices, and there was no obvious incentive for behaviour change	Reduction of unacceptable meat from 97.5% to 78.5% ($p<0.001$); significant improvements in KAP after training; cost of training was US$9 per butcher and estimated gains through diarrhoea averted was US$780 per butcher	Improved KAP after training; significantly higher milk production after training and tendency for reduced mastitis; significant sector benefits in several sites	Improved KAP after training; satisfaction with training

Continued

Table 9.5. Continued.

Particulars	Kenya	Senegal	Ibadan, Nigeria	Assam state, India	Kampala, Uganda
Policy influence	High: legislation changed and new institutions	None	Low: only engagement with market authorities	High: new institutions but no change to legislation	Some: linked to broader ILRI policy processes
Current status of the initiative	Training and certification are episodic and project-led, but trained vendors have an important share of the market	None: one-off training	The pilot was intended to investigate efficacy and acceptability and did not have a strategy for sustainability	Training and monitoring are ongoing and supported by the government	Training is being supported by donors
Reference(s)	Kaitibie *et al.* (2010a,b); Omore and Baker (2011); Alonso *et al.* (2018)	Submitted	Grace *et al.* (2012a)	Lapar *et al.* (2014); Lindahl *et al.* (2018)	Ongoing

KAP, knowledge, attitudes and practices.

be presumed to have nutritional benefits while acknowledging that there had been insignificant efforts to measure these benefits (Bouis, 2000).

Delgado *et al.* (2001) examined the effects of income growth on diets using Chinese panel data. As incomes improved, Chinese consumers shifted from high-carbohydrate foods towards high-fat, energy-dense foods, with these changes varying by income levels. These income effects suggested that increased incomes could affect diet and body composition in ways detrimental to health; moreover, the biggest harm would fall on low-income groups due to their increasing incomes. The study argued that higher incomes might reverse health gains achieved in the preceding two decades if diet-related non-communicable diseases could not be controlled (Delgado *et al.*, 2001).

In 2003, for the first time, an ILRI programme was initiated with an explicit focus on improving human health through livestock by considering both the associated benefits and risks of livestock to people's health. The new ILRI Livestock Keeping and Human Health Impacts programme focused on nutrition, zoonoses and food safety. This programme sought to leverage expertise through partnerships, and commissioned some important evidence syntheses. These concluded that the available evidence suggested that interventions to promote livestock were generally positive for nutrition, although few high-quality studies took into account the complex links between livestock and nutrition, and most had substantial methodological weaknesses (Leroy *et al.*, 2006). The project also developed an influential conceptual framework (Fig. 9.1) articulating the links among livestock, nutrition and human health (Randolph *et al.*, 2007). These links are context specific. To begin teasing out the roles of different species, a study conducted in Ethiopia demonstrated that ownership of small stock did not contribute to improved child nutrition within the household, whereas poultry might provide direct benefits through egg consumption (Good, 2009).

An external review (Science Council/CGIAR, 2008) recommended that human nutrition not be a focus for ILRI. This led to fragmentation of ILRI's first human health programme, and for several years little research was done at ILRI relevant to human nutrition. However, the launch of A4NH in 2012 provided an opportunity to revive this important area of research.

ILRI leveraged external expertise to re-establish nutrition work. This included collaborations with senior nutritionists at Emory University in Georgia, IFPRI, the London School of Hygiene and Tropical Medicine, UK, and Washington State University. Exploratory work and pilots were conducted in several field sites. Highlights include the following:

- An ILRI study conducted with households representing low, medium and high levels of dairy intensification in rural Kenya indicated that women's increased labour demands as households intensified their dairy production were associated with poorer nutritional outcomes for their young children; in contrast, children in households of high dairy intensity received more milk than children in lower-intensity households (Njuki *et al.*, 2015).
- ILRI produced the first reported study showing a link between aflatoxin in milk and child stunting (children who are too small for their age) in two low-income areas in Nairobi (Kiarie *et al.*, 2016).
- ILRI conducted a project to develop tools for rapid, integrated assessment of food safety in value chains. Studies in five countries documented the potential importance of livestock products to nutrition and how these were being eroded by poor food safety (El-Tholth *et al.*, 2018; Häsler *et al.*, 2018, 2019; Roesel *et al.*, 2019; Nguyen-Viet *et al.*, 2019).
- ILRI conducted an analysis of the demand for livestock products, the drivers of this demand and the barriers to consuming livestock products among poor households in Nairobi. Price was found to be the most important barrier to consumption, while taste was reported as the main driver for consumption. Estimated demand elasticities indicated that increases in total food expenditure would lead to the greatest increase in demand for beef meat. Price reductions would increase the demand relatively more for fish, other meats and dairy products (Cornelsen *et al.*, 2016).
- A systematic review suggested that food scares linked to livestock disease outbreaks and FBD could harm nutrition due to consumers avoiding the implicated foods (Green *et al.*, 2017).
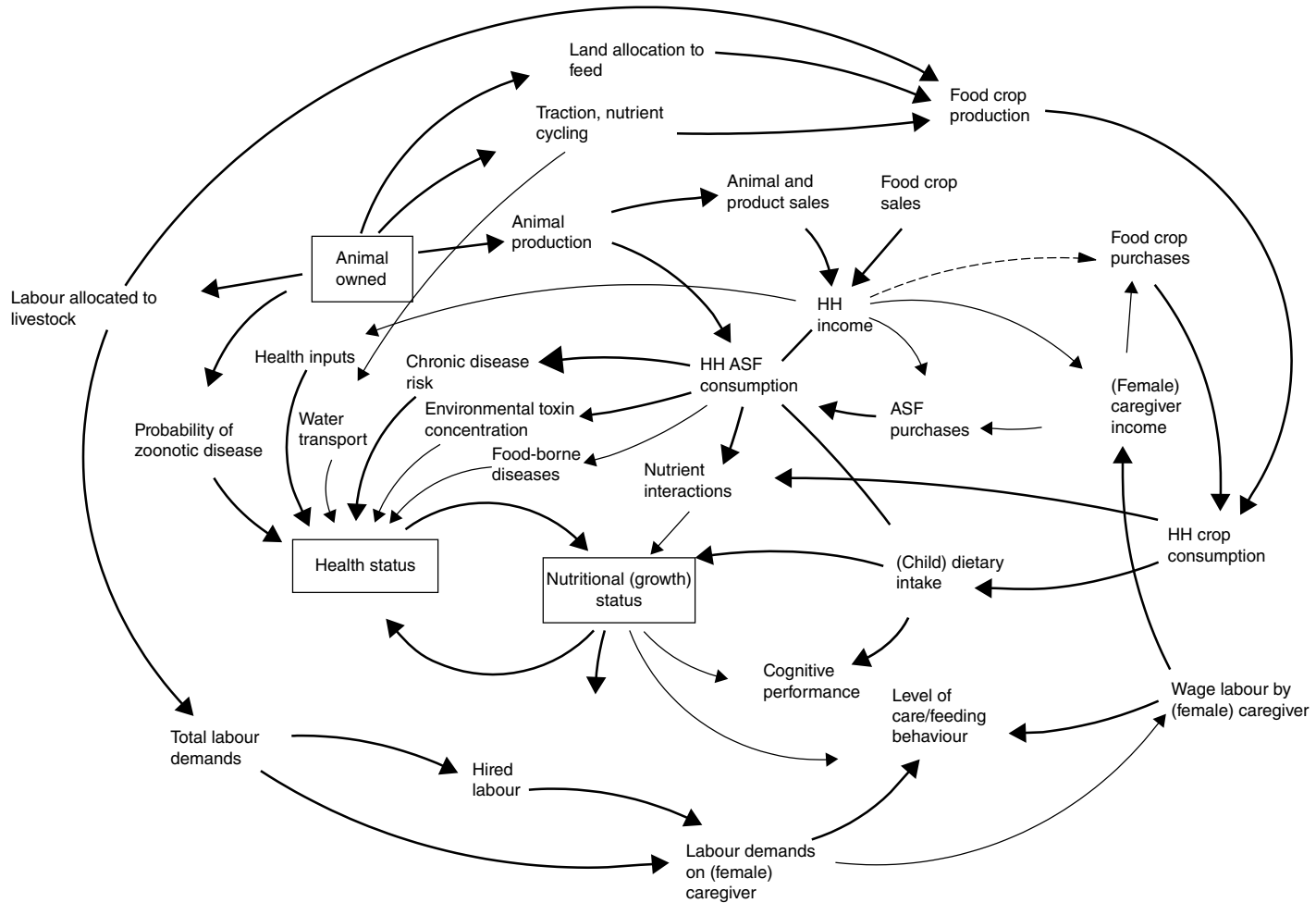
Fig. 9.1. Impact pathways among livestock keeping and human nutrition and health outcomes among the poor. (Adapted from Randolph *et al.*, 2007.) ASF, animal-source foods; HH, household.

- A study in Tanzania suggested that participation in a pro-poor agricultural intervention to improve milk production may improve women's milk consumption (Mishkin *et al.*, 2018).
- A Women Empowerment in Livestock Index, based on a widely used index to measure empowerment of women in agriculture and adapted to livestock keepers, incorporated nutrition and was used to identify dimensions of empowerment associated with dietary diversity and food security (Galiè *et al.*, 2018).
- Work with FAO on the challenges of ensuring livestock interventions in the Sahel had positive nutritional benefits and led to a reformulation of relevant FAO guidelines (Dominguez-Salas *et al.*, 2019).

As ILRI also endeavoured to engage with the Millennium Development Goals and the subsequent Sustainable Development Goals, there were increasing efforts to understand the appropriate contributions of livestock products to human diets, especially given the wide and sometimes conflicting concerns about undernutrition, overnutrition, the environmental externalities of livestock systems, livestock-associated human diseases and animal welfare. A series of papers looked at some of the synergies and trade-offs among these societal goals (Enahoro *et al.*, 2018; Salmon *et al.*, 2018; Sirma *et al.*, 2018). ILRI increasingly engaged in broad platforms that addressed all these issues. These included livestock initiatives taking on greater nutritional focus, such as the multi-stakeholder Global Agenda for Sustainable Livestock partnership, the Livestock Data for Decisions project, the Global Livestock Agenda to 2020 initiative and the Global Livestock Advocacy for Development project. The links among livestock, livestock-associated disease and human nutrition were also set out in several influential publications that ILRI authored or co-authored (Grace, 2015a, 2016, 2017; ILRI, 2019). ILRI's collaboration with Chatham House produced a widely cited and evidenced-based synthesis of livestock-enhanced diets in the first 1000 days of life (Grace *et al.*, 2018a).

A few ILRI projects have aimed to improve nutrition through consumption of livestock products as opposed to better understanding this issue or advocating for it. ILRI participated in an mNutrition initiative that involved mobile phone companies providing mobile phone-based health, nutrition and agriculturally based information services to the poor. ILRI helped to build the capacity of local partners to develop appropriate nutrition messages and to ensure the quality of the messages (CABI, 2017). More than 5 million people were reached with these nutrition messages. There was evidence of some behaviour change due to implementing this service, but it proved difficult to develop business models to keep the service going because people were generally unwilling to pay for mobile phone-based health information. A rigorous external evaluation of this project is under way. Preliminary results indicate that aspects of the approach are attractive to mothers, but considerable technological and sociological barriers challenge access and uptake (https://perma.cc/7QSA-Z9DF; accessed 19 August 2020).

Another large ILRI-led project focused on behavioural communication change messages to promote dietary diversity, including livestock products, in Kenya. This project gave more than 5000 women training in nutritional issues and reached over 50,000 infants via nutritional messages to their mothers (Kiome *et al.*, 2019). This was not a research project and the impact is not clear. Another project in Rwanda aimed to evaluate the nutritional impacts of a social and behavioural change communication intervention combined with a government initiative dubbed 'One Cow per Poor Family' (Flax *et al.*, 2017). The final results of this project are not yet available, but initial results confirm that families who are given a free cow had lower stunting prevalence than families who were eligible but had not yet received a free cow (Flax *et al.*, 2019).

ILRI projects have also been the entry point for other nutrition projects. The ILRI-led African Chicken Genetic Gains (ACGG) project in Ethiopia has partnered with a Food, Agriculture and Natural Resources Policy Analysis Network (FANRPAN) project which will promote chicken and egg consumption in the ACGG households benefiting from ACGG provision of 25 imported tropically adapted chicken strains and locally developed indigenous strains. Again, work is ongoing and findings are yet to emerge.

In conclusion, the contribution that livestock make to human nutrition has evolved at ILRI from an assumed but unexamined premise,

to an active area of research, to relegation outside of ILRI and finally back to renewed recognition that this should be an important focus of ILRI's agenda. The very small investments in this area to date have necessarily constrained its impacts. Research studies did produce useful information on links among livestock keeping, livestock product consumption and nutrition. There were also methodological advances in tools for assessing nutrition in value chains, for formulating diets and for measuring women's empowerment. ILRI advice has also been incorporated in many guidelines. While recent decades have seen livestock production coming under increasing criticism in high-income countries because of environmental, health and animal welfare concerns, the increasing numbers of high-level reports and global engagements on nutrition and livestock issues are likely to draw attention to the importance of livestock and livestock-derived products for nutritionally vulnerable populations

The Future

ILRI and partners have been studying food safety in informal markets for more than a decade. This work has helped confirm the hypothesis that food safety is an important and probably growing constraint to smallholder value chains because of its multiple burdens on human health, livestock production and product marketing. Over the same period, our understanding of the global burden of FBD in developing countries has greatly increased, validating ILRI's emphasis in this area, especially the importance of zoonotic disease and animal-source foods, areas where ILRI is mandated to research.

ILRI research on FBD has resulted in many science outputs, including some genuinely innovative tools and approaches, and has already demonstrated outcomes at community, national and regional levels. These include substantial inputs into global, regional and national strategies and national training programmes. The major development-oriented approach – the triple-path for training, motivating and enabling of informal market agents – has been shown to be both scalable and sustainable. While questions remain about its lasting effects on food safety and its application outside those few countries where its success has been demonstrated, the next few years should bring further evidence about this, with benefits lasting for many decades to come.

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10 Ticks and Their Control

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Executive Summary

The problem

Ticks are bloodsucking external parasites. They are responsible for decreased productivity due to blood loss from the host animal and 'tick worry', the irritation resulting from their feeding activity. Other negative effects include the injection of toxins, transmission of endemic and emerging diseases (such as heartwater, African swine fever and Congo-Crimean haemorrhagic fever) and tick-associated disease (such as dermatophilosis). Tick-borne pathogens affect 80% of the world's

cattle population and are ubiquitous in the tropics and subtropics. Countering these negative effects requires expensive control measures. Global costs associated with ticks and tick-transmitted pathogens in cattle alone were estimated years ago at above US$13.9 billion and US$18.7 billion, respectively (de Castro, 1997) and costs have doubtless increased in this century. Climate change and transboundary trade in livestock have recently begun to drive ticks into new areas where animals have less resistance to both ticks and tick-borne diseases. In Africa, ticks and tick-borne disease appear at the top of several rankings of important livestock diseases; notably, diseases transmitted by parasites, such as trypanosomiasis and East Coast fever (ECF), ranked high in International Livestock Research Institute (ILRI) prioritizations of livestock disease across regions and production systems of sub-Saharan Africa (Perry *et al.*, 2002).

The most common control methods are the use of genetically resistant animals and the application of acaricides. Acaricides may be applied through dips, sprays or pour-on formulations as well as intra-ruminal boluses, ear tags and footbaths. Resistance to acaricides is the ability in a strain of ticks to tolerate doses of acaricides that would prove lethal to most individuals in a normal population of the same species, and this is a major and growing problem. An anti-tick vaccine is commercially available for only a single tick species. Pasture management also has a role in integrated control.

ILRI's role in the global context

Because of its geographical location, abundant infrastructure and technical expertise, ILRI was and remains in a powerful position to contribute to the global understanding of African ticks and tick-borne diseases. In 1979, the International Laboratory for Research on Animal Diseases (ILRAD) Tick Unit was established as a resource – a provider of skills and materials that could be used in ILRI's research and, potentially, by others as well. The unit was built primarily to support research on ECF. The control of ECF and other such diseases is inextricably linked to ticks and their control, so ILRI, although it lacked a systematic tick research programme – a programme aimed at some specific component of tick biology

or control – was soon involved in diverse areas of tick research.

Following flagship projects at ILRAD, ILRI conducted important research on tick biology, tick population dynamics, the impact of ticks and tick control using chemicals. Apart from ECF, a major ILRI research theme, other haemoparasites and, more recently, viral pathogens were studied.

Scientific impacts

Sustainable strategies for the control of ticks and tick-borne disease involve a complex interplay between parasite and host species, available control technologies and a range of environmental factors. In this challenging situation, ILRI's contributions were a continuum from laboratory-based science, through field experimentation, to practical advice and policy recommendations.

ILRI made early and ongoing contributions to our understanding of 'endemic stability'. This occurs when rates of infection are sufficient to maintain a level of acquired immunity that minimizes clinical disease in a population. The concept was developed to describe patterns of tick-borne disease in cattle but has since been applied more broadly in veterinary and human health.

ILRI's field experiments in Kenya, Ethiopia and Uganda led to recommendations for on-farm tick control. For example, in Kenya, acaricide treatment improved weight gains where keeping unvaccinated cattle without acaricides was uneconomical. Rotation of acaricides could potentially mitigate resistance, so ILRI scientists conducted the first field examination of acaricide rotation, finding it was advantageous.

More laboratory-based research into tick biology was greatly facilitated by the existence of the Tick Unit, described above. ILRI developed an artificial feeding system for ticks and methods for maintaining tick colonies (four stocks for over 30 years, and six for more than 20 years). In addition, tick-breeding research established high- and low-infectivity lines for ECF: seven different stocks and lines of ticks from eastern and southern Africa, which include low (refractory) and high (susceptible) genetic tick lines. Vector biology studies included understanding population genetics of ticks in East Africa and molecular taxonomy of Afro-tropical ticks, tick ecology,

and disease dynamics at the wildlife and livestock interface. ILRI developed maps of tick distribution and models that explained the spread and the subsequent disappearance of an especially problematic tick species after its introduction to Zimbabwe.

The Tick Unit has adapted protocols for detecting and quantifying chemical resistance in ticks to backstop similar efforts by regional veterinary services. Pen and field trials of new acaricide formulations are being tested as alternatives to existing compounds to mitigate acaricide resistance in tick vectors of veterinary importance.

ILRI has played a significant role in the international effort to apply a range of molecular technologies to improve the scientific understanding of ticks and future means of their control. As genomic technologies emerged globally, ILRI's scientists played a valuable part in sequencing tick genomes as they did for ECF. Significant research was conducted on anti-tick vaccine evaluation and antigen identification, vector genomics and vector–pathogen interactions. The involvement in the identification of novel tick antigens continues.

According to Altmetric (www.altmetric.com/; accessed 24 February 2020), ILRI contributed to 2% of the research outputs on ticks.

Development impacts

The most visible development achievement is an ECF vaccine, which is covered in Chapter 6 (this volume). The Tick Unit and the tick research have been essential components of this major commitment by ILRI. The organization has played a key role in the development of a recombinant ECF vaccine and an important part in the development of the infection-and-treatment regime, which has been shown to have a significant impact in Tanzania. A significant and practical outcome of the Tick Unit and ILRI's research includes sharing knowledge and advice with the Centre for Ticks and Tick-Borne Disease (CTTBD), an animal vaccine production facility in Malawi.

Studies of heartwater, an important tick-borne disease affecting small ruminants, generated evidence on economic impacts and a potential market for a vaccine.

ILRI developed recommendations on tick and tick-borne disease control and acaricide usage for farmers but since uptake of this information is indirect, via extension services, its final impact is not known.

Policy influence and advice

ILRI generated evidence on the adverse consequences of stopping state-supported tick control in Zimbabwe and advised on better control approaches. A consultancy to the Director of Veterinary Services in Zimbabwe recommended tick control strategies at a critical time for livestock production in that country.

Capacity development and partnerships

ILRI has built capacity in tick research and control for students, extension workers and farmers. Supported by the Wellcome Trust, ILRI and government officials set up meetings between farmers and researchers, to identify problems associated with ticks and tick-borne disease, including tick sampling with farmers. In addition, tick scientists from Sudan, Kenya, Malawi and Ghana have come to ILRI to be trained on tick dissections and tick management. To strengthen future research capacity, the institute has trained more than 20 PhD and MSc students and Fellows. The close link on the ILRI campus between advanced molecular sciences and practical tick culture and control have often been a key competitive advantage.

National and international partners have included the Wellcome Trust, the UK Biotechnology and Biological Sciences Research Council (BBSRC), the Brazilian Federal Agency for Support and Evaluation of Graduate Education (CAPES), Genesis Labs, the University of Bern and the Directorate of Veterinary Services in Kenya.

Introduction

From the early days of ILRI, the impact of African tick species on animal productivity, the complexity of their control in the field and their activity as vectors of diseases such as ECF, babesiosis, anaplasmosis and heartwater have all engaged ILRI's scientists. Supporting these practical issues has been research into fundamental

aspects of tick biology. The aggregate contribution of ILRI's scientists to tick research over the decades has been considerable. However, from the beginning, the major focus of animal health research in ILRI has been on a small number of tightly defined areas such as vaccination against ECF and trypanosomiasis. Perhaps for that reason, ILRI has typically lacked a single, focused tick programme, and its engagement in tick research has often seemed to be ambivalent. Increasing this ambivalence may have been a reluctance to intrude where other African institutions could claim involvement. An additional consideration may have been the fact that tick control depended largely on either the use of indigenous livestock by smallholders or the application of chemical acaricides manufactured by global animal health companies. Hence, the role of an institution like ILRI was not so clear.

The lack of a coherent strategy had two broad consequences. First, as the research activities that were undertaken reflected either the specific needs of other projects or a scientist's personal interest, ILRI's contributions to tick research cover an extremely diverse set of topics. In contrast with other, more focused areas of activity within ILRI, it is therefore harder to point to major, quantifiable impacts. This is the downside of the somewhat piecemeal approach ILRI took to tick research. On the upside, as the contributions were mostly a result of individual initiatives, they were typically dependent on external collaborations. They therefore constitute an excellent example of ILRI's capacity to engage productively in multi-organizational projects. The number of collaborating institutions involved in ILRI's published tick research is large. In what follows, the focus is on areas where, subjectively assessed, ILRI's contributions have been major or at least essential to the final result.

In reviewing this diverse effort, it is convenient to break it generally into two components. The first is work that has been largely field based, focusing on the practicalities of tick control. The second is work that has been more laboratory based. Significant contributions have been made to practical tick control by quantifying the impact of ticks, in understanding the dynamics of tick populations on a local and landscape scale, and in providing input to the effective use of pesticides (acaricides), including the economic cost and benefit of their application. The more laboratory-based research has focused on developing research capacity through the ILRI Tick Unit and the acquisition of techniques such as *in vitro* tick feeding and genomic technologies. In turn, this has led to application in the development of vaccines for ECF, an understanding of the genetic diversity of the major ECF vector species, *Rhipicephalus appendiculatus*, and progress in the development of anti-tick vaccines. Each of these areas will be addressed in turn.

A note on nomenclature: *Boophilus* ticks were long classified as a genus and in all of the literature pre-2001 are cited as such. Approximately 15 years ago, the suggestion was made, on the basis of molecular evidence, that the genus should be considered a subgenus of *Rhipicephalus* (Barker and Murrell, 2004). The coherence of the genus *Rhipicephalus* as it stands has also been questioned. Hence, in the literature a species may be described as *Rhipicephalus decoloratus*, *Rhipicephalus* (*Boophilus*) *decoloratus* or *Boophilus decoloratus*. In what follows, to cover all possibilities, the *Boophilus* ticks will be referred to as *Rhipicephalus* (*Boophilus*) spp. or *R.* (*Boophilus*) spp.

Practical Tick Control

The impact of ticks as vectors of disease has been quantified by groups working on these diseases, principally, in the case of ILRI, ECF (Minjauw and McLeod, 2003). The direct effect of ticks themselves has been less examined, although it is a major concern in countries such as Australia and much of Central and South America. There were, however, several early attempts to quantify production losses due to ticks. De Castro *et al.* (1985a) used Boran cattle immunized against *Theileria* spp. to examine the effects of acaricide treatment. Five tick species were found to infect the cattle, although in smaller numbers on acaricide-treated animals, which also showed higher live weight gains. Overall, however, the conclusion was that it was possible to keep Zebu cattle without chemical tick control, once immunized against *Theileria* spp. Estimates of the direct impact of *R. appendiculatus* on productivity were low. In another study published in 1985, only relatively small and transient effects were found from the infestation of cattle with up to 400 *R. appendiculatus* a week for 24 weeks.

There was some suggestion of acquisition of immunity to the ticks (de Castro *et al.*, 1985b). Morzaria *et al.* (1988) returned to the question, finding that, for cattle vaccinated against ECF, acaricide treatment improved weight gains, while keeping unvaccinated cattle without acaricide treatment was simply uneconomical.

In Africa, as throughout the rest of the world, if tick control is consciously applied, it is most likely to be through the application of synthetic acaricides. The scientific challenge is to identify the optimal acaricide treatment regime, one that balances the negatives of cost and potential environmental and health impacts with the positives of the control of tick-borne disease and the minimization of production losses through the direct effects of ticks themselves. Within this question lies an extremely complex set of issues. Are the animals to be treated – usually cattle – indigenous or exotic breeds? Which are the most important tick species and what is their distribution, both spatially and temporally? Which acaricides are available and what is their efficacy? The choice of acaricide may be affected by issues such as the cost and the occurrence of acaricide resistance. 'Acaricides' will include not only commercial products of certified quality but also market-derived treatments of uncertain origin, quality and efficacy. This, in turn, is affected by national and regional registration procedures, which may be rigorous or disturbingly lax. All these issues may be regarded as essentially scientific or technical. The final set of complexities relate to infrastructure and human behaviour: the availability of dips or other treatment facilities, the distance between the farmer and the treatment facility, and the fact that acaricide application, regardless of the efficacy of the chemical itself, is frequently done so poorly that treatment is ineffective.

An event in recent African history provides a good example of the benefits and risks of tick control, especially in the absence of a scientifically sound and enforceable policy. Andy Norval, who was head of the ILRI Tick Unit from 1987 to 1989, had in earlier work noted that the most common tick in Zimbabwe in overgrazed tribal areas was *R.* (*Boophilus*) *decoloratus*, while in well-managed commercial farms, the diversity of species was greater but the economically most important one was *R. appendiculatus*. Until the early 1970s, ticks and tick-borne diseases were controlled efficiently through a programme of intensive dipping. The low incidence of tick-borne disease led indirectly to overgrazing in communal areas. Then, between 1973 and 1978, a weakening of the dipping programme was followed, typically after 1–3 years, by increases in the population of *R.* (*Boophilus*) *decoloratus* and hence outbreaks of babesiosis and anaplasmosis. Cattle numbers plummeted; then, with reduced animal numbers, grazing pressure reduced, grass cover increased and *R. appendiculatus* and *Amblyomma hebraeum* re-established in these areas. This, in turn, was followed by outbreaks of theileriosis and heartwater (Norval, 1979; Lawrence *et al.*, 1980). These disease outbreaks were attributed to a loss of immunity to the tick-borne diseases, i.e. a loss of endemic stability because of a long-term lack of exposure to ticks and the diseases they transmit. Subsequently, serological surveys in 1981–1982 suggested that endemic stability was being regained in cattle on communal land, and the suggestion was made not to reintroduce intensive dipping (Norval *et al.*, 1992).

Over the years, ILRI has made a number of contributions to such complex situations. Although there has been little direct involvement in the evaluation of acaricides in straightforward field situations, there are exceptions. For example, in 2003, there was a 1-year longitudinal study of 92 smallholder dairies in Kenya to evaluate the efficacy of deltamethrin in the control of the major tick-borne diseases and trypanosomiasis. Four application regimes were compared – biweekly, monthly and bimonthly treatment and untreated controls – and the conclusion was reached that monthly treatment could reduce the incidence of tick-borne diseases to a statistically significant degree (Muraguri *et al.*, 2003). In 2003 and 2004, the efficacy of cypermethrin on four tick species was investigated in Ethiopia and it was found that application every 3 weeks provided good protection (Mekonnen *et al.*, 2004).

The complex issue of optimal frequency of acaricide treatment in the absence of pesticide resistance has been examined by ILRI and their collaborators in a variety of production settings. The population dynamics of four major tick species on indigenous and cross-bred cattle in a dry or semi-arid area of Uganda were examined for cattle given biweekly, monthly or no acaricide treatment. There were effects of lactation and

year-on-year variation but only on the cattle given biweekly treatment were the overall numbers of ticks reduced significantly (Okello-Onen *et al.*, 1999). In a companion paper published in 1998, the variable costs of acaricides, drugs and labour, and the benefits in live weight gains, were together used to calculate the most economically beneficial treatment frequency for indigenous cattle. The conclusion was that a biweekly dipping strategy did not offer benefits commensurate with costs, while the monthly treatment gave clear economic benefit (Okello-Onen *et al.*, 1998), a conclusion that seemed somewhat at variance with the finding on tick numbers. The authors returned to the question in 2003, again examining the effect of biweekly and monthly dipping on indigenous breeds over a period of almost 3 years. The biweekly dipping improved milk offtake and pre-weaning growth rates (Okello-Onen *et al.*, 2003). As they currently stand, such discrepant results would be difficult to translate into a clear message for farmers.

Scientifically more interesting was a paper derived from an ILRI–Kenya Agricultural Research Institute (KARI) collaboration that addressed an unresolved issue in acaricide usage (Kamidi and Kamidi, 2005). *Boophilus* spp. in particular have a pronounced capability to develop resistance to a range of acaricides. The example of resistance in *Rhipicephalus* (*Boophilus*) *microplus* is astonishing and very well documented. It is known that, with the possible exception of amitraz, resistance once acquired can persist for a very long time, even in the absence of chemical selection pressure. Commonly, the market offers an odd mix of different acaricides that are used by farmers in a fairly random way. On occasion, attempts have been made to regulate a chaotic situation by enforcing the serial use of acaricides with the idea of exhausting one before applying another. An alternative approach would be to use acaricides in a structured rotation, although the benefits of this for tick control have not been established.

Rotation of pesticides from different chemical groups has been used in the management of some crop pests to reduce the probability of the emergence of strong resistance. This has never been systematically studied with acaricides for tick control. There has been one published laboratory-based test of the idea that the emergence of resistance could be delayed by the rotational use of two different acaricides in a controlled way. The results were encouraging (Thullner *et al.*, 2007). However, the work reported by Kamidi and Kamidi (2005) is perhaps the only published example where this has been examined in a field situation. The work described the consequences of three different acaricide treatments on a single smallholder farm with exotic dairy cattle over 7.5 years. Initially, ticks were controlled by weekly spraying with amitraz. Then, when resistance developed after 3 years, this was replaced by fortnightly treatments with an organophosphate, although it was known that resistance to this chemical group occurred in the district. A dramatic increase in tick-borne disease followed. The final strategy was a regime of fortnightly spraying, using amitraz and the organophosphate in rotation. This resulted in the lowest incidence of tick-borne disease of the three strategies.

These observations raise interesting questions. First, it is striking that, although both acaricides were expected to achieve at best partial tick control used separately, the rotation seemed to be effective. Second, the cost of acaricide was, inevitably, very high, although perhaps less than might have been incurred with an increased incidence of tick-borne disease. Finally, of course, the long-term financial and biological sustainability of intensive pesticide treatment in the face of known resistance must be doubtful.

Several publications have attempted to take the issue of ticks from the field to the landscape scale. During the 1990s, the evolving situation in Zimbabwe was a focus, and the approaches included: (i) examination of the field distribution of particular species, often supplemented by ecological and climatic modelling; (ii) studies on current acaricide usage and practices; and (iii) economic analysis of preferred strategies. For example, factors contributing to the spread of *R. appendiculatus* in Zimbabwe after its introduction and its subsequent disappearance were examined using a climate model. It was concluded that the chief causal factor was a wet–dry climate cycle (Norval and Perry, 1990).

On a number of occasions, these concerns evolved into policy advice. The focus on Zimbabwe may have been a result of the dramatic effects of a failure in tick control during the civil unrest. In 1990, Perry and Mukabeni of ILRI, and Norval, who had recently shifted to the University of Florida, together with Barrett, in the

Department of Veterinary and Tsetse Control Services, submitted a report containing recommended tick control strategies to Zimbabwe's Director of Veterinary Services (Perry *et al.*, 1990a). Twenty-five years later, the report still encapsulates many of the typical issues: political imperatives, changing disease epidemiology, the cost of acaricides, the paucity of methods to control tick-borne disease, and so on. To briefly recap this history: prior to the independence war of the 1970s, intensive acaricide treatment had led to the eradication of ECF and the control of other tick-borne diseases. The highly regulated system of treatment was, however, increasingly unpopular. It collapsed during the war, as noted previously, with consequent severe outbreaks of disease and the death of approximately 1 million cattle. Subsequently, there was evidence that endemic stability to these diseases was re-established or in the process of being re-established, and there seemed to be the opportunity to pair satisfactory disease control with reduced use of expensive (state-purchased) acaricides. The catastrophic loss of cattle, however, had reawakened a demand for intensive dipping, which was reintroduced for political reasons. By the time of the ILRI consultancy, the costs were becoming unsustainable.

The policy advice that flowed from this consultancy was complex. It divided communal lands into four categories, based largely on the probable but different impacts of babesiosis, anaplasmosis, heartwater and theileriosis. A reduction in acaricide treatment with a move, where possible, to minimal acaricide application was proposed. The target was to achieve endemic stability to the various diseases, supported by vaccination. Significant cost-saving was envisaged, although the costs of vaccinations were uncertain (Norval *et al.*, 1992).

These ideas were revisited again in 1994. The concern was specifically with heartwater and its vectors, the ticks *A. hebraeum* and *Amblyomma variegatum* (Norval *et al.*, 1994). *A. hebraeum* was then widely distributed in the dry southern Lowveld with some foci in the wetter areas of the Highveld, while *A. variegatum* occurred in the Zambezi Valley and surrounding dry Lowveld areas. The distribution of *A. hebraeum* had changed over the preceding 70 years, while that of *A. variegatum* had remained static. The distribution patterns of both species in

Zimbabwe displayed anomalous features: the ticks occurred in areas of lowest predicted climatic suitability for survival and development and in areas where the densities of cattle, the most important domestic host, were lowest. The only factor favouring the survival of the species in the Lowveld habitats in which they occurred was the presence of alternative wildlife hosts for the adult stage. Norval *et al.* (1994) concluded:

> Their absence from more climatically favourable Highveld habitats appears to have been the result of intensive acaricide treatment of cattle over a long period and a historic absence of significant numbers of wildlife hosts. Eradication of *A. hebraeum* and *A. variegatum* by intensive acaricide treatment of cattle can be achieved in the absence of significant numbers of alternative hosts, because of the long attachment and feeding periods of the adults of these tick species. However, eradication becomes impossible when alternative hosts for the adult stage are present, because a pheromone emitted by attached males attracts the unfed nymphal and adult stages to infested hosts. The unfed ticks are not attracted to uninfested hosts, such as acaricide-treated cattle.

In the face of a probable reduction in intensive acaricide treatments, due to the cost to the government, the authors suggested two potential alternative strategies: to establish a buffer zone to restrict disease spread, or to allow the ticks to spread and to control heartwater by immunization.

By 1998, there was evidence that the heartwater vectors were, in fact, spreading (Peter *et al.*, 1998). A study reporting the results of a survey in 1995–1996 (Perry *et al.*, 1998) returned to the question of *A. hebraeum*, *A. variegatum* and heartwater. The dynamics of tick control were changing. The government, under financial pressure, had abandoned intensive dipping, and wildlife species were moving back into the Highveld. Suggestions were made on how to deal with the increased disease risk. The overuse of acaricides remained a concern. It was noted that intensive acaricide treatment (i.e. more than 30 times a year) was associated with a higher risk of heartwater than on farms using more strategic dipping.

Given the very strong focus in ILRI on ECF, the distribution of *R. appendiculatus* was a longstanding interest. The example of the spread of *R. appendiculatus* in Zimbabwe is given above. A broader consideration of the distribution of

R. appendiculatus in Africa based on climate and vegetation was published by Perry *et al.* (1990b). The starting point in this research was a predictive model of tick distribution based on climatic factors. The model was originally developed by the Commonwealth Scientific, Industrial and Research Organisation (CSIRO) to better understand the distribution of *R. (Boophilus) microplus* in Australia (Sutherst, 2003). Here, it was to be applied to *R. appendiculatus*. The authors found that the ecoclimatic indices of suitability correlated well with known tick distributions in eastern Africa but were insufficient as a single-factor explanation in central and southern Africa. Cold stress and vegetation microenvironments were also considered to be important. Factors such as cattle and wildlife distributions and acaricide control (if any) were hypothesized to be relevant, although the data to test that hypothesis were insufficient. Predictably, too, this focus on tick distribution and climatic factors was combined into an attempt to understand the epidemiology of *Theileria parva* using additional information from geographic information systems (Lessard *et al.*, 1990).

Development of Research Capacity

A mix of fundamental methodology, facilities, equipment and hands-on experimental expertise underpins all scientific research. ILRI played a significant role in developing such scientific capacity in at least two areas of tick research. The first was through the establishment of a Tick Unit for the development and maintenance of tick colonies together with the acquisition of techniques needed for tick and tick-borne disease research. The second was via the involvement of ILRI staff in tick genomics and other molecular technologies.

The ILRI Tick Unit

The ILRI Tick Unit was built around experimentally valuable infrastructure: fly- and tick-proof animal isolation rooms (pens) with a capacity for 16 cattle, tick culture and incubation rooms, small-animal facilities and associated laboratory space. More important were and are the bio-

logical resources. Currently, the ILRI Tick Unit has in culture representatives of three genera of ticks, including the subgenus of *Boophilus*. These genera are *Rhipicephalus*, *Rhipicephalus (Boophilus)*, *Hyalomma* and *Amblyomma*. The species in culture are *R. appendiculatus*, *Rhipicephalus zambeziensis*, *Rhipicephalus evertsi*, *A. variegatum*, *R. (Boophilus) decoloratus*, *R. (Boophilus) microplus* and *Hyalomma anatolicum*. The diversity of *R. appendiculatus* cultures is a focus of the collection, with seven different lines from eastern and southern Africa, including selected lines derived from the Kiambu stock that differ in susceptibility to *T. parva* infection and lines from South and eastern Africa selected for experiments on the impact of diapause on disease transmission, as well as geographically diverse isolates, including two from Zimbabwe and three from Zambia. The expertise of the ILRI Tick Unit currently is in tick culture, performance of animal trials under controlled conditions and the process of producing sporozoites for ECF projects. These skills continue to underpin basic research into *T. parva* (e.g. Henson *et al.*, 2012).

Ticks share with many other parasites the irritating characteristic that, while they are exceedingly difficult to kill in the wild, they are often very difficult to maintain under controlled conditions. Hence, it is an achievement that of the *R. appendiculatus* stocks, four have been maintained for over 30 years and six for more than 20 years. Two of the other species have been in culture for over 30 years and one for more than 20 years. Admirable though this is, it is also a cause for concern. Experience with *R. (Boophilus) microplus* in Australia showed that a much-used reference tick colony, maintained for even longer, showed declining viability and then sudden collapse.

Artificial feeding systems

To understand and, if necessary, dissect the process of tick feeding on a mammalian host (cattle) and thus acquiring a disease organism such as *T. parva*, it would be experimentally useful to be able to feed ticks in a less physiologically and biologically complex situation than on the natural host. For *R. appendiculatus*, this problem was tackled in the 1990s. Slightly earlier work at

ILRI with *A. variegatum* showed that it was possible to feed the ticks on rabbit or cattle skin membranes, with high carbon dioxide concentrations and a temperature of 37°C being important for success. Adult female and male ticks were fed to engorgement over a period of up to 16 days. All stages of the tick fed successfully and although engorgement weights were less than on natural hosts, egg laying was successful. Ticks fed *in vitro* successfully transmitted *Theileria mutans* and *Ehrlichia ruminantium* to cattle (Voigt *et al.*, 1993).

For a number of reasons, use of an artificial membrane rather than animal skin is desirable, but success with such membranes is easier to achieve for ticks with long mouth parts than for ticks with short ones, such as *R. appendiculatus* (Young *et al.*, 1996a). Nevertheless, in 1995, successful feeding of nymphal *R. appendiculatus* on an artificial membrane was described. When the system was used to feed nymphal ticks on blood infected with *T. parva* piroplasms, the prevalence of infection was high and comparable with results achieved with ticks feeding on blood donor cattle (Waladde *et al.*, 1995). The status of such feeding systems was reviewed (Waladde *et al.*, 1996; Young *et al.*, 1996a).

Genomics and molecular biology

By the middle of the first decade of the 21st century, the biological revolution precipitated by full-genome sequencing of many organisms was well under way. Just as important as the genome sequences themselves were the new experimental approaches and techniques that evolved, drawing on the enormous quantities of new information. For ticks, the start was slower than for many other organisms, including a variety of other parasites and disease organisms. The lower priority attached to veterinary diseases, particularly of developing economies, and the smaller size of the research community were probably two reasons for this. More significant, however, was the sheer size of the tick genomes. Depending on species, size estimates varied from one-third that of the human genome to more than twice the size. The first full tick genome sequencing project to be launched was for one of the

smaller genomes, that of the North American tick, *Ixodes scapularis* (Hill and Wikel, 2005), which was of only indirect relevance to African issues. By 2016, this first tick genome had been thoroughly explored and now undoubtedly represents an important resource for ongoing research into all tick species (Gulia-Nuss *et al.*, 2016). By 2006, high in the priority list for tick genomes was *R.* (*Boophilus*) *microplus* because of its economic importance. In this case, the size of the genome, considerably larger than the human genome, was daunting (Ullmann *et al.*, 2005; Guerrero *et al.*, 2006). Nevertheless, by 2010, considerable advances had been made in assembling sections of the genome. In this international effort, ILRI's scientists played a valuable part (Guerrero *et al.*, 2010).

In the specific area of genome sequencing, African tick species lagged behind. Nevertheless, large quantities of interesting sequence data for African species were being accumulated. The focus usually was on the salivary gland, a logical choice. The pharmacologically and physiologically active factors necessary for maintaining the tick's attachment site pass through the salivary gland. The salivary gland is also the route of transmission of tick-transmitted diseases as well as often being a site for their development. In 2002, a complementary DNA (cDNA) library was generated from the salivary gland of feeding *A. variegatum* females. Sequencing of random clones from the library gave more than 2000 non-redundant sequences, 39% of which could be tentatively identified with known proteins based on sequence similarities. Abundant families of cement proteins, anti-haemostatics and also possible anti-inflammatories were identified, all proteins expected to be important to the success of tick feeding (Nene *et al.*, 2002).

Somewhat more targeted approaches were adopted in two subsequent studies. In 2004, cDNA libraries were prepared from the salivary glands of *R. appendiculatus* infected with *T. parva* and from uninfected salivary glands. Over 9000 sequences were collected from each sample, with the intention of identifying genes specifically up- or downregulated as a result of the *T. parva* infection. No major differences between the abundantly expressed genes in the two samples were found, although the sequences themselves represent a repository of useful information (Nene *et al.*, 2004).

Secreted proteins are often identified by a signal sequence, a relatively short peptide sequence necessary for their export from cells. A novel method using a 'signal sequence trap' was used to identify possible secreted proteins from both *R. appendiculatus* and *A. variegatum*. Given the already extensive databases of known proteins existing in 2005, it was interesting that of 61 *R. appendiculatus* sequences, only 15 could be tentatively identified. For *A. variegatum*, the proportion was just one out of seven (Lambson *et al.*, 2005). This underlines, if such emphasis was needed, the paucity of fundamental information about tick genes and proteins.

The reason for the sheer size of the tick genomes continues to be of interest. A recent ILRI shed some light on this question. Relatively small segments of high-molecular-weight DNA from *R. appendiculatus* were shown to have large numbers of degenerate transposable elements. By extrapolation, the authors suggested that there could be about 65,000 copies of a single family of these repetitive elements; in basic terms, this means that the size of the tick genomes could be, in part, due to the accumulation of such elements of unknown (if any) function over evolutionary time spans (Sunter *et al.*, 2008).

A recent and rather different 'molecular' study offers a new solution to an old problem. This chapter has already described historical changes in tick distribution that affect the occurrence of tick-borne disease. These are not isolated instances. Rather, the speed, scale and potential impact of such changes in tick distribution appear to have increased, while climate change, animal movements, trade and the multiplicity of associated factors will probably ensure that such changes continue.

Coping with changes in tick distributions demands reliable knowledge of the identity and distribution of ticks. This requires the collection of large numbers of ticks across broad areas and then the accurate identification of species. This has previously been done either morphologically or using DNA-based analysis or a combination of both. The former requires a trained scientist to distinguish closely related species. DNA-based methods tend to demand expensive equipment and reagents, time and expertise. Rothen *et al.* (2016) described an alternative, the use of matrix-assisted laser desorption/ionization (MALDI-TOF) mass spectrometry. The essential piece of scientific equipment needed for such analyses is complex and expensive, while the skill needed to operate it is considerable. The intuitive response to the idea of using MALDI-TOF to identify ticks could well be that the idea is scientifically interesting but impractical. However, preparation of samples for MALDI-TOF analysis is simple and cheap, the instruments are high throughput and analyses are commonly carried out in a specialized, central facility (in the case of this study in Japan). These factors together have the potential to change the feasibility of using this technology. As reported, a collection of 398 African ticks of the genera *Rhipicephalus*, *Rhipicephalus* (*Boophilus*), *Hyalomma* and *Amblyomma*, in total ten species, were identified morphologically and by cytochrome C oxidase DNA sequencing. Of these, 48 individual ticks were then used to construct a reference database of mass spectra. Subsequently, the remaining ticks were identified by mass spectrometry using this database. Overall, a sensitivity of 96.1% and a specificity of 99.7% were achieved. The potential usefulness of this methodology for field surveys is considerable.

Application of Research Capacity

Ticks as vectors, with a focus on *R. appendiculatus* as the vector of *T. parva*

Ticks and their biology are inextricably linked with the epidemiology, impact and control of tick-borne diseases. The special complex of *R. appendiculatus* and *T. parva* (i.e. ECF) has been central to ILRI's animal health research from the institute's beginning.

ECF is the subject of a major chapter in this book (Chapter 6). Given that, this section will deal only with a few specific questions where the dominant research issue concerned the biology of the tick vector rather than that of *T. parva*. Some aspects have been described already. Disease epidemiology depends on knowledge of the incidence and distribution of the tick vectors; ECF control in most areas relies heavily on tick control via the use of acaricides. ILRI's contributions to both these areas have been discussed.

A major practical achievement by ILRI has been its contribution to the development of an infection-and-treatment method (ITM) vaccine for ECF. The ability to produce such a vaccine depends on quality-controlled tick colonies and the technical ability to perform all stages of vaccine production (Patel *et al.*, 2016). ILRI remains a resource of knowledge and hands-on expertise for this vaccine production.

As with many other vector-borne diseases, in the case of ECF, the tick is not merely a biological syringe. Rather, it is the site of complex developmental changes in the *T. parva* organism involving a range of specific and poorly understood interactions between the two species. A number of papers in the early- to mid-1980s addressed various aspects of the tick–*T. parva* interaction. Some were practical. Irvin *et al.* (1981) established a rapid method for staining salivary glands of *R. appendiculatus* infected with *T. parva*, and then used it to follow the dynamics of infection and parasite maturation. Later, a method of transplanting *T. parva* kinetes to establish infection in a single tick salivary gland acinus was described, a method that the authors suggested could be applied to the development of cloned parasites (Fujisaki *et al.*, 1988). Other research was more fundamental. The site of *T. parva* developmental changes, the type III acinus in the tick salivary gland, was first examined (Fawcett *et al.*, 1981) before the ultrastructure of the sporogony of the parasite in the salivary gland was investigated (Fawcett *et al.*, 1982). Then, in 1993, it was shown that both a crude extract of tick salivary gland and interleukin-2 as a single, pure cytokine could enhance the susceptibility of bovine lymphocytes to infection by *T. parva* sporozoites (Shaw *et al.*, 1993). In a general sense, this ability of salivary gland material from the tick vector to facilitate infection was subsequently rediscovered for a number of tick-transmitted viral diseases (Nuttall *et al.*, 2008).

The fact that vector competence of *R. appendiculatus* varies with tick isolate and that these differences are heritable has been examined several times. In 1995, estimates of heritability were obtained for *T. parva* infecting two tick stocks, Kiambu and Muguga (Young *et al.*, 1995), and the point was made that the heritabilities were high enough to allow selection of tick strains for high and low susceptibility to infection. This was, in fact, done, as noted in the discussion of the tick stocks of the ILRI Tick Unit. Subsequently, the competence of seven different stocks of *R. appendiculatus* and *R. zambeziensis* as vectors of two different stocks of *T. parva* was examined (Ochanda *et al.*, 1998). Reproducible differences were found.

In a slightly earlier paper with significance for ECF epidemiology, the transmission of *T. parva* by nymphal and adult *R. appendiculatus* was examined using two isolates of *T. parva*. With both, infection levels were much higher in adult than nymphal ticks, a contributory factor being the large difference in the number of requisite structures, type III acini, in the salivary glands of the different tick instars (Ochanda *et al.*, 1996). The authors suggested that transmission by nymphal ticks, representing a lower challenge dose of *T. parva*, might cause milder infections and lead to immunity in the cattle host rather than death, a factor in the establishment of endemic stability. Field evidence from Zimbabwe was consistent with this hypothesis.

Then, in 2009, there was a re-examination of the differences between ticks using the same Muguga and Kiambu isolates, although this time the differences were examined by the modern techniques of quantitative and nested polymerase chain reaction (PCR) (Odongo *et al.*, 2009). These techniques were shown to be more sensitive than traditional microscopy, and it was confirmed that, for the Kiambu isolate, a higher proportion of ticks became infected and parasite numbers within adult salivary glands were also higher. It is interesting that these differences between tick isolates persisted through an additional 20 years of continuous tick culture. These observations would make possible the examination at the level of gene expression of factors that might explain the differences in *T. parva* susceptibility.

Finally, an older paper exemplifies the use that can be made of large databases in understanding disease. Much information had been recorded on the transmission of the Muguga stabilate of *T. parva* to Boran cattle using two isolates of *R. appendiculatus*. Between 1986 and 1991, 1241 records of tick batches harvested from 286 infected cattle had been compiled, from which a total of 812 records were selected as suitable for analysis. This database was interrogated using statistical modelling procedures searching for relationships between a long list of

factors and the prevalence, abundance and intensity of salivary gland infection in both female and male ticks (Young *et al.*, 1996b). Twenty-four factors or interactions were found to be statistically significant. Some factors might have been intuitively expected; others were more unexpected. Consistently among the most important factors, however, were the piroplasm levels on the day of harvesting ticks and the month in which the ticks were harvested. The latter finding is surprising, although a tentative correlation between time of nymphal engorgement and the climatic conditions (temperature and humidity) at the time was noted. The final models were complex and with significant error margins, with the consequence that they had limited predictive value. There does not appear to have been subsequent follow-up using this statistical approach.

The genetic complexity of *R. appendiculatus*

As described above, it had long been known that strains of *R. appendiculatus* had various capacities to act as vectors of ECF and that this capacity was heritable. This raises the question of the genetic complexity of this tick species and the extent to which it relates, for example, to geographical distribution.

Kanduma *et al.* (2012) utilized the database of expressed genes coding for salivary gland proteins developed by Nene *et al.* (2004) to identify 29 polymorphic markers. These they then used to discriminate among populations of *R. appendiculatus* and among *R. appendiculatus* and four other *Rhipicephalus* spp. using ten field populations and ten laboratory stocks (Kanduma *et al.*, 2012). Distinguishing *R. zambeziensis* from *R. appendiculatus* was difficult, although the other species were satisfactorily separated. Within *R. appendiculatus*, clustering into two populations occurred, which did not, however, correlate with a field/laboratory culture division. The authors proposed two preferred sets of markers, one optimal for distinguishing between species and the second for intraspecies comparisons.

Subsequently, the question of genetic diversity in *R. appendiculatus* populations was addressed again, this time using two mitochondrial genes,

12S ribosomal RNA and cytochrome C oxidase subunit 1, as well as a third gene that, ultimately, was not informative. Analysis of sequence variation in these genes in ticks sampled from different geographical locations, from different hosts and from laboratory and field isolates (the three chief variables examined) identified 28 haplotypes clustering into two haplogroups. These groups could not be defined by geographical origin, host species or the laboratory/field divide. Based on these observations, the authors suggested that two major genetic groups of *R. appendiculatus* existed in Kenya, with possible broader distribution in eastern and southern Africa. It was considered possible that the existence of two genetic groups could have had implications for the spread of the tick and for the transmission dynamics of ECF (Kanduma *et al.*, 2016a).

The authors returned to the issue in a second publication in the same year (Kanduma *et al.*, 2016b). Ticks from ten locations in Kenya were collected, associated with three grazing systems: cattle, cattle and wildlife co-grazing, and wildlife without livestock. Numerous individual ticks from ten closed laboratory colonies plus ticks of five other *Rhipicephalus* species were included in the analysis. On this occasion, the conclusions appeared to be somewhat different. There was a low degree of genetic differentiation in the field samples, and no relationship, as before, between the genetic diversity and either geographical location or host species. The ten laboratory strains, as well as the other species, were strongly differentiated. In addition, some of the laboratory strains were differentiated from current field samples taken from the same geographical point of origin as the original laboratory strain. The key conclusion, in terms of disease transmission and control, was that there was in fact little genetic diversity in the *R. appendiculatus* populations, perhaps as a result of livestock and wildlife movements through the country. This conclusion can also be compared with the results of analysis of the diversity of protein sequences in a single protein, Ra86, which will be discussed in the following section on vaccines. Even more recently, an array of gene markers was used to look at the broader phylogeny of *Rhipicephalus* and *R.* (*Boophilus*) species, with the results demonstrating once again that much remains to be resolved (Kanduma *et al.*, 2019).

Tick vaccines

There has been occasional interest in the development of tick vaccines since the early days of ILRAD, although initially this was as a minor contributor to antigen discovery research initiated elsewhere. Certainly, this was the case with an anti-tick vaccine effort driven by the International Centre of Insect Physiology and Ecology (ICIPE) in Nairobi (Mongi *et al.*, 1986).

From the late 1990s onwards, there was a more consistent interest in the field. Three factors account for this. First, as had long been the case for all parasite vaccines, the ability to express recombinant proteins offered at least a potential pathway to practical application of antigen discovery programmes. This was as true of ticks as it was of ECF. Second, the steady accumulation of tick genomic information, referred to previously, was a useful source of novel information. Third, in 1988 and 1989, an Australian group patented an antigen from the tick *R.* (*Boophilus*) *microplus* that, when expressed as a recombinant protein in a commercially viable way, gave useful protection against field infestations of ticks. Soon two commercial vaccine developments were under way, one in Australia and the second in Cuba, leading to the release in the early 1990s of two vaccines, TickGARD and GAVAC (Willadsen, 2004).

There were several aspects to ILRI's response. The Australian work gave a stimulus to antigen discovery in a number of laboratories and countries. ILRI collaborated, although as a minor partner, in the evaluation of several antigens, for example, work on the recombinant p29 antigen from *Haemaphysalis longicornis* (Mulenga *et al.*, 1999) and other work that remains unpublished. ILRI has also engaged in *de novo* antigen discovery. An early effort led to the identification of a cement protein, RIM36, from *R. appendiculatus* (Bishop *et al.*, 2002). This was shown to be the target of a strong antibody response by cattle naturally exposed to the tick but, apparently, was of little use as a protective antigen. ILRI has contributed to ongoing, basic research on tick proteins (Costa *et al.*, 2017; Seixas *et al.*, 2018), some of which had no obvious connection to vaccine research. Recently and more encouragingly, it was shown that recombinant glutathione *S*-transferase from *H. longicornis* induced 67% protection against *R. appendiculatus*, although it was ineffective against *Rhipicephalus sanguineus* (Sabadin *et al.*, 2017). This is not only positive news for control of the tick of greatest interest to ILRI but also another example of the unpredictability of cross-immunity among tick species, something explored in greater detail by ILRI and other laboratories with respect to the Bm86 antigen.

Rather more effort went into exploring the potential of Bm86 homologues in the control of endemic African tick species. This was (and remains) a tantalizing scientific and practical issue. It was shown early on that the sequence of the Bm86 molecule was quite strongly conserved across tick genera and species, although with variation (Willadsen, 2004). Even within isolates of *R.* (*Boophilus*) *microplus* itself, sequence differences of up to about 5% have been reported. Sequence differences did not, however, translate into differences in protection against tick infestation in any predictable way. The most striking example was *Rhipicephalus* (*Boophilus*) *annulatus*, a species closely related to *R.* (*Boophilus*) *microplus*. Vaccination with recombinant Bm86 typically gave 80–90% protection against *R.* (*Boophilus*) *microplus* on cattle, but effectively total protection against *R.* (*Boophilus*) *annulatus*, protection that was also sustained for a longer period. The reason is still unclear. Practically, however, the obvious question was: what is the protection of Bm86 against *R.* (*Boophilus*) *decoloratus* or *R. appendiculatus*?

First, it was shown by Odongo *et al.* (2007) that antisera to Bm86 reacted with the *R.* (*Boophilus*) *decoloratus* tick gut, the location of the antigen in *R.* (*Boophilus*) *microplus*, and that *R.* (*Boophilus*) *decoloratus* feeding on vaccinated cattle showed vaccination effects similar to those recorded for *R.* (*Boophilus*) *microplus* on TickGARD-vaccinated cattle: reduced tick numbers and reduced overall fertility, measured as total egg production, reductions of 46 and 61%, respectively. Although less than the effects seen with *R.* (*Boophilus*) *microplus*, these results were certainly encouraging. The presence of two variants of Bm86 was shown, Bd86-1 and Bd86-2, with amino acid sequences that were 86% and 85% identical to the original Bm86. Recombinant Bd86-1 reacted strongly with antisera from TickGARD-vaccinated cattle. Two linear peptide epitopes shared between the Bd86 molecules and Bm86 were identified that, it was suggested, could be the basis of a peptide-based vaccine.

Unfortunately, the Bm86 vaccine had no effect on feeding *R. appendiculatus*. The obvious question was whether a sequence difference between the Bm86 antigen used for the vaccination trials and the homologues in *R. appendiculatus*, named Ra86, was sufficient to explain the lack of protection against that tick species. One problem was the presence of at least two variants of Ra86, which themselves showed only 80% amino acid sequence identity, exceptionally divergent for the 'same' protein (Kamau *et al.*, 2011). Evidence was obtained that both variants could be present in a single genome but that when both were present, one of the two would be transcriptionally dominant.

Further research showed the situation to be even more complex. Nineteen Ra86 sequences were obtained from the laboratory Muguga strain of *R. appendiculatus*, defining two alleles differentiated by insertions or deletions (indels) and different in length by 39 amino acids. Then a further 20 sequences of Ra86 were obtained from each of four field sites in central and western Kenya, revealing a further three different size types, differentiated by 39–49 amino acid indels and hence a total of five indel-defined genotypes. The longest sequence was found only in the laboratory strain. Analysis clustered all Ra86 sequences and Bm86 into four major clades based on amino acid substitutions. Although there was evidence that selection contributed to the sequence variation, there was no evidence that the groupings correlated with geographical separation of tick populations (Kamau *et al.*, 2016).

With such diversity – which has not been reported in *R. (Boophilus) microplus* in Australia or Central and South America – is the idea of vaccination using a Bm86 homologue impractical? Olds *et al.* (2012) vaccinated cattle with a mixture of two recombinant forms of Ra86 and challenged them with Muguga strain ticks. There was no significant effect on adult mortality, engorgement weight or weight of eggs laid, although there was an interesting decrease in egg hatching, which grew more pronounced in late-laid eggs. There was a slight but statistically significant decrease in moulting of nymphs to adults. These figures, incorporated into a tick population model, showed the potential for a useful, although extremely gradual, decline in tick numbers. There was also a slight decline in the infection levels of ticks fed on *T. parva*-infected cattle vaccinated with Ra86 compared with non-Ra86-vaccinated controls. Clearly, a more efficacious vaccine would be necessary, as such a vaccine, even if theoretically useful, would be unattractive to farmers.

A recent study examined the potential of an antigen cocktail to give protection against tick infestation and/or *T. parva* transmission (Olds *et al.*, 2016). The cocktail used antigens selected from the literature: the tick antigens chosen were subolesin, TRP64 (the cement protein from *R. appendiculatus*) and three tick histamine-binding proteins, while from *T. parva*, the sporozoite antigen p67C was selected. All of these antigens had separately shown promise in vaccination trials, although the tick species, host and challenge model all varied. In this trial, cattle were vaccinated, produced good antibody responses and were challenged with the normal Muguga isolate of *R. appendiculatus* and the Muguga 'lowline' ticks that had been infected with *T. parva*. No significant effects on either tick engorgement and fertility or disease transmission were found. There were, however, some differences in the susceptibility of the two isolates of tick used, emphasizing the potential importance of isolate variation in the field. The authors stressed the desirability, in future work, of early assessment of any tick antigen in the natural tick–host relationship.

Another aspect of this deserves to be noted. The idea of antigen cocktails as a means to improve the efficacy of vaccines is frequently touted, not only for tick vaccines but for many other anti-parasite vaccines as well, to the extent that it has become an important but poorly acknowledged rationale for much antigen research. The concept is experimentally testable, but reports of tests are scarce and those of success even scarcer (Willadsen, 2008). The fact that ILRI carried out such a test, and reported failure, is a worthwhile contribution.

The tantalizing dream of tick vaccine research is a vaccine that protects against multiple species. The partial cross-protection induced by Bm86, despite the variability of protection across species, seemed to offer some hope. This was explored further in a study that used a peptide from Bd86 to raise monoclonal antibodies that were found to cross-react with *R. (Boophilus) microplus*, *R. (Boophilus) decoloratus*, *R. appendiculatus* and

Hyalomma anatolicum anatolicum (Kopp *et al.*, 2009). The degree to which such cross-reactivity translates into protection is unknown.

Recent Developments

As the 21st century progressed, ILRI's interest in ticks, with the exception of molecular approaches to tick biology and vaccine development, appeared to decline. The result was that pointers to the future, when they came, were from other institutions and scientists. Three issues emerged: the impact of climate change, the spread of *R. (Boophilus) microplus* through East and southern Africa and its accidental introduction into West Africa, and finally the evidence of significant acaricide resistance in African tick species.

Today, any discussion of the future of disease control is likely to begin with the anticipated impacts of climate change. The idea, supported by a growing body of evidence, that shifts in vector populations will greatly change the epidemiology of many diseases has been well explored. Changes to tick distributions and hence, for example, to ECF are expected (Grace *et al.*, 2015).

ILRI had earlier played a role in understanding the dynamic nature of ticks and tick-borne disease. The strongest indication that this would be an ongoing if not escalating problem came from *R. (Boophilus) microplus*. In contrast to other tropical and subtropical parts of the world including Australia, Central and South America and large parts of south and eastern Asia, Africa was until recently fortunate in being spared any major impact from this tick species. The situation has changed over the last two decades. From small populations in eastern South Africa (Natal), the tick has spread through much of South Africa, displacing endemic *R. (Boophilus) decoloratus* (Tønnesen *et al.*, 2004). In Tanzania, tick surveys conducted between 1998 and 2001 were compared with historical (40-year-old) data, with the results showing that, while *R. (Boophilus) decoloratus* had largely retreated to high-altitude areas in northern and central Tanzania, *R. (Boophilus) microplus* had invaded all but the driest and coldest parts of the country (Lynen *et al.*, 2008). This seemed not to have happened by 2007 in Rwanda (Bazarusanga *et al.*, 2007).

In a review published in 2006, Estrada-Pena *et al.* (2006) identified only limited confirmed records of *R. (Boophilus) microplus* in Africa, all in the south-east. West Africa was still considered free of the tick. Then, in 2007, its discovery was reported in Ivory Coast as a result of an accidental introduction (Madder *et al.*, 2007). A second independent introduction was found to have occurred in Benin in about 2005. Since then, it has continued to spread (Madder *et al.*, 2011, 2012; de Clercq *et al.*, 2012), apparently displacing other *Boophilus* spp. as it invades. The tick has now spread throughout Ivory Coast and far into the north of Benin. In November 2012, *R. (Boophilus) microplus* was discovered as intense field infestations in south-western Burkina Faso and Mali (Adakal *et al.*, 2013). It continues to spread within Burkina Faso. Its spread has been accompanied by decreased milk production, uncontrolled tick populations, inappropriate acaricide use and cattle deaths (Madder *et al.*, 2011; Adakal *et al.*, 2013).

Surveys in Cameroon in 2013 at a number of sites, involving the identification of 20,000 ticks, showed that *R. (Boophilus) microplus* seemed not to have reached that country. However, there appeared then to be no ecological reason why it would not eventually (and probably rapidly) spread through much of West Africa, south of the Sahel (de Clercq *et al.*, 2013, 2015)[1]. This expectation has regrettably been confirmed. Recent evidence, which has involved several ILRI scientists, has shown that the species is now present in large numbers throughout much of Cameroon, apparently displacing *R. (Boophilus) decoloratus* as it spreads (Silatsa *et al.*, 2019a,b).

In more detail, *R. (Boophilus) microplus* has become the dominant tick species on cattle in south-western Burkina Faso and southern Benin. A full year survey at three sites in Benin and three in Burkina Faso showed that the abundance of *R. (Boophilus) microplus* was over 50% of all ticks collected of all species at five of the six sites. When tick counts were averaged over the full year, the daily numbers of *R. (Boophilus) microplus* collected were Gogounou (38), Ouangolodougou (113), Farnifaso (164), Okpara (249), Kpinnou (465) and Kimini (710). At Gogounou, in the northern part of Benin, *A. variegatum* was the most abundant species at 26% of the total count, although the relative abundance of *R. (Boophilus) microplus* was almost identical at 25%, suggesting that *R. (Boophilus) microplus*

is continuing to expand its range towards drier areas. Ongoing spread along the tropical, wetter near-coastal regions is, of course, almost certain to occur.

No scientific studies have as yet been carried out to measure the impact of such tick numbers on local cattle. However, based on Australian experience, the blood loss from a daily tick count of 100 or above would have significant effects on productivity, and the higher numbers could easily result in mortality, particularly at times of nutritional stress. Anecdotal evidence from farmers confirms this expectation.

The next evolving problem is that of the spread of acaricide resistance. In work led from Obihiro University of Agriculture and Veterinary Medicine in Hokkaido, Japan, and involving a number of collaborating institutions in Uganda, ticks were collected from 30 farms across Uganda, all having a history of acaricide failure (Vudriko *et al.*, 2016). Such reported failures can be due to acaricide resistance, as is usually assumed, but other factors are commonly part of the explanation. The major tick species were *R. appendiculatus* and *R.* (*Boophilus*) *decoloratus*. Acaricide resistance assays showed that 90% of the samples were resistant to synthetic pyrethroids and 60% of the total were highly resistant, i.e. the acaricides had effectively no lethal activity. Resistance was high against a combined organophosphate/synthetic pyrethroid product and was significant against organophosphates and amitraz. Resistance to multiple acaricides was detected in about half of the samples. Over a 2-year period, three-quarters of the farms had used two or more acaricides, and of these, over half had used chemical rotations that made no sense scientifically.

The work is significant for a number of reasons. Most obvious is the worryingly high frequency of resistance and the occurrence of multiple resistance to diverse chemical groups. Second, the study underlines the importance of incorrect acaricide usage and the frequency with which it happens. Third, there is the fact that resistance to acaricides was found in over 40% of the *R. appendiculatus* samples. It was once a common speculation that resistance would evolve slowly, if at all, on multi-host ticks compared with the single-host *Boophilus* spp., with the alternative hosts perhaps providing a chemical-free refuge.

Clearly, under the conditions of cattle farming in Uganda, this has not been the case.

The Future

Given the diversity of tick-related problems, where might ILRI best make its future research contributions? Its greatest competitive advantage over most other research providers is the close juxtaposition of facilities for large-animal experimentation and parasite culture with laboratories capable of advanced molecular research. This is more than a huge experimental advantage. In a more indefinable but still important way, it brings together the molecular scientist and the livestock target of the scientist's research. This juxtaposition could be utilized in many ways, but three examples suffice. First, as is clear throughout this chapter, current tick and tick-borne disease control depends heavily on synthetic acaricides. Resistance to these is an increasing problem. No effective resistance management strategy can be developed until resistance can be rapidly and accurately diagnosed, which itself presupposes an understanding of resistance mechanisms. Current methods of diagnosis have not changed significantly in decades, are often slow and are too frequently inaccurate. To do better is a challenging research problem.

The second area where the close association of scientist/laboratory/experimental animal is beneficial is in vaccine research. This is as true of anti-tick vaccines as it is of ECF vaccines. Interest in this approach to tick control for African ticks is developing. Despite ILRI's worthwhile contributions to this area, the institute has always lacked a tick vaccine programme. As described above, the wealth of genomic information and associated experimental techniques together offer abundant new opportunities and approaches (de la Fuente *et al.*, 2016). If the promise of these is yet to be convincingly realized, it is undoubtedly true that the combination of new science, traditional biology and large-animal evaluation is a powerful combination that ILRI is well placed to exploit.

A third possibility is the investigation of the genetics of within-breed and between-breed variation in the ability of livestock, especially

cattle, to become resistant to ticks. This has been a major component of the management of *R.* (*Boophilus*) *microplus* both in Australia and South America. In the African context, questions of fundamental scientific interest and practical importance are unanswered. For example, to what degree are indigenous cattle resistant to ticks? Are there between-animal differences in heritability high enough to be useful? To what degree is the acquisition of resistance effective against multiple tick species? ILRI possesses the scientific skills, the biological resources and, importantly, the infrastructure and field stations to address such questions.

Each of these options would be about developing technologies, at best partial solutions to practical problems. As has been described above, a robust solution to the control of ticks and tick-borne disease requires an understanding of tick distributions and economic impacts; the current and future effects of climate change; and the regulatory system and the production environment in which tick control is to be applied. ILRI has skills in all of these areas and a strong focus on at least one target group, the smallholder livestock farmer. Thus, ILRI has, in principle, not only the potential to develop new technologies but also the infrastructure and experience to facilitate their effective adoption.

Acknowledgement

Note

[1] The TickRisk project, led by Maxime Madder and Eva De Clercq and based largely in Benin, and the WecatiC project, led by Hassane Adakal, have provided the above data, mostly collected during 2012–2013.

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Preface to Part II:
Research Spending and Publications on Primary Production

This preface first shows the estimated spending in the principal fields corresponding to the four chapters in the domain of primary production– rangeland ecology, forage diversity, planted forages and multidimensional crops.

The preface then presents 'scientific impact' as a function of International Livestock Centre for Africa (ILCA)/International Laboratory for Research on Animal Diseases (ILRAD)/International Livestock Research Institute (ILRI) publications and citations extracted from the Scopus and Google Scholar databases using search keywords relevant to the four fields, and software from Aria and Cuccurullo (2017).

Research Spending on Primary Production

Data from the financial and annual reports of ILCA, ILRAD and ILRI were used to compile a spending database for 1975–2018 (www.ilri. org/dataportal/impact/finance). Current spending for each year and institution was assigned to scientific domains using spending detail by project, by scientists' fields of expertise and, occasionally, from cost accounting by the institutions. Current annual spending in US$ was converted to constant annual spending in 2015 US$ using the global Manufacturers' Unit Value Index.

ILRI and one of its predecessors, ILCA, made comparatively modest investments in primary production investigations (Fig. PII.1)[1]. ILCA scientists (1974–1994) worked on primary production in four broad branches – rangeland production systems, forage diversity, planted forages and multidimensional crops. Subclasses such as the nutritional quality of feeds and farming practices related to plant productivity would have been included within 'rangeland production systems' or in 'planted forages'. This work incurred some US$26 million (in 2015 US$) in the 20 years of ILCA's existence, or 4.1% of the ILCA/ILRAD total of US$636 million. Spending at ILRAD on plant production from 1974 to 1994 was negligible. ILRI lifetime (1975–2018) spending on primary production was some US$111 million, or roughly 6.4% of the lifetime total.

Bibliometrics

About 280 papers were produced by ILCA in the four branches of the primary production domain. The mean number of citations per paper in that domain was 29 and the median was 12 during the ILCA era. The scientific return on primary production research was 11 papers and 309 citations per US$ million in the ILCA era.

The mean number of citations per paper was 22 and the median was ten during the lifetime of ILRI (1975–2018) in a sample of 1558 papers. The scientific return on lifetime (1975–2018)

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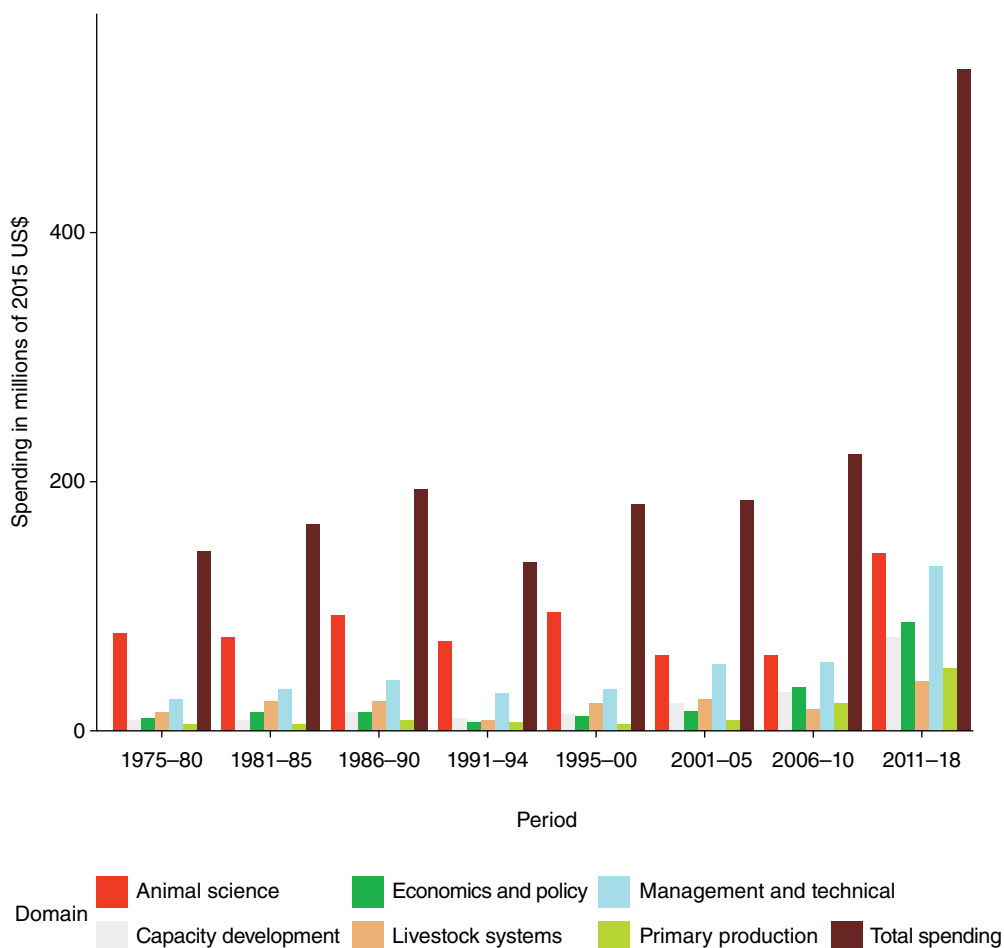
Fig. PII.1. Primary production research has been a small share of total ILRI spending, 1975–2018. (Data from ILCA/ILRAD/ILRI Annual Reports and Financial Reports.)

primary production work was 14 papers and 308 citations per US$ million of spending.

Rangeland Ecology

Published work by ILCA, ILRAD and ILRI on rangelands comprises the disparate domains of field investigations proper, such as those done in the 1970s and 1980s in Mali, Ethiopia and Kenya and later in Niger, and the landmark work in this century on mixed wildlife–livestock systems in Kenya and Tanzania. At the same time, much of the work on animals held by pastoralists, including studies of

bovine immunology, veterinary epidemiology and the interactions of wildlife with domestic livestock, is indirectly related to rangelands. The bibliometrics must therefore be interpreted carefully.

Using the Altmetric database, which covers social and academic media, ILRI has contributed some 1.3% of global research papers identified by the search terms 'grazing', 'rangelands', 'pasture' and 'grassland' (www.altmetric.com/; accessed 2 April 2020). The corresponding ILRI share of global Altmetric citations on those terms is less than 1.5%. The ILRI share of such papers in Africa, including North Africa, is 37%, with a similar fraction for citations.

The major papers on rangelands tend to be older, including the work of Sandford (1983) on pastoral development, King (1983) on water, Coppock (1994) on Borana in Ethiopia, Solomon Bekure *et al.* (1991) on Kajiado county in Kenya, and Reid and Ellis (1995) on South Turkana, Kenya. More recent work, such as Thornton *et al.* (2009), focuses on climate change, or wildlife–livestock management (Lamprey and Reid, 2004; Hobbs *et al.*, 2008). After the studies of the colonial era and the decades of the 1960s and 1970s, ILCA and ILRI research held a dominant position in rangelands work in both East and West Africa.

ILRI produced some 975 rangelands/grasslands papers over its lifetime (1975–2018), a mean number of citations per paper of 25 and a median of 11 (Fig. PII.2). An approximation of the importance of 'climate change' papers within the domain of rangelands is the finding of some 182 ILRI lifetime papers treating some aspect of climate change within rangelands research, with a mean number of citations per paper of 45 and a median of 14.

The recent burst of new research (as shown in Fig. PII.2) on the broadly defined field of 'rangelands' has occurred outside ILRI and is largely a function of studies of climate change as it affects, and is affected by, the use of global rangelands (see Chapter 16, this volume). Despite landmark work in this field by ILCA/ILRI scientists, the complexity and scale of African
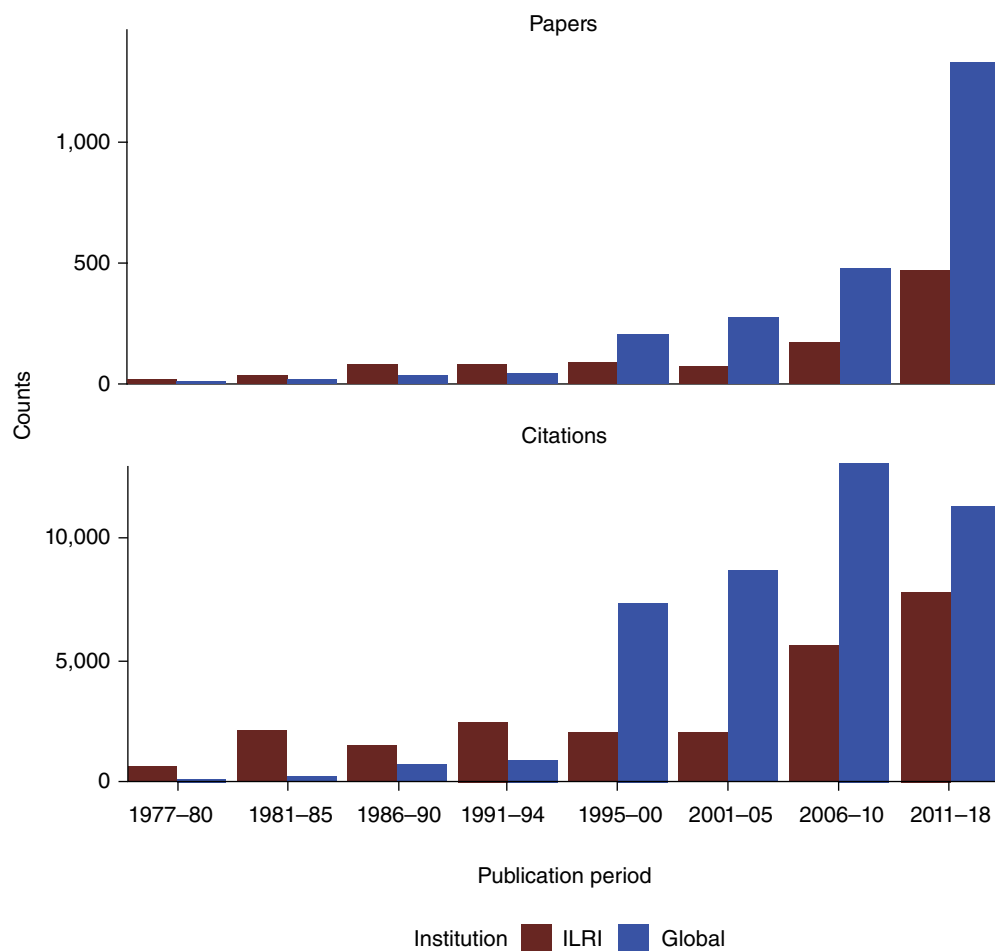
Fig. PII.2. ILRI work has been a large share of global publications on rangelands and related problems, 1977–2018. ILRI sample = 974 papers; global sample = 2,351. (Data from www.scopus.com/.)

rangeland problems, and their roles in global climate and livelihoods, are far greater than the limited resources spent on those problems by ILRI and its predecessors; the scarcity of research resources in this field will of course be made worse by the growing impact of climate change in arid areas.

Forage diversity and planted forages

Publications in the field of forage diversity are chiefly the work of the forage gene banks. As such, published work (Fig. PII.3) does not capture well the value of the forage gene banks, which is mainly held in the plant collections.

Because that value is better expressed by the distribution of materials, the scientific impact of the ILRI forage gene bank, developed, maintained and used in close collaboration with the gene banks of the International Center for Tropical Agriculture (CIAT) and the International Center for Agricultural Research in the Dry Areas (ICARDA) for more than 35 years, has been extensive (see Chapter 12, this volume), even though it cannot be monetized by commercial sales.

ILRI's publications record in planted forages has two parts. The first 'global' part is global and regional analyses of the roles of various resources, including planted forages, in livestock feed systems. The second 'experimental' part comprises plot and laboratory work on forage yields and forage characteristics, including feed
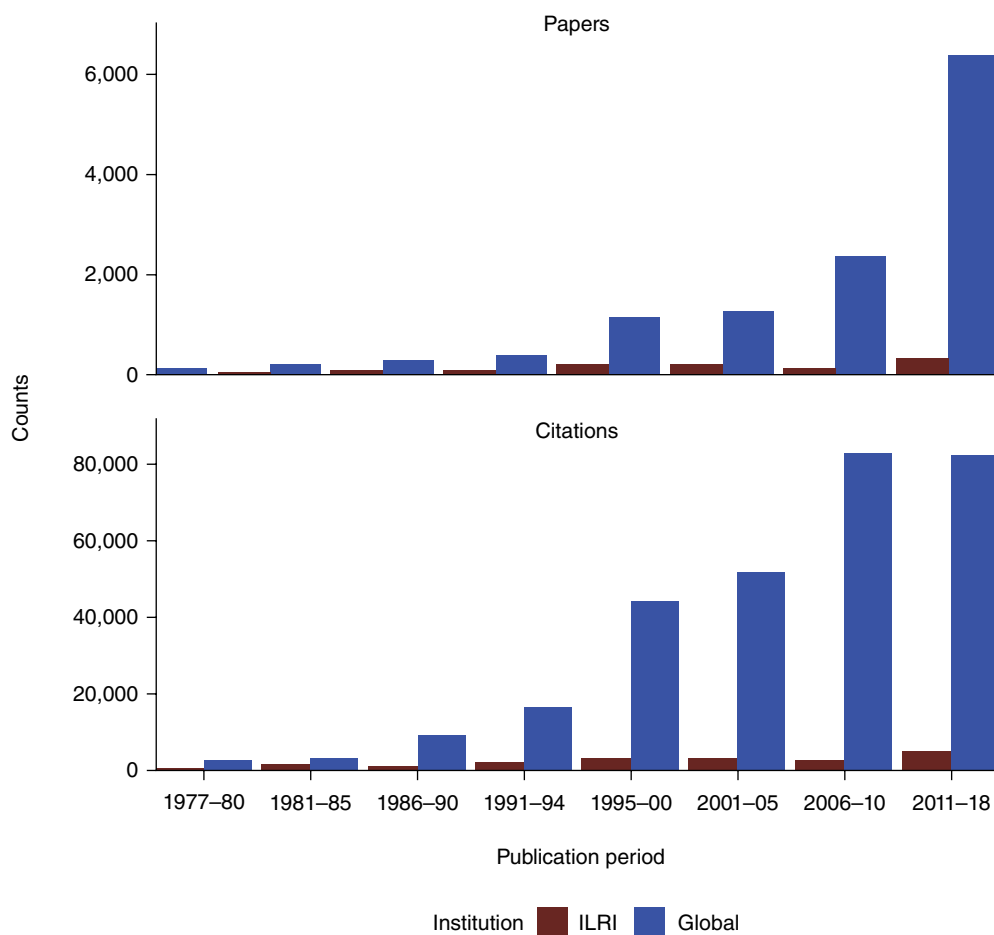
Fig. PII.3. ILRI work has been a small share of global publications on planted forages, 1977–2018. ILRI sample = 927 papers; global sample = 12,032. (Data from www.scopus.com/.)

digestibility. The 'experimental' part has become less important in ILRI's portfolio in this century and hence is less capable of supporting technology development in forages and in contributing to explanations of why introduced forages have not generally succeeded on smallholdings in the tropics.

ILRI's work in this area has become a smaller part of global work in this century. ILRI papers in forage diversity and planted forages were about 6.3% of global papers and about 5.6% of global citations in that domain over the period 1975–2018. One reason is that the boom in papers on plant biomass as an energy source has depressed ILRI's share of the global spread of work in all subfields related to primary production.

ILCA/ILRAD (1975–1994) produced about 163 papers with a mean of 33 citations per paper and a median of 11. Over its history, ILRI (1975–2018) produced about 928 papers in the broad domain of forage diversity and planted forages, with a mean of 21 citations per paper and a median of 9. ILRI produced about 8.3 papers per US$ million, generating about 174 citations per US$ million. In addition to the falling ILRI shares of total papers and total citations, mean citations per paper fell from 33 citations per paper in the period 1975–1994 (median of 11) to 21 (median of 9) over the lifetime period 1975–2018 at a time when mean citations per paper were growing in most fields.
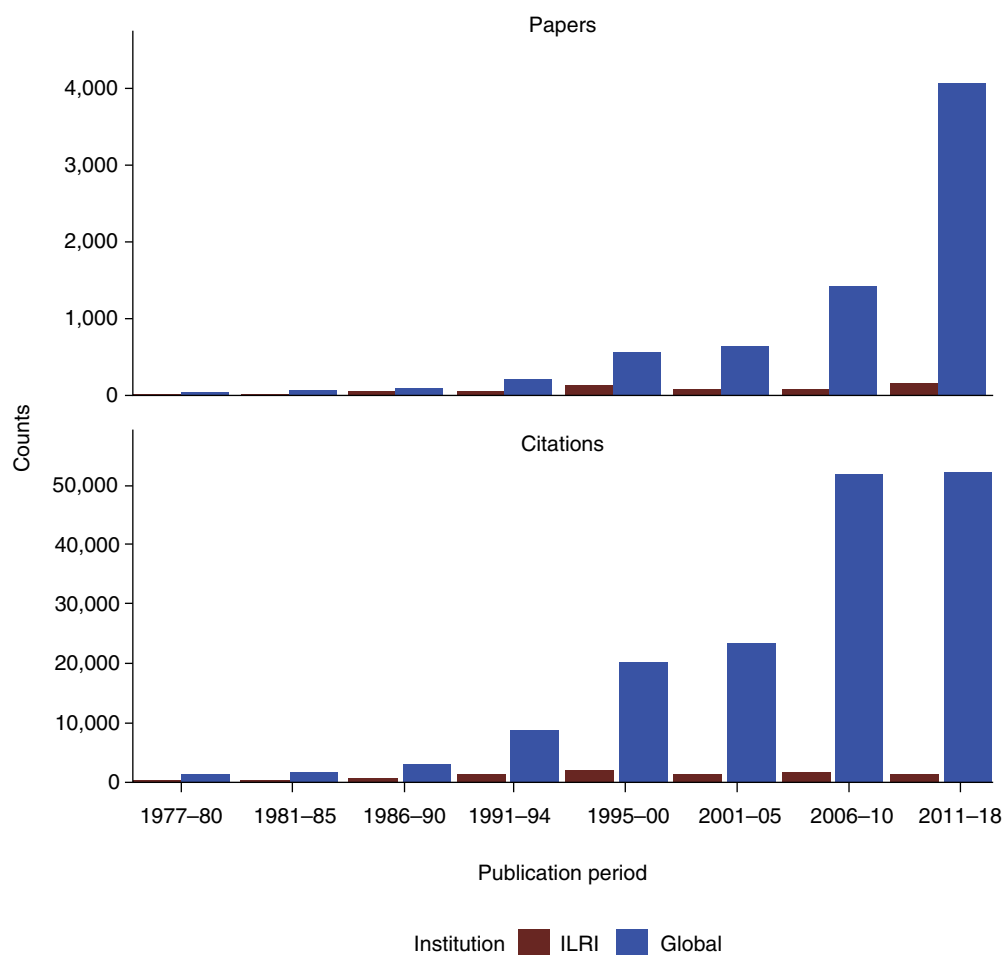
Fig. PII.4. ILRI has made niche contributions to multidimensional crops research, 1977–2018. ILRI sample = 506 papers; global sample = 7,105. (Data from www.scopus.com/.)

Multidimensional Crops

ILRI's published record in multidimensional crop research is substantial. Most of the relevant ILRI output in this field is due to the dedication of Ercole Zerbini and the late Michael Blümmel, who collaborated for many years with scientists of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in Hyderabad, India, on fodder improvement in pearl millet, sorghum, maize and grain legumes (Fig. PII.4). That work has created the empirical basis of a new model of multiple traits – food and fodder – in single crops for both grasses and legumes.

During the ILCA/ILRAD period, there were nearly 100 papers, with a mean number of citations per paper of 32 and a median of 10. There were approximately 506 papers with at least one ILRI author on some aspect of multidimensional crops published between 1975 and 2018. The long-term mean citations per paper in multidimensional crop research was 19 (median of 8).

Despite the accomplishments of ILRI research on multidimensional crops, the global importance of ILRI in that field has fallen over time. The ILCA shares of global papers and citations were 16% and 17%, respectively, from 1975 to 1994. The long-term ILRI shares
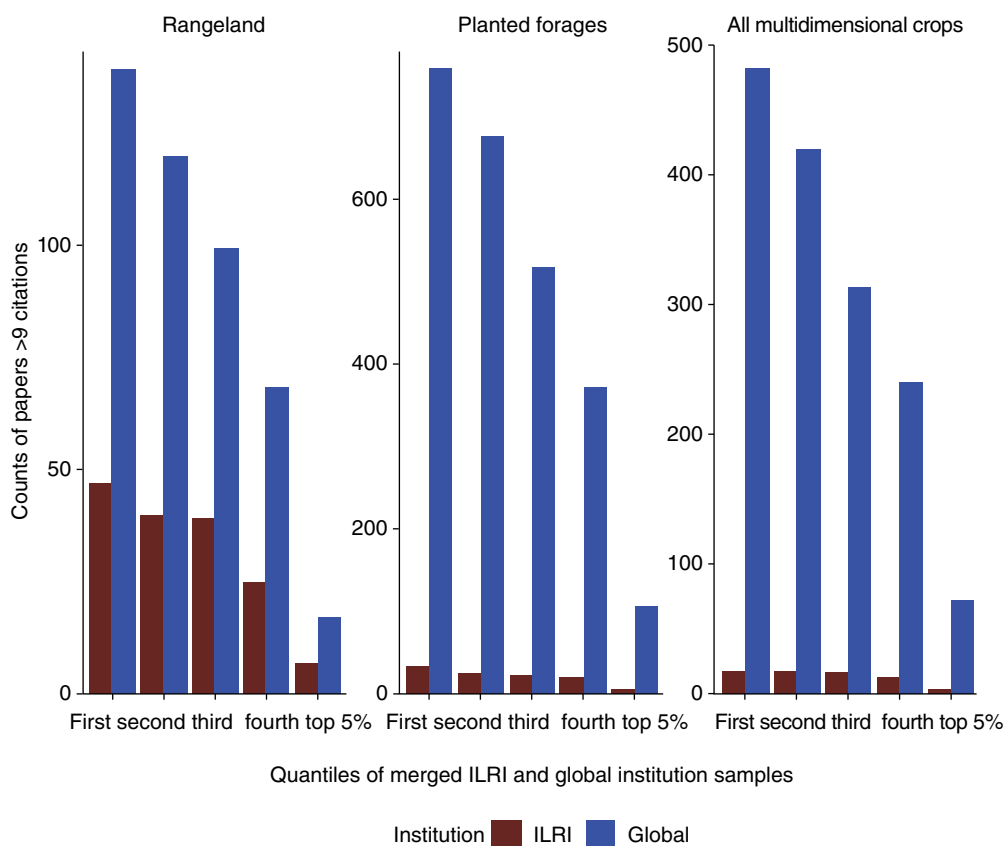
Fig. PII.5. Frequency of citations of ILRI and global institutions in primary production research by quantile, 1977–2018. Papers published from 1977 to 2018 with more than nine citations. ILRI (global) rangeland papers = 478 (1,045); ILRI (global) planted forage papers = 402 (6,021); ILRI (global) multidimensional papers = 230 (3,489). (Data from www.scopus.com/.)

(1975–2018) were 5.4% and 5.8%. The declining weight of ILRI papers in this field is due to the recent global boom of papers on the use of biomass, including cereal crop residues, for energy.

High citation papers

One measure of major ILRI scientific contributions is the share of ILRI papers in the top 5% of citations in a given field, compared with the share of all papers – ILRI plus global – in the top 5% (Fig. PII.5). This subset was limited to papers having at least ten citations. ILRI's global leadership in studies of extensive rangelands systems is evident on this metric. The ILRI share of all rangelands papers was about 32%; the ILRI share of papers in the top 5% of citations was about 40%. The corresponding shares of ILRI papers in planted forages and multidimensional crops were in the range of 5–7%.

Note

[1] Spending data from the International Center for Tropical Agriculture (CIAT) and the International Center for Agricultural Research in the Dry Areas (ICARDA) were not available.

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11 Rangeland Ecology

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Executive Summary

The problem

Sub-Saharan Africa rangelands are vital to the livestock economy of the subcontinent. They cover roughly 9 million km^2 or about 40% of the areas with potential for livestock production. The majority of African livestock – chiefly cattle, sheep, goats, camels and donkeys – live on rangelands at some point during the annual production cycles. Most of the range is managed by mobile groups who constitute perhaps one-fifth of poor livestock owners in sub-Saharan Africa. Grazing areas have limited vegetative production because of low and variable rainfall – they receive less than 600 mm annual rainfall – shallow and eroded soils, and inadequate forage due to reduction and fragmentation of the rangeland areas resulting from cropland and urban expansions. For all these reasons, it has been difficult to make sustained improvements in range productivity, even under controlled management, despite several decades of research and development interventions.

ILRI's role in the global context

The International Livestock Research Institute (ILRI) and its predecessor, the International Livestock Centre for Africa (ILCA, 1974–1994) have worked for more than 40 years on rangeland ecologies of sub-Saharan Africa. ILCA's rangelands research focused on the monomodal rainfall areas of the West African Sahel in Mali, the inner delta of the Niger River in Mali, Niger and Senegal. ILRI's historical sites in East Africa were the bimodal rainfall areas of Kenya and Ethiopia. A novel feature of ILRI research since the 1990s has been integrative studies on the rangelands of southern Kenya, in areas of intensive livestock–wildlife interactions in Amboseli National Park, Nairobi National Park, the Mara Reserve and the Serengeti in Tanzania (with collaborative tasks on rangeland management in southern Ethiopia/Borana region).

Impacts of ILRI's research

Scientific impacts

There were a number of scientific impacts of ILRI's range research:

- Integrated studies of domestic livestock, vegetation, water, crop and management interactions with original data from field conditions.
- Identification of determinants of plant and animal productivity under arid and semi-arid conditions.
- Definition of constraints to growth of pastoral systems.
- Development and refinement of research methods – for animal counts, techniques for vegetation surveys, participatory household surveys, application of remote sensing to African environments, and joining of biophysical process models to agent-based household models.
- Extension of range science methods and models to problems of climate change.
- Extension of range science methods to problems of interactions between wildlife and livestock.

- Elucidation of the economic and biological rationale of transhumant pastoralism.
- Refinement of estimates of greenhouse gas emissions from range components (animals, plants, soils, water and infrastructure).

Development impacts

The chief development impact of range science followed from the defence of the economic and biological rationale of extensive pastoralism. This defence, made on theoretical grounds following the emergence of density-independent models in the 1980s, and on empirical grounds following the ILCA/ILRI studies of pastoralism, has prevented bad policies (such as certain forms of group ranges and grazing reserves) from being imposed on pastoral groups. As it has done so, it has preserved pastoral livelihoods and limited rising inequality; an example of this scientific and development impact can be seen in the Kenyan Mara Community Conservation Planning Framework.

Introduction

This chapter summarizes the impact of research by ILRI[1] and collaborators on rangeland ecology in East and West Africa.

In East Africa, the research topics included identifying the drivers of rangeland vegetation, such as rainfall, animal density, bush and crop encroachment, and increased landscape fragmentation. A second group of topics was establishing the importance of wildlife–livestock interactions in Kenya and Tanzania, given the significant and diverse wildlife populations in those countries. This led to a process to foster innovations in conservation area management, better incorporating pastoral livestock production with wildlife. Simultaneously, modelling of coupled systems was ongoing to better capture multiple drivers of change in rangelands and examine both the impacts of landscape fragmentation and the growth of agriculture on livelihoods and ecosystem services. These results highlighted the need to view humans, cattle and wildlife as integrated components of ecosystems when making management decisions

In West Africa, ILCA research focused on comparative evaluations of pastoral and agropastoral systems in central Mali (Niono) and the inner delta of the Niger River (Macina) in the mid-1970s, which led to an understanding of seasonal vegetation growth under the influence of rainfall, flooding, grazing and cropping. The impact of the most severe drought in history that hit the Sahel in 1982–84 was assessed on the pastoral systems of the Gourma region in northern Mali in 1983 and was followed by a monitoring of the rangeland recovery over a decade. Later West African studies documented the impacts of grazing on pastures, including through recycling of nutrients via excretions, based on long-term research in the Fakara region of Niger. Related studies of herder decisions about animal movements, in response to changes in rainfall, cropping intensity and wage opportunities, built on the characterizations of rangeland productivity and its determinants.

Main Trends in African Range Systems

Map 2 (see p. xviii) shows the main research areas of ILRI and its predecessors. General trends around those areas can be described for human populations, livestock populations, climate, vegetation, mobility and grazing access.

Arid and semi-arid pastoral systems are found across much of sub-Saharan Africa. In Kenya, Mali, Niger, Nigeria and Sudan, they are the largest livestock systems by land area. Although sometimes considered 'marginal' in terms of public expenditure priorities, these systems contribute significantly to agricultural gross domestic product, household food and nutritional security, and to ecosystem maintenance in dry areas. In Kenya, over 80% of domestic meat consumption is produced in pastoral systems; Sudan has been exporting around 1.8 million animals annually for decades; and in the Horn of Africa, livestock and meat export values may have exceeded US$500 million by 2010 (Catley *et al.*, 2013, p. 7). In West Africa, these pastoral systems contribute many of the young males and interact with more intensive and sedentary livestock production systems via seasonal mobility.

Human populations

Significant increases in human populations are noted in East and West Africa alike. In West Africa, Touré *et al.* (2012) estimated an increase

of 2.6% per year in the overall rural population of the drylands between 2005 and 2010, with 3.6 times more people in 2010 than in 1960. de Haan *et al.* (2016) assumed a 2.5–3% annual increase for the future.

Livestock populations

After the severe losses during the droughts of the early 1970s and early 1980s (Toulmin, 1987) livestock populations have increased rapidly as well, with the Food and Agriculture Organization Corporate Statistical Database (FAOSTAT) showing rates of growth of between 3.1% and 4.4% from 1980 to 2010. In both East and West Africa, the small-ruminant population has grown faster than cattle. Detailed data on national level species distributions are lacking in most places; however, unique data from Kenya based on 30 years of aerial surveys shows that cattle numbers have declined as camel and small ruminants have increased (Ogutu *et al.*, 2011). The same study found significant declines in wildlife numbers.

Climate

West Africa is characterized by a south–north climate gradient ranging from humid/subhumid on coast lines to semi-arid/arid in the north. Transhumant pastoralism has dominated in the arid Sahelian zones, with herders migrating among rangelands and water sources. At the end of the rainy season, herders move to areas with available grass or crop residues, often southwards or in wetlands but also more opportunistically. Over the past three decades, 'these movements have become longer and more dispersed' (Touré *et al.*, 2013, p. 14) and conflicts with sedentary farmers and in protected areas have increased (Turner *et al.*, 2011). This is for various reasons, including changes in traditional land uses around water points and increased livestock numbers. Although many transhumance corridors have been legally recognized since colonial times, transhumance corridors are not always respected (Niamir-Fuller, 1999; Turner *et al.*, 2016) and failure to respect them sometimes leads to violent conflicts among herders and between herders and crop farmers.

In East Africa, with bimodal rainfall in some areas, dry-season movements are shorter and more opportunistic. Increased fragmentation of rangelands due to expansion of cropping and other activities and exclusion from dry-season water and grazing further limit seasonal mobility. The observation of range fragmentation was a motivation for much of ILRI's research as scientists sought to understand its impact on rangeland, livestock and wildlife productivity.

Vegetation

Long-term trends are extremely difficult to detect in the East African rangelands. First, the cost of long-term field studies of vegetation and land use make them infeasible in some instances. Second, the high temporal and spatial variability of precipitation and vegetation make it problematic to project from shorter periods and smaller study areas (Homewood, 2008; Oba, 2013). Third, changing drivers such as drought frequency, recent fragmentation and the spread of invasive plant species disturb historical patterns of land use. As Homewood (2008, pp. 65–72) explains, dryland rangelands go through periods of vegetation fluctuation in response to different drivers, in particular climate variability. In East Africa, there is no consistent long-term evidence or trend in rainfall, although heavy grazing from sedentarization or restriction of mobility can degrade rangelands (Galvin *et al.*, 2002), and hence increased fragmentation is a threat to the sustainability of rangelands.

Long-term dry matter (DM) production per hectare above the 600 mm isohyet in West Africa is in the order of 600–2400 kg DM/ha. Rainfall and vegetation improved after the droughts of the 1970s and 1980s, and the subsequent 'regreening' of parts of the Sahel has been notable (Hiernaux *et al.*, 2009c; Dardel *et al.*, 2014b) including for the woody population in rangelands (Hiernaux *et al.*, 2009b; Brandt *et al.*, 2016a) and agroforestry parklands (Reij *et al.*, 2009; Sendzimir *et al.*, 2011).

Galvin *et al.* (2002) summarized the research, concluding that woody plants have expanded across most rangelands globally, in response to both grazing management and

global increases in carbon dioxide and nitrogen emissions.

Mobility and grazing access

Associated with the growth in population density in East and West Africa has been an expansion of cropping. The area expansion of cropped fields reduces grazing areas on average and typically limits seasonal grazing, such as on wetlands, even more sharply (Haywood, 1981; Marie, 2000; Schlecht *et al.*, 2001).

Increased private ownership and enclosure of rangelands, particularly in East Africa, including 'land grabbing', and the erosion of some traditional practices governing common lands has restricted grazing even more. The loss of mobility and grazing access through public use planning, enclosures and urbanization (Galaty, 2013a) ultimately threatens rangeland integrity (Galvin *et al.*, 2008a,b). Formal tenure is now more important as a tool for pastoralists to secure rights to access lands; however, this poses challenges, because Hobbs *et al.* (2008) has argued that fragmentation results from modern land tenure.

The Central Problems of Tropical Range Ecology

A summary of the central problems of tropical range ecology would be the following questions:

- What are the technical and economic feasibility of measures to raise plant productivity under arid conditions?
- What is the technical and economic feasibility of raising livestock at given levels of feed resources?
- What are the short- and long-term effects of climate and climate change in primary and secondary range productivity?
- What are the effects of rangeland use for livestock, crops, wildlife and tourism on soils, nutrient flows and transfers, vegetation, water and greenhouse gas emissions?
- How have land rights evolved under pressure from competing uses in crops and other sectors, and what are their effects on

the seasonal, annual and spatial mobility of livestock?
- What is the appropriate use of equilibrium and non-equilibrium models as explanatory frameworks and policy guides?

This chapter first presents these issues schematically before discussing the evidence produced about them by the studies of ILRI, its predecessors and its collaborators in sub-Saharan Africa.

The technical and economic feasibility of measures to raise primary productivity under arid conditions

Efforts to raise pasture yields in dry areas without added water have failed systematically. Pratt and Gwynne (1977, pp. 100–128) showed that the economics of range improvement – by water development, fencing, overseeding of the range, managed grazing and seeding with new species of grasses – were unfavourable in drier conditions and risky in wetter ones. These findings were generally confirmed in Le Houérou's (1980) book on browse and in Sandford's (1983) global review of pastoral development.

Le Houérou (1989, pp. 149–155) synthesized the Sahelian experience with native pasture improvement over many years and concluded:

- Irregular rainfall, a long dry season and competition from native grasses and forbs made the introduction of higher-yielding plant species unsuccessful.
- There had been no commercial success in reseeding pastures at rainfall around the 550 mm isohyet, with local or introduced grasses or with legumes; the same was true of 'rotational or deferred grazing'.
- '...of the 80 herbaceous tropical arid zone species of forages which have been tried at Niono (550 mm) in Mali in 1977–1980, not one single species became established and amenable to produce a grazing impact'.
- There was one success – with *Acacia tortilis* and *Acacia senegal* near M'Bidi, Senegal – in establishing browse species at rainfall less than the 400 mm isohyet in West Africa.
- The high cost of fencing, firebreaks and water made it nearly impossible to achieve higher plant yields, even if browse and

pasture production could be improved under experimental conditions (see also Montgolfier-Kouèvi and Le Houérou, 1980).

The short- and long-term effects of climate

Climate is the key determinant of rangeland productivity, especially in the arid and semi-arid areas where extensive animal production predominates. In East Africa, these systems receive no more than 600 mm of rainfall annually and often only 200–300 mm (Ellis and Swift, 1988; Oba, 2013). Higher aridity means greater rainfall variability in time and space, and in much of East Africa, the rainfall is bimodal. Inter-annual variability in precipitation is a major driver of herd and grazing management. In East Africa, rainfall is the primary driver of vegetation, with vegetation growth closely following rainfall amount, frequency and duration (Coppock, 1994; Coppock *et al.*, 2017).

In West Africa, the monsoon drives a climate gradient from subequatorial humid in the south to desert margins in the north. In the arid and semi-arid Sahel, rainfall varies from 100 to 600 mm annually in a period of 1–4 months, with the more southerly regions receiving from 600 mm to more than 1200 mm over periods of up to 8 months. Although the monsoon occurrence is predictable, it occurs only in one season and the distribution of rain across this season is unpredictable (Hiernaux and Le Houérou, 2006). There is a marked contrast in the Sahel between fodder quality in the wet and dry seasons.

Forage availability and quality are the primary drivers of variability in livestock production. Primary production, in turn, is highly variable over time and space because the major determinant of plant growth is available soil moisture and fertility. Shortages in forage availability arise from drought, constrained access (e.g. due to disease, distance and access to water, or to conflict) or changes in palatability. Most rangelands include a mix of vegetation types including an herbaceous layer and scattered woody plants. These rangelands return quite rapidly to peak production after drought once the rains return, as documented by long-term research (Hiernaux *et al.*, 2009a,c; Miehe *et al.*, 2010).

Major livestock losses do occur, with severe droughts, which is one reason why herd sizes need to be large enough so that production can return to trend within 3–5 years (Ellis and Galvin, 1994). These droughts are often cumulative, with several successive 'failed' seasons ultimately leading to major hardship and loss of animals, as lack of feed and water plus diseases lead to mortality (Toulmin, 1987). Drought recovery is mostly related to levels of herd die-off, as population is mostly related to lagged rainfall variation; however, drought intervals are also important (Lesnoff *et al.*, 2012). Long-term shifts in climate, compounded by persistent growth of human populations and of cultivated areas into rangelands, explain some of the shift in West Africa into small stock in western Niger (Turner, 1999).

The effects of rangeland activities

Pastoralists have for centuries managed the spatial and temporal variability of water and pasture by moving animals annually and seasonally, as shown in the early compilations of Monod (1975) and ILCA (1975). Seasonal mobility in West Africa follows the monsoon along the south to north gradient, while in East Africa, the movements are more opportunistic and local owing to variability in altitude and in the bimodal rainfall regime. Pastoralists also move to avoid seasonal disease outbreaks, often caused by vectors influenced by rainfall patterns. Traditionally, pastoral and agro-pastoral producers managed access to and availability of grazing and water through complex rules and agreements, sometimes including specialized institutions, so that in drought years reserves would still be available (Gallais, 1984; ODEM/CIPEA, 1983). In addition to the ecological drivers, security and access to markets also influence movements. Homewood (2008) noted that the need for flexibility made pastoral systems vulnerable to land loss and exclusion from customary ranges; losses of land access to fragmentation threaten the viability of pastoralism.

Equilibrium and non-equilibrium models

Equilibrium models from temperate systems (on which many of the papers in ILCA's first major

book relied; ILCA, 1975) influenced the early studies of tropical arid and semi-arid rangelands. These equilibrium models focused on livestock densities and carrying capacities, and blamed livestock for overgrazing and environmental degradation.

The early ILCA studies in Mali (Hiernaux, 1983; Wilson *et al.*, 1983; Wilson, 1986; Wilson *et al.*, 1988) and later work in the Gourma in northern Mali (de Leeuw *et al.*, 1992), and further in western Niger (Hiernaux *et al.*, 2009a) formed some of the empirical basis of non-equilibrium models, which became dominant in the 1980s and 1990s (e.g. Ellis and Swift, 1988; Behnke and Scoones, 1993; Scoones, 1995).

The 'Synthesis Paper' of Ellis and Swift (1988) (Table 11.1) contrasted equilibrium and non-equilibrium systems in four domains. Equilibrium systems operate through biotic feedbacks, such that rangelands have a density-dependent carrying capacity. Non-equilibrium systems are density independent and respond to stochastic events such as rainfall and fire, rather than to livestock populations. Semi-arid rangelands in bimodal rainfall systems such as in southern Ethiopia behave more as equilibrium systems (Coppock *et al.*, 2017), while the behaviour of Sahelian rangelands under monomodal rainfall regime clearly affiliates to non-equilibrium (Hiernaux, 2004).

Vetter (2005) summarized the equilibrium/non-equilibrium debate over arid and semi-arid rangelands. She concluded that: 'most arid and semi-arid rangelands encompass elements of both equilibrium and non-equilibrium behaviour, and management must account for the high temporal variability and spatial heterogeneity'.

The African Rangelands Research Environments

East Africa (southern Ethiopia, Kenya, Tanzania)

The rangelands of Kenya, Tanzania and southern Ethiopia are noted for bimodal rainfall, which heightens the seasonal, inter-annual and spatial variability characteristic of arid and semi-arid areas. The short rains occur in October–December, with the long rains in March–May. The lowlands of Ethiopia and northern Kenya are arid and semi-arid, while southern Kenya and northern Tanzania are semi-arid to dry–subhumid with patches of greater humidity.

Historical rangelands research at ILCA focused on the Borana Plateau of southern Ethiopia (Coppock, 1994). The Borana areas have a semi-arid climate (400–600 mm of rain) with a complex mix of vegetation consisting mainly of perennial grasses and shrubs.

ILCA's initial range research in Kenya was in Maasailand in Kajiado County of south-eastern Kenya (Solomon Bekure *et al.*, 1991). ILRI's later work concentrated on the rangelands of southern Kenya, especially areas of intensive livestock–wildlife interactions in Amboseli National Park, Nairobi National Park, the Mara Reserve and the Serengeti in Tanzania. The rangelands of northern Tanzania and southern Kenya are more varied in terms of rainfall (400–1200 mm), with national parks occupying some of the wetter areas (Amboseli National Park and Maasai Mara National Reserve). These parks are among the most popular for wildlife tourism, and the challenges of integrating

Table 11.1. Contrasts between equilibrium and non-equilibrium systems. (From Ellis and Swift, 1988.)

Domain	Equilibrium systems	Non-equilibrium systems
Abiotic patterns	Vegetative conditions relatively constant; wetter	Highly variable conditions; typically, drier; monomodal rainfall
Plant–herbivore interactions	Deterministic from livestock to vegetation with limited feedback	Weak determinism from livestock to vegetation; plants under 'abiotic control'
Population patterns	Density-dependent carrying capacity; animal 'populations track carrying capacity'	Density independent; 'abiotic cycles'; carrying capacity random
Ecosystem characteristics	Typically more humid and densely populated	Typically more arid and less densely populated than equilibrium system

wildlife tourism with livestock production remain significant. Vegetation in the Mara is more productive than in more arid Kajiado, but both areas are predominantly tall- and short-grass plains interspersed with woodlands and shrubs. Some of ILRI's research focused on the Athi-Kaputiei Plains, in northern Kajiado district and bordering Nairobi National Park (Reid *et al.*, 2008). Rainfall ranges from 500 to 800 mm. The soils are derived from phonolitic lava and contribute to a nutrient-rich savannah with both grasses and trees that can support considerable wildlife biomass. For at least 400 years, Maasai have occupied this area. Over the 20th century, this pastoral–wildlife system has become more fragmented and compressed, which was the subject of ILRI's research.

Further south in Kajiado, on the border with Tanzania, the Amboseli ecosystem has long been considered a conservation jewel. However, its ongoing transition from extensive pastoralism to intensive pastoralism carried out on individual land parcels is threatening both wildlife in and around the Amboseli National Park and livestock production by the communities (Burnsilver *et al.*, 2008). The constraints on mobility and fragmentation of the resource base has altered the landscape, modifying wildlife habitat and increasing competition among wildlife and livestock for pasture and water.

Over to the west in Narok County, the Mara ecosystem is one of the wettest pastoral savannahs in East Africa and is the northern site of wildebeest, zebra and Thomson's gazelle migration from the Serengeti in Tanzania. The Maasai Mara National Reserve is limited to wildlife tourism but is surrounded by group ranches to the north and east. It receives relatively high rainfall (up to 1200 mm annually) and is a productive range that supports a high density of wildlife, especially from July to October when animals migrate north from Tanzania. Some research also occurred in the Ngorongoro Conservation Area adjacent to the Serengeti, which is a designated multiple-use area with important objectives for both wildlife conservation and human welfare. Over 50,000 Maasai pastoralists and their livestock live in the area (Boone *et al.*, 2002). The Tarangire–Simanjiro–Manyara pastoral ecosystem, south-east of the Serengeti in Tanzania, was also a site for some of ILRI's work.

West Africa (central Sahel in Mali, Inner Delta, Gourma, western Niger, northern Nigeria, Senegal and Gambia)

Rangeland production in the Sahel occurs under monsoon conditions and is characterized by high spatial, seasonal and annual variability (Ayantunde *et al.*, 1999; Hiernaux and Le Houérou, 2006). The Mali studies of the late 1970s to the early 1990s would have occurred in a period of exceptionally low Sahel rainfall, which would not have been true of the East Africa studies (Nicholson, 2000; Nicholson *et al.* 2018). Mean primary production ranges from 600 kg DM/ha in the northern Sahel with 200 mm of rainfall to 2400 kg DM/ha in the southern Sahel with 600 mm rainfall, but there is no linear relationship between rainfall and herbage production (Hiernaux *et al.*, 2009c; Dardel *et al.,* 2014a).

Herbage production is characterized by a wide local variation due to differences in soil type, runoff water patterns based on topography and geomorphology, and dominant plant species (Hiernaux and Le Houérou, 2006). The feed quality of herbage is often inversely proportional to the amount of water infiltrated in the soil during the growing season, at least for a given soil texture and fertility (Breman and de Wit, 1983). Free-ranging ruminants are selective in choosing their diets (Ayantunde *et al.*, 2007), and therefore spatial heterogeneity in herbage mass and quality affects the spatial distribution of grazing animals (Turner *et al*., 2005; Schlecht *et al.*, 2006).

ILRI's pastoral research in West Africa has focused on the Sahel, in view of the importance of these arid rangelands to livestock production. ILRI research on rangeland ecology started in Mali in the 1970s in Niono (central Mali) and then expanded to Macina (the inner delta of the Niger River). In 1983, 25 rangeland sites were established in Gourma and were monitored by ILCA from 1984 to 1993, and then irregularly until 1998. The site monitoring continued from 2000 to 2009 under the African Monsoon Multidisciplinary Analysis (AMMA) project (Mougin *et al.*, 2009) and is still going on under the AMMA-CATCH (Coupling the Tropical Atmosphere and the Hydrological Cycle) research network (www.amma-catch.org; accessed 25 March 2020) although the observations had to be scaled down from 2012 because of civil

insecurity. In Niger, 71 vegetation monitoring sites were established in Fakara and were monitored from 1994 to 2006 under ILRI research activities. The monitoring of these sites is continuing within the AMMA-CATCH network (Cappelaere *et al.*, 2009). In addition, there were grazing studies conducted on-station at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Sahelian Centre in Sadoré, Niger, and at the Niger government cattle ranch in Toukounous.

The Gourma monitoring sites are spread along the south–north bioclimatic gradient from Boulakessy at the border with Burkina Faso to Gourma Rharous on the Niger River via Hombori and Gossi. Gourma is in the Sahelian agroecological zone with average annual rainfall of between 200 and 500 mm (Hiernaux *et al.*, 2009b,c). It is dominated by annual herbaceous plants and a few tussock perennials towards the driest end, with widely scattered shrubs and small trees.

Fakara is a small natural region of western Niger covering about 6000 km² between the confluent valleys of the Niger River to the West and the fossil valley of the Dallol Bosso to the East (Hiernaux and Ayantunde, 2004). The study site covers 500 km² (included within latitude 13°20′–13°35′N and longitude 2°35′–2°52′E) all falling within the central Sahel bioclimatic zone with annual precipitation of between 400 and 500 mm.

The study site in Toukounous is a 4474 ha ranch situated in the central Sahel, 14°33′N and 33°17′E, at an altitude of 290 m above sea level. The ranch is fenced into 30 paddocks, varying in size from 49 to 283 ha. The local climate is typical Sahelian semi-arid tropical with monomodal rainfall from July to September. The long-term annual rainfall (mean±standard deviation) is 336±105 mm. Like any other Sahelian site, the vegetation is dominated by annual herbaceous species. The study on the effect of grazing regimes on cattle performance was conducted between 1995 and 1997 (Ayantunde *et al.*, 1999).

The study site in Sadoré (13°14′N, 2°16′E) at the ICRISAT Sahelian Centre in Niger is situated about 45 km south-east of Niamey. The climate is typical south Sahelian with an annual precipitation of between 450 and 600 mm. Most grazing studies were carried out at an enclosure that was established in 1982.

Key predecessors and partners

The early ILCA work in Niono, Mali, was developed alongside a Malian–Dutch research programme called 'Primary Production in the Sahel' (Penning de Vries and Djiteye, 1991). Pierre Hiernaux was among the first to set up systematic monitoring of rangeland sites for long-term analysis, complementing others in Senegal (Valenza, 1984; Gaston and Boerwinkel, 1982; Miehe *et al.*, 2010). ILCA researchers contributed early studies on livestock productivity, mobility and transhumance within the Macina flood plain (ODEM/CIPEA, 1983) and in central Mali. Toulmin *et al.* (2002) and Cotula *et al.* (2004) conducted research on pastoralist mobility and conflicts over land, especially between herders and farmers, in the 1990s, which highlighted changing land-use dynamics in response to different legal and administrative changes. Turner (1992, 1999, 2017) contributed to this line of research by examining how community resource management to 'clarify rules' of access actually runs the risk of increasing local ecological and economic vulnerabilities, given both the agro-ecological realities and the range of resources needed to sustain both crop and livestock production. Turner highlighted the trend of a greater year-round presence of livestock in the former 'agricultural' zone as a significant factor changing resource access and needs and leading to conflict.

In East Africa, key researchers who were working at the same time as ILRI (and in some cases were ILRI collaborators) on issues of land use and livestock included Peter Coppolillo, Lane Coppock, Solomon Desta and Katherine Homewood. Galaty (1994a, 2013b) noted in particular the negative trends towards excluding livestock or selling lands for other, crop-based, purposes. McCabe found similar issues in Tanzania in long-term research on Maasai livelihood diversification (McCabe, 2003; McCabe *et al.*, 2010), as did Homewood (2008) and collaborators from ILRI. Coppolillo (2000) described factors affecting the distribution of animals across landscapes and found that the distribution of dry-season water was a major influence throughout the year, not only in the dry season. He also noted variability in herder practice and cattle productivity.

Desta and Coppock (2002, 2004) summarized the long-term data on cattle populations,

rainfall and changing access to rangeland resources in the Borana region of southern Ethiopia. Their 2002 study convincingly demonstrated the 'boom-and-bust' cycle of livestock losses associated with periodic rainfall deficits. Their 2004 study documented a trend of declines in per-capita livestock holdings due to resource pressure/population increase and reduced access to key grazing areas (similar to trends documented in southern Kenya by Solomon Bekure *et al.*, 1991, and Galaty, 1994b, among others). This was leading some families to try cultivation as well as privatizing some grazing areas. They suggested that these patterns are broadly predictable and hence development interventions should reflect these system dynamics and respond to growing resource pressure.

Homewood *et al.* (2001) summarized long-term changes in land cover in Serengeti–Mara focused on wildlife rather than livestock per se. Comparing the Kenyan side to the Tanzanian side, they found a marked decline in species and rapid land-cover change only on the Kenyan side. Their analysis concluded that the Kenya–Tanzania differences were primarily due to landowners responding to market opportunities for mechanized agriculture and less to cattle numbers or to population growth. Homewood went on to collaborate with ILRI and other colleagues on the book *Staying Maasai: Livelihoods, Conservation and Development in East African Rangelands* (Homewood *et al.*, 2009), which focused more on livelihood diversification in the context of changing land-use dynamics.

Gufu Oba conducted long-term research in southern Ethiopia and northern Kenya on rangeland dynamics, exploring herder management of grazing areas and herder perceptions of land-use change and responses to these changes (Angassa and Oba, 2007, 2008; Oba *et al.*, 2000). His research contributed evidence on the interactions among rainfall, plants and grazers, and documented herder management of rangelands for animal and rangeland performance.

The main research questions in ILRI

The research was organized into four main areas: (i) quantitative assessment and monitoring; (ii) effects of grazing regime and intensity; and (iii) grazing access and mobility; and (iv) interactions among people, livestock and rangelands.

Quantitative assessment and monitoring

Quantitative assessment and monitoring of rangeland resources included detailed mapping in the large study zones of central Mali, the Macina flood plains, the Niono ranch, Gourma and later in the Fakara of Niger. The assessment and subsequent monitoring in the 1970s and 1980s were important to document how vegetation behaved in response to rainfall and soil properties. These studies also contributed to a broader understanding of the variation between rangeland types in different parts of Africa, again in relation to soil properties (fertility) and rainfall. To date, the monitoring and assessment of rangeland resources in Gourma, Mali (1984–2006), and in Fakara, Niger (1994–2006) (which have then continued under AMMA and AMMA-CATCH) are the only such long-term studies in the West African Sahel. Other investigations were mainly short-term studies of grazing or of conflict between farmers and herders.

Grazing regimes

A second area of research sought to explain the effects of grazing regimes and grazing intensity on animal performance, rangeland vegetation and forage production, and on the physical and chemical properties of soil. ILRI researchers sought to understand the relationships between animal productivity and rangeland management, including the impacts of livestock grazing on rangeland properties and cropped areas (e.g. through nutrient redistribution). The answers to the first two questions also contributed empirical evidence to the debates about whether arid and semi-arid African rangelands behave as equilibrium or non-equilibrium systems (Behnke *et al.*, 1993). These debates and the evidence underlying them has significant implications for rangeland management (see Homewood, 2008, Chapter 4, and Vetter, 2005). They also contributed to the related debates about whether the Sahel was under a process of desertification and if livestock systems had particular responsibility in the process (Hiernaux *et al.*, 2016).

Access to grazing resources

The third area was research on access to grazing resources and livestock mobility in relation to vegetation resources and the livelihoods of pastoralists and agropastoralists. These studies led to an understanding of how livestock keepers used mobility to actively manage their herd productivity, given the high temporal and spatial distribution of vegetation in the rangelands. In West Africa, reciprocal relationships with croppers have historically been important for the mutual benefits that pastoralists received by grazing their animals in wetter areas and croppers received from the manure deposited by transhumant animals.

Interactions among people, livestock and rangelands

A common area of research in East and West Africa was to document interactions among people, livestock and the range. This research built upon the characterization, assessment and monitoring work in West Africa to take into account the new dynamics, especially changes in cropping patterns, increased fragmentation, livestock population dynamics and the impact of declines in previously reciprocal arrangements and the failures of formal land tenure. In East Africa, the research combined modelling with ground observations, resulting in key findings about the impacts of fragmentation (in particular) on rangeland, wildlife and livestock performance (Galvin *et al.*, 2008c). This also resulted in the development of several modelling exercises to better understand the impacts of changing rangeland dynamics, and a new model. In addition, Reid *et al.* (2004, 2008) sought to understand complementarities between livestock production and wildlife management in southern Kenya, leading to significant innovations in land management around the Nairobi National Park and the Maasai Mara National Reserve.

Principal Findings

East Africa

ILRI hosted the Land Use Change, Impacts and Dynamics (LUCID) network, beginning in 2000.

The general goal was to promote biodiversity conservation and prevent land degradation through research to provide tools for understanding key changes. The network specifically sought to 'examine the causes and consequences of land degradation and the biophysical systems that underlie changing patterns of land use within East Africa land-cover/land-use changes in response to multiple drivers' (www.lucideastafrica.org; accessed 25 February 2020). Three foci were: (i) the drivers and impact of agricultural expansion into grazing areas; (ii) the transition of agro-pastoral systems in semi-arid areas; and (iii) the impacts of land-use change on biodiversity.

Over 48 working papers were published covering 30 years of land-use change across East Africa, primarily in subhumid and semi-arid zones where cropping, livestock production, protected areas and wildlife commonly overlapped. The main findings on the agro-pastoral systems transition and the impacts of land-use change on biodiversity (Maitima *et al.*, 2004) included:

- Causes of land-use change in agro-pastoral systems: the research found that the fluidity of land-tenure arrangements and quite major changes around who has rights to use land and decide how it should be used was most marked in agro-pastoral areas. The trend was a movement away from common management to private and individual arrangements such as subdivision of former group ranches (Olsen *et al.*, 2004), including fencing and smaller grazing areas, as well as more crop-based agriculture.
- Beneficial impacts of grazing on rangeland vegetation: moderate grazing was found to support native vegetation and local diversity.
- Impacts of the increased competition for key land and water resources: this was resulting in the restriction of herding and an increase in cropping and transition of some households to agro-pastoral production. In addition, there were restrictions on movement of wildlife and loss of access to wetland areas and key migration corridors and resources (Reid *et al.*, 2004; Lamprey and Reid, 2004).
- Impacts of restrictions on wildlife and livestock movement: despite the gazetting of national parks and reserves, dispersal of

animals into adjacent areas or for seasonal movements was still critical. Unfortunately, the increased competition for land also increased human–wildlife conflicts.

Extending the LUCID work while adding unique data on wildlife and livestock populations over time across Kenya, Joseph Ogutu and colleagues documented the impacts of pastoralism and protected areas on wildlife numbers. The first studies focused on the Mara ecosystem, where they documented the decline in a number of wildlife species, which corresponded with habitat deterioration and in some cases increased numbers of people and settlements (Ogutu *et al.*, 2009). This trend was continuing by 2011, but they noted the importance of ranches around the park as wildlife dispersal areas, which led to a recommendation that land use and poaching needed to be regulated (Ogutu *et al.*, 2011). The finding on the importance of pastoral areas to support protected areas emerged again, as these areas provide corridors between seasonal grazing areas (Ogutu, 2013; Ogutu *et al.*, 2017). The 2017 study estimated that Kenya's communally and privately protected pastoral areas support 65–70% of the country's wildlife population. This is because the national parks and reserves are too small for many of the large wildlife who must access areas outside the protected areas either seasonally or year-round. This research influenced the support community conservancies around the Maasai Mara National Reserve, Nairobi National Park and Amboseli National Park through the Reto-o-Reto project.

ILRI researchers engaged in over a decade of research on land-use change, land management, biodiversity and livestock across the arid and semi-arid regions of southern Kenya and northern Tanzania. This collaboration produced a book in 2008, drawing on some of the LUCID studies and others, entitled *Fragmentation in Semi-Arid and Arid Landscapes* (Galvin *et al.*, 2008d). This edited volume is a comprehensive overview of why and how fragmentation has occurred across a range of arid and semi-arid ecosystems and the implications of this fragmentation for people and animals. An increase in the 'exclusivity of use' across rangelands has restricted movements across landscapes, limiting access to resources. Given that mobility is key to managing the temporal and spatial heterogeneity of water

and forage resources, the research found that limitations on mobility were having serious impacts on rangeland ecology as well as on livestock and people. Their thesis was that fragmented landscapes are less productive than unfragmented ones. They attributed fragmentation to modern systems of land tenure, which are not suited to arid and semi-arid rangelands (Hobbs *et al.*, 2008).

Reid *et al.* (2008) describe the Athi-Kaputiei Plains near Kitengela, Kenya, which they studied intensively on the ground and in aerial surveys during the period 1977–2002. The area is an unusual example of a fragmented pastoral ecosystem that still supports migration of large wildlife despite its proximity to Nairobi. At present, the fragmentation is exacerbated by fencing of land parcels. Fences had a particularly negative impact on livestock movements and grazing/foraging. This research informed the Wildlife Conservation Lease Program, which paid Kitengela residents to allow free movement of wildlife on their lands, to avoid poaching and to avoid fencing of land. Initiated in 2000 and expanded in 2007, the programme had the potential to be a promising innovation, but it fell short of success. Although Osano (2013) found some positive impacts, for example in terms of more lions and payments to beneficiaries, the programme stopped in 2012 when the donor funds closed.

The conflict between wildlife and livestock

Reto-o-Reto sought solutions to land-use change and wildlife conservation problems with a more action-oriented approach. It engaged pastoral communities in solutions to balance poverty alleviation and wildlife conservation in pastoral systems. The research approach described in Reid *et al.* (2016) was one of 'continual engagement' between scientific researchers and community members which produced new knowledge and solutions. They intentionally used collaborative research-facilitator teams to better engage with communities and bridge across nested institutions from community up to the global level. This approach produced several key pieces of hybrid knowledge, from the Kitengela conservation payments to the Amboseli modelling work on the impacts of subdivision and the Mara Community Conservation Planning Framework.

Community-based conservation has emerged as a promising approach for resolving conflicts stemming from wildlife–livestock–pastoralist interactions, and the Reto-o-Reto approach supported the establishment of a network of conservancies around the Maasai Mara National Reserve. This began with four in 2009, which expanded to 14 by 2013 when the Mara Wildlife Conservancies Association was formed. At the heart of the conservancy model is that payments from tourists are used to compensate pastoral communities for adhering to rules about when and where they are permitted to graze their animals, in order to ensure that wildlife have enough area and forage. The community management model offered by the conservancies was strengthened by the 2013 Wildlife Conservation and Management Act and the 2016 Community Land Act. Today, all conservancies across Kenya are members of the Kenya Wildlife Conservancies Association and strive to offer a sustainable model that protects both wildlife and pastoral livestock production.

The final outcome for which the Reto-o-Reto work is known was the 2010 Greater Kitengela Land Use Master Plan, the first ever for a pastoral area. This plan evolved with support from research that showed, for example, that compensating pastoralists for loss of access to grazing lands could increase their resilience. The multiple pressures on land in Kitengela, and the cessation of funds for the compensation scheme, have compromised the objectives of the plan. As discussed at the end of the chapter, participatory land-use planning with communities is still one of the most promising solutions for improved management of rangeland ecosystems.

Modelling

The Colorado State University (CSU)/ILRI collaboration also led to innovations in modelling rangelands and pastoral households. Research spanning the 1990s and early 2000s sought to quantify different alternatives in the rangelands of sub-Saharan Africa resulting from the increasing pressures on natural resources owing to human population growth and the resultant conflicts among wildlife, cattle and agriculture (Galvin and Thornton, 2001). The major research questions were the effects of landscape fragmentation (in the case of southern Kenya,

the subdivision of group ranches) and the growth of agriculture (Thornton *et al.*, 2003, 2006; Boone *et al.*, 2005, 2006) on livelihoods and ecosystem services. The coupled model was subsequently used to explore the possibilities of schemes of payment for ecosystem services in areas of southern Kenya where agriculture is expanding rapidly, to compensate pastoralists for losses arising from more wildlife-compatible forms of land use (Bulte *et al.*, 2008). A third set of studies investigated the impacts of climate variability on livelihoods and on the economic benefits of using weather forecasts (Galvin *et al.*, 2004; Thornton *et al.*, 2004). This work was later extended to more generalized studies of the relationship between fragmentation and rainfall variability (Boone, 2007; Boone and Wang, 2007).

The CSU/ILRI collaboration on integrated assessment modelling was founded on the SAVANNA model, originally developed by Coughenour (1985, 1992) for Turkana District, Kenya, but further developed and applied in many other settings in Africa, Asia and North America since. SAVANNA models primary ecosystem interactions, simulating functional groups for plants and animals over periods from 10 to 100 or more years in a spatially explicit way.

For household modelling a simple structure was built – the Pastoral Household and Economic Welfare Simulator (PHEWS). This tracks the flow of cash and dietary energy in pastoralist households using a simple set of management rules that describe a reasonably realistic hierarchy of goals at the household level. PHEWS was used to model households of varying sizes and assets and with different access to natural resources. PHEWS was built using survey data regarding household size, structure and income; species, numbers and sexes of livestock held; and cultivated area (Thornton *et al.*, 2003). A coupled SAVANNA–PHEWS model was calibrated for sites in northern Tanzania and southern Kenya (Thornton *et al.*, 2006, 2007; Galvin *et al.*, 2006) using ecosystem and household data collected in the previous decade.

SAVANNA–PHEWS was innovative in at least two ways. First, it is worth noting that SAVANNA itself is a complex and sophisticated model, and even now represents a summit of the ecosystem modeller's art. PHEWS, on the other hand, occupies the other end of the spectrum: it is simple, requires relatively few data to calibrate,

was developed very quickly and can easily be adapted to new situations. PHEWS was an early example of a 'disposable' model: because the builder invests only limited time and energy in assembling it, the model can easily be thrown away and a new start can be made, as there is little lost. The nature of the relationship between model complexity and model utility is probably not as straightforward as is often imagined; this is borne out by recent trends in some quarters towards model simplification. Second, despite the disparities in the detail and elegance of the models, SAVANNA and PHEWS were tightly linked, and were run as part of the same simulation. At each time step modelled, SAVANNA passed information about livestock to PHEWS, and PHEWS passed information about the sale or purchase of animals back to SAVANNA, where herd sizes were adjusted accordingly.

PHEWS was essentially a population-based model, and it was used as the basis for developing an agent-based approach to investigate similar questions. Like PHEWS, the DECUMA model (Decisions under Conditions of Uncertainty by Modelled Agents) was tightly linked with SAVANNA to represent livestock-owning and cultivating households. As an agent-based model, DECUMA simulates in a relatively complex way individual households on a landscape in a spatially explicit way (unlike PHEWS), adjusting livestock distributions on a weekly basis and making other household decisions on a monthly basis (Boone *et al.*, 2011; Boone and Lesorogol, 2016). One potentially important document from all this work, unwritten as yet, is a comparison of SAVANNA–PHEWS and SAVANNA–DECUMA simulations for the same situation: we have calibrated applications of both coupled models for the same part of Kajiado district, Kenya. Such a comparison would throw light on the added value of a more complex household model (DECUMA) compared with a very simple model (PHEWS).

Beginning in 2012, ILRI worked with CSU on a simulation tool that could be used to project global rangeland changes in response to trend climate and climate variability. This led to a process-based simulation model that is spatially explicit and of moderate complexity, called G-Range. Several needs guided the design of G-Range:

- A simulation tool for global rangelands that captures main primary production and its dynamics.

- A tool of moderate complexity – one that could be useful to a new user in a week or less.
- A monthly time step, with simulations that run for 5–100 years or more.
- Representation of global vegetation at least at the scale of herbaceous, shrubs and trees.
- The ability to include natural or management modifications to rangelands, such as fire and fertilization.
- Programming structures and portable code, allowing the software to be run on different platforms including multiprocessor clusters or networks.
- Output mostly as straightforward spatial surfaces, without complex summary analyses that are more readily done in other packages.

The idea was not to program G-Range from scratch but to use components from published models. The Century model (Parton *et al.*, 1993) was used as the core of the soil modelling and physiological aspects of the G-Range model, given Century's wide use in rangelands over the past 20 years or so. Other aspects of G-Range were influenced by SAVANNA. G-Range does contain some new contributions, notably in modelling plant populations.

There are several insights from the CSU/ILRI collaboration on the modelling of coupled systems. An early synthesis of the coupled modelling work supported the hypothesis that a household's capacity to stresses is governed by flexibility in livelihood options (Thornton *et al.*, 2007). Households cope with stresses through intensification, diversification and off-farm economic activities. Viable options depend on household objectives and attitudes as well as on access to natural resources, inputs and output markets. The study also highlighted the fact that generally it is the poorer households that can gain the most from implementing risk-management options. Furthermore, there are limits to the adaptive capacity of households in the absence of access to off-farm resources, and these limits likewise depend on local context. Much of the CSU/ILRI work around rangeland fragmentation has been summarized in Hobbs *et al.* (2008) and Galvin *et al.* (2008b,c) as discussed above.

A general insight from the modelling work was the view of humans, cattle and wildlife as

components of an integrated ecosystem (Galvin *et al.*, 2008a), if technical, advisory and policy-related interventions are to be appropriately targeted. A thread that remains to be unravelled is the appropriate use of integrated models to resolve conflicts between conservation and people in the rangelands (Galvin *et al.*, 2006).

Simulations with G-Range summarized projected climate change impacts on livestock across Africa, using a review of literature and model results (Thornton *et al.*, 2015; Boone *et al.*, 2015). While there are many options that can help livestock keepers adapt, there appear to be no widely applicable and unconstrained options (Boone *et al.*, 2018; Thornton *et al.*, 2019).

West Africa: assessment and monitoring of rangelands

This was one of the major areas of research begun by ILCA in Mali, as a contribution to the study of livestock production in a diversity of pastoral and agro-pastoral systems (Wilson *et al.*, 1983, 1988; ODEM/CIPEA, 1983) continued in Niger by ILRI (Hiernaux and Ayantunde, 2004; Hiernaux and Turner, 2002). ILCA researchers invested large efforts to characterize, quantify and spatially assess forage resources across different regions. Field observations of 331 sampled sites across central Mali from 1976 to 1980 (Wilson *et al.*, 1983) encompassed a large area in order to include most of the seasonal movements of herds managed by Macina Fulani pastoralists as well as a diversity of livestock production systems. The observations defined bioclimatic zones and noted how the forage species composition varied with these zones (Hiernaux and Le Houérou, 2006). Within the zones, the distribution of woody plant species depends on soil texture first and then moisture regime and terrain topography (Sankaran *et al.*, 2005). Beyond that, land-use history, especially clearing for cropping, was found to modify the composition of woody plant species (Cissé and Hiernaux, 1984; Achard *et al.*, 2001). The distribution of herbaceous species, which are mostly annuals, is less consistently sensitive to these same factors as well as to the shadow of woody plants. This is due to large inter-annual variations in species composition in relation to variations in rainfall

distribution as well as changing soil seed stocks (Hérault and Hiernaux, 2004). Analysis of aerial photographs confirmed the match between geomorphology and vegetation type (Hiernaux and Haywood, 1978).

Additional observations of 169 sites across the Macina floodplains from 1979 to 1983 (ODEM/CIPEA, 1983) demonstrated that biogeographic zoning only affected unflooded islands or edges, along with land-use history including cropping and wood exploitation. In the flood zones, the perennial herbaceous vegetation is determined by the inter-annual variations in flooding regime (Hiernaux and Diarra, 1986). Although poor in species diversity, they were highly productive. The patchy distribution required large-scale mapping, which was also a methodological innovation (Marie, 2000).

Observations across the 25 sites in the Gourma transect (Hiernaux *et al.*, 2009b,c) following the 1983/84 drought confirmed the earlier Mali findings that vegetation is organized by bioclimatic zones and then based on edaphic conditions within these zones. Land-use history had little impact. Soil type and rainfall distribution determined where herbaceous and woody plants were located and distributed. Analysis of satellite images for the same region also indicated that vegetation types can be mapped to edaphic zones and surface hydrology and soil type (Breman and de Ridder, 1991; Gal *et al.*, 2016). Field observations supported the building up of a novel primary production model, STEP (Sahelian Transpiration, Evaporation and Productivity model) to simulate annual herbaceous growth relying mainly on a soil water balance and meteorological control of plant photosynthesis (Lo Seen *et al.*, 1995). The model was validated with field monitoring data on the Ferlo and Gourma rangeland vegetation (Mougin *et al.*, 1995; Tracol *et al.*, 2006). The herbaceous vegetation decay and decomposition with or without grazing is also simulated in STEP and has had a number of applications in assessing seasonal fodder resources (Diawara *et al.* 2018) and impact on the environment (Delon *et al.*, 2015; Pierre *et al.*, 2015). STEP was further adapted for particular perennial grasses growing in flood plains (Léauthaud *et al.*, 2018).

Observations a decade later in the Fakara region of south-western Niger, a more densely populated area with more sedentary populations,

found that vegetation distribution was explained by both the edaphic environment and land use (Turner and Hiernaux, 2015). The generally poor soil fertility explained the poverty of the vegetation floristic composition. These findings were confirmed by analysis of high-resolution photographs and satellite images, which also were used to distinguish cropping land-use types (Schlecht *et al.*, 2006; Tong *et al.*, 2020).

The assessments were also combined with monitoring of herbaceous biomass and floristic composition at the same sites, observing variation in vegetation production over time (e.g. before, during and after droughts); across topography (lowlands versus uplands; sandy soils versus clay soils); and in response to burning and grazing. The results confirmed the high spatial heterogeneity of Sahelian rangeland forage resources, in response to rainfall, runoff and soil properties. Land-use change was also found to be a factor in data collected from 1994 to 2006 in Fakara, Niger. Finally, woody plants were also assessed and monitored during the same time and over the same sites to observe how their growth, phenology and distribution were affected by soils and rainfall as well as grazing and cropping (Hiernaux *et al.*, 2009a, 2019).

Overall, this body of research was novel in several respects. First was the quantification of forage resources expressed in seasonal capacities per landscape unit (Marie, 2000; Hiernaux, 2005; Auda *et al.*, 2012; Hiernaux *et al.*, 2015). Second were a number of methodological innovations. The assessment of the contribution of woody plants to livestock nutrition led to new woody plant population survey methods (Hiernaux, 1980; Franklin and Hiernaux, 1991; Brandt *et al.*, 2016a,b), development of allometric relationships between woody plant size and foliage and fruit masses (Cissé, 1980), and surveys to characterize the phenology of the main woody plant species (Hiernaux *et al.*, 1994b). It also led to a number of methodological advances in systematic field observations (Hiernaux, 1982, 2016; de Leeuw and Hiernaux, 1990), aerial surveys (Milligan, 1982; Milligan *et al.*, 1982) and remote sensing using aerial photos and satellite images (Hiernaux, 1988; Hanan *et al.*, 1991). One of the principles put forward in field methodology is the stratified random sampling along linear transects (Hiernaux, 2016), as a more efficient strategy to account for the high spatial heterogeneity and patchy pattern of the vegetation. Consideration of the significant seasonality of vegetation growth in arid to subhumid West Africa was a driving principle in screening for more efficient metrics of forage resources assessment by satellite remote sensing such as normalized difference vegetation index (NDVI) metrics used to assess herbaceous and crop production (Hiernaux, 1988; Bégué *et al.*, 2014) and also woody plant crown cover and foliage mass (Brandt *et al.*, 2016a,b).

Indeed, the strength of the seasonality of the Sahel ecosystems, including the complex situations created by the combination or rainfall and flood seasons in the Macina flood plains (Hiernaux, 1983), forced the assessments to go beyond static survey and to quantify, explain and attempt to predict the seasonal and inter-annual variations in forage resources. Repeated measures of vegetation in rangeland grazed or protected from grazing together with rainfall records, soil moisture and main nutrient (nitrogen, phosphorus) contents were decisive to better understand what the limiting factors of rangeland production were (Buerkert and Hiernaux, 1998; Hiernaux and Diawara, 2014). They led to the development of simulation models of the vegetation growth (Lo Seen *et al.*, 1995; Mougin *et al.*, 1995), grass tillering under grazing condition (Hiernaux *et al.*, 1994) and also of the straw and litter decomposition during the dry season depending on grazing and trampling intensity (Hiernaux *et al.*, 2014).

Stratified sampling along a linear transect has been adopted in many rangeland resources assessment and monitoring such as the monitoring by the Centre de Suivi Ecologique in Senegal (Diouf *et al.*, 1998), the Institut de l'Environnement et de Recherches Agricoles (INERA) national pastoral resource survey in Burkina Faso (Kiema, 2015), the carbon balance study in Widou Thiengoly in Senegal (Assouma *et al.*, 2018). Similarly, the stratification of woody plants when assessing their density by an unbiased distance method known as the 'point-centred quadrant' (Pollard, 1971) with points distributed at regular intervals along the same linear transect, associated with classical dendrometry on woody plants sampled by the method and allometric relationships (Cissé, 1980; Henry *et al.*, 2011), is increasingly used to efficiently assess the contribution of woody plant population (Hoffmann *et al.*, 2006).

The seasonal curve integral of the NDVI during either the growing season (herbaceous) or the dry season (woody plants) is widely used in satellite remote sensing the vegetation production, as well as metrics based on seasonal NDVI maximum, mean or percentile values (Tucker *et al.*, 1985; Hiernaux, 1988; Fensholt *et al.*, 2004; Dardel *et al.*, 2014a), and based on STI in the dry season (Jacques *et al.*, 2014; Kergoat *et al.*, 2015). Accounting for the woody phenotypes improved the assessment of woody plant cover and foliage masses (Brandt *et al.*, 2016a,b, 2019).

The simulation models developed and calibrated using field data collected by ILRI in Mali, Niger and Senegal have been used to predict vegetation production from rainfall, flood and grazing scenarios (Dardel *et al.*, 2014a,b; Diouf *et al.*, 2016; Diawara *et al.*, 2018), and also to assess the risks of soil erosion by wind (Pierre *et al.*, 2015), carbon sequestration, carbon and nitrogen emissions to estimate (Le Dantec *et al.*, 2009; Delon *et al.*, 2015) and to calculate the main nutrient balance in a pastoral ecosystem (Schlecht *et al.*, 2004; Assouma *et al.*, 2018).

The quantitative assessments of grazing livestock impact on the ecosystem in the short and medium term, and the derived model tools have been used to advocate for protecting and ensuring livestock seasonal and regional mobility in pastoral systems (Hiernaux *et al.*, 2015). They contribute to discussions on the desertification paradigm in the Sahel and policies developed at national and international scales to combat alleged desertification (Dardel *et al.*, 2015; Hiernaux *et al.*, 2016).

Quantifying the carbon and nutrient recycling role of livestock in pastoral and agro-pastoral systems has been used to diagnose the corralling practices of agro-pastoralists in western Niger and suggest improvements (Gandah *et al.*, 2003; Powell *et al.*, 2004; Djaby, 2010; Hiernaux and Diawara, 2014; Coppock *et al.*, 2017). More generally, this knowledge was used to assess the contribution of livestock to cropping intensification with a perspective of ecological sustainability and improvement of agro-pastoralist welfare (Hiernaux, 1996, 2013; La Rovere *et al.*, 2005).

Effects of grazing regimes on animal and rangeland performance

A series of experiments were carried out across the various West African sites to try to address concerns that grazing livestock was a driver of environmental degradation. These experiments were aimed at measuring the impact of livestock grazing regimes on short (within season) and medium (inter-annual) time frames. The ILRI experimental work clearly separated the impact during the short growing season from that during the long dry season (Hiernaux and Diarra, 1986; Hiernaux and Le Houérou, 2006).

Grazing experiments across three sites and over two decades, in fenced paddocks, demonstrated that herbaceous annuals responded to grazing during the growing season with regrowth, but this decreased rapidly in response to repeated grazing on the same plants. The short-term impacts depend on the timing and intensity of the grazing (Hiernaux and Turner, 1996). Grazing during the dry season was found to accelerate the decomposition of straw and litter, so that, at most, livestock intake reaches a third of the herbaceous biomass at the onset of the season (Hiernaux *et al.*, 2015). In the particular case of the Macina grasslands, which are adapted to temporal floods, dry-season regrowth was found to depend on grazing timing and intensity, with an optimum frequency specific to each grassland type (Hiernaux, 1984). The longer-term effects of grazing observed on species composition and vegetation productivity are minor compared with the effect of clearing a land to crop or for forestry exploitation (Hiernaux, 1998; Achard *et al.*, 2001; Hiernaux and Turner, 2002). They depend on the timing and intensity of grazing and involve forage intake but also trampling and livestock excretions (Diarra *et al.*, 1995; Schlecht *et al.*, 1998). Another set of experiments assessed soil seed stocks and germination patterns; these were found to be transient, with most seeds germinating during the wet season following dispersion, particularly due to the capacity of annuals to produce large numbers of seeds, which were rapidly dispersed.

Another line of research observed the effects of grazing regimes on diet selection and animal performance. This demonstrated that grazing ruminants selected forages that were more nutritious and digestible than an overall pastural evaluation would suggest. Night-time grazing was found to increase forage intake and hence animal productivity, especially during the dry season, as the quality of available forage decreases in the dry season. Supplementation is necessary

for animals to maintain their body weight in the late dry season. The foraging behaviour of free-grazing livestock differs by species, with goats being the most selective and sheep the patchiest.

A domain of the grazing livestock impact on which the ILRI team particularly focused their research, especially when studying agropastoral systems, was the recycling of organic material and minerals through faeces and urine excretions. Faeces and urine excretions were studied in controlled conditions, in barns and metabolic cages at Sadoré research station (Fernández-Rivera *et al.*, 2005), but also on grazing cattle on the ranch at Toukounouss (Ayantunde *et al.*, 1999) and on cattle, sheep and goats in village conditions (Schlecht *et al.*, 1998). In the latter case, the results indicated that grazing livestock through their local mobility with grazing–walking and resting–rumination areas achieved a spatial transfer of organic matter and nutrient to the benefit of resting points such as paddocks and corralling spots (Hiernaux *et al.*, 1998). These nutrient concentrations are key to cropping intensification and diversification (Hiernaux and Diawara, 2014).

Turner (1999) and Turner *et al.* (2005) looked at the issue of whether grazing livestock in mixed crop-grazing areas could possibly lead to grazing-induced degradation. Their results indicated this is possible if there is not enough labour/expertise to manage the animals or if they are constrained in finding enough free-grazing areas. Turner and Hiernaux (2002) worked with livestock herders to document how they moved their grazing animals across landscapes. This approach resulted in better information on the spatiotemporal distribution of livestock across agro-pastoral landscapes, as this distribution reflects local land-use patterns, topography, vegetation, settlements and water points.

Mobility and access to grazing

Given the previously summarized evidence that livestock keeper management of grazing is critical to how much feed livestock are able to access as well as the distribution of nutrients across landscapes, the studies that researchers associated with ILCA and later ILRI conducted on mobility and access to grazing resources are relevant.

Research from central Mali (Niono and Macina) in the late 1970s and early 1980s described the daily and regional grazing routes used by pastoralists. The ILCA/ODEM project in Macina mapped transhumance routes and documented the local governance and access rules. In Niono, the researchers found that integrated crop–livestock production was increasing. Contractual agreements and grazing rights and institutions were declining in terms of authority/formal recognition. Similar research in Gourma, Mali, also found diversities of pastoral and agropastoral systems and a tradition that fixed grazing rights through access to water points. Research from Fakara in the mid-1990s that was followed up in 2007 found that grazing management of most village livestock depended on movements outside the village territory, especially during the rainy season to avoid damage to crops and to have access to natural pastures as there is always restricted livestock mobility during the cropping season. Second, the presence of extra-village movements of village livestock is higher in areas of higher population density, which is expected due to declining grazing areas as a result of demographic pressure. Third, the perceived advantages of herd mobility are to better provide livestock with pasture and water and, at least during the rainy season, to avoid crop damage. The perceived disadvantages of herd mobility are losing access to milk and other livestock products, not finding dry-season pasture or water outside the village territory and spending more energy trekking the herd.

Research on farmer–herder relationships and conflict management in agro-pastoral systems of Niger from 1995 onwards produced novel findings (Turner *et al.*, 2012; Turner 2017). Community informants stated their preference to resolve conflicts without involving customary or government authorities, particularly at supra-village levels, as they did not believe that higher authorities could settle conflicts in a lasting fashion. Second, most of the farmer–herder disputes occurred during the cropping season and involved active mediation by customary authorities at the local level, resulting in a crop damage fine. These fines were paid by the herding family or livestock owner. These disputes are better managed when there is a convergence of productive interests across herding and farmer social groups and a high perceived degree of interdependence. Later research in Mali (Turner *et al.*, 2014)

confirmed that increases in the number of conflicts due to unauthorized grazing of crop residues is a reflection of the change in farmer–herder relationships from that of mutual trust that characterized manure and entrustment contracts to more inherently conflictual relationships based on wage and tenancy contracts.

Conclusions and the Future

Rangelands research in arid and semi-arid sub-Saharan Africa has been reinvigorated by renewed government and donor interest in pastoral livelihoods. The challenges facing productive rangelands remain competition over resources, which has been exacerbated by armed conflict; overuse of some rangelands as fragmentation continues; and the failure of many technical and governance interventions, as summarized by Reid (2012). These challenges cannot be met without a long-term core-funded research investment, as has been achieved in the pastoral areas of the USA, Australia, New Zealand and the Mediterranean Basin.

Despite the recent revival of interest in pastoral problems in the drylands, the Altmetric results highlight the serious underinvestment in African range sciences. Searches for the expressions 'range ecology', 'pasture', 'pastoralism' and 'grazing' show that papers from African sites, of all institutional affiliations, are only about 5% of global papers and barely 4% of global citations.

The unresolved development challenges of pastoralism in East and West Africa make it essential to renew long-term empirical research to understand rangeland dynamics and to develop appropriate public policies. The rangelands research agenda at ILRI focuses on: (i) governance for better rangeland management; (ii) monitoring rangeland conditions to improve development interventions; (iii) understanding the interactions between climate change and the rangelands; and (iv) improving rangelands productivity for pastoral resilience.

Range governance

As most rangelands are common pool resources that are shared by communities, development partners have been testing community-based approaches in different settings. Evidence of what works to make participatory and community-based rangeland management successful is accumulating, but researchers have not yet systematically consolidated this evidence. For example, evidence is emerging to suggest that simple interventions by communities to establish (or re-establish) seasonal grazing patterns can have a quick and significant effect on rangeland condition. In order to convince various investors of the feasibility of rangeland management, however, we need more action research and trials of interventions such as seasonal planned grazing, rangeland rehabilitation and management of bush encroachment. This needs to be coupled with impact assessments of the social and biophysical impacts of past and ongoing management initiatives, as well as cost–benefit analysis of the relative benefits of rangeland management. Finally, we lack evidence of how community-level restoration interventions interact with socio-ecological dynamics and larger landscape scales.

Monitoring rangeland conditions

Quick successes in restoration often build the confidence of community institutions to take on bigger challenges. However, scaling out these local successes often proves challenging, given the seemingly intractable challenge of securing access to resources while also maintaining the flexibility needed to manage these resources. While rangeland management needs to be participatory, this participation may differ by social, institutional and biophysical context. Supporting, validating and disseminating evidence for appropriate models of governance that build on community-based approaches, further enabling them with higher-level institutional arrangements, is thus another priority. While evidence suggests that community governance needs to be enabled by higher-level arrangements, such as national land-tenure policies or district land-use plans, again little systematic analysis of these nested models has been consolidated.

Mitigating climate change and the rangelands

Documentation of the ecosystem services provided by rangelands shows that they can generate a

competitive return on new investment. Much of ILRI's previous work on ecosystem services focused on wildlife biodiversity. However, recently, carbon sequestration has attracted more interest, as an option to offset greenhouse gas emissions from other sectors. While the potential for carbon sequestration in rangelands is high, there is little empirical evidence about what is achievable in arid and semi-arid environments (Milne *et al.*, 2016).

Adapting to climate change in the rangelands

Adapting rangelands to future climate change is an overarching priority. Climate change will bring hotter temperatures and different rainfall patterns, with accompanying changes in the composition, quantity and quality of forage. Models like G-Range are a major step forward in studies of climate change and rangelands and

can advance investigations of adaptation and mitigation options there. Work is under way on coupling G-Range with household models to allow integrated scenarios of ranges, animals and households.

Rangeland productivity

With the increased interest in stimulating more market orientation and commercialization of pastoral and agro-pastoral systems, many development partners are forced to address the question of forage availability. While substantial new fodder production is available from crop residues and potentially from the introduction of new planting materials in mixed systems, it is inevitable that most rainy-season forage will be produced on rangelands. With greater investment in tools such as land-use planning, rangeland management can be stimulated by the commercial opportunities.

Note

[1] 'ILRI' refers to 'ILCA and ILRI' unless a specific distinction is needed.

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12 Forage Diversity, Conservation and Use

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Contents

Executive Summary

The problem

Managing biological diversity has long been recognized as an essential component of crop improvement to ensure a pool of genetic material for selection and breeding for current and future needs arising from agricultural development, population growth and growing food demand. Tropical and subtropical forage genetic resources are particularly important because with few tropical forage breeding programmes of limited species coverage, forage germplasm remains the basis for selection and development of new feeds. With increasing demands for feeds for livestock intensification, rapid rates of genetic erosion of forage diversity in many regions and the need to select new higher-yielding and better-adapted genotypes, the in-trust forage collections held in the International Livestock Research Institute (ILRI), the International Center for Tropical Agriculture (CIAT) now part of the Alliance of Bioversity International and CIAT after the first mention of CIAT and the International Centre for Agricultural Research in Dry Areas (ICARDA) are crucial. The knowledge generated from research on forage diversity allows scientists to identify genotypes with higher potential and to support innovative genotype selection and breeding programmes.

Scientific impacts

The principal scientific impacts have been in germplasm collection, characterization and distribution.

Collections

The three collections at ILRI, CIAT and ICARDA comprise an estimated 72,000 distinct accessions of 1600 species of tropical and subtropical forage grasses and herbaceous and woody legumes. With the large number of plants that can be used as forage, this is likely to be less than 20% of global tropical forage biodiversity. The regional origins of the collections are about 30% each from Latin America and the Caribbean, West Asia and North Africa, and sub-Saharan Africa, and the remaining 10% mostly from tropical Asia and South-east Asia. Much of the forage diversity is found in the rangelands of sub-Saharan Africa, and conservation efforts including protected areas for wildlife conservation and tourism will protect remaining forage diversity *in situ* for the foreseeable future. These collections constitute stocks of current and future value that can be used in crop and animal production.

Characterization

The CGIAR forage germplasm collection is continuously characterized for morphological traits, with about 60% already completed and species with high potential as feed (grasses: *Brachiaria*, *Cenchrus*, *Chloris*, *Panicum* and *Pennisetum* spp.; herbaceous legumes: *Arachis*, *Centrosema*, *Desmodium*, *Lablab*, *Medicago*, *Stylosanthes*, *Vicia* and *Vigna* spp.; fodder shrubs and trees: *Cratylia*, *Desmanthus*, *Flemingia*, *Leucaena* and *Sesbania* spp.) already evaluated for biomass production, nutritional value and some adaptive traits, often via multilocational trials with national partners. Species characterization and evaluation have

identified promising genotypes, some more productive than current named cultivars, for a range of environments. The information generated has been used to identify genotypes for core collections, for use in selecting parents for grass breeding programmes and for users to better select genotypes best suited to their needs.

Technical advances in collection management have been possible as information has been generated on environmental adaptation, seed production and seed longevity. Improvements in procedures, such as breaking seed dormancy and seed production, and understanding the longevity of forage seeds has led to more efficient management of the large collections held in CGIAR. Costing of gene bank operation methodology developed by the Systemwide Genetic Resources Programme and applied to the different areas of gene bank operations has shown the areas of highest cost and risk. This allows management to focus on these areas where efficiencies and savings can be made without compromising genetic integrity and long-term conservation of the germplasm.

Gene bank management of forages is a complex operation because of the large number of wild species and the diversity of morphotypes and botanical species that are used as forages. Knowledge management tools such as the Crop Genebank Knowledge Base have been developed to share knowledge from the CGIAR centres and assist gene bank managers both inside and outside CGIAR to better manage their collections. Forage networks have made significant contributions to forage selection and use, and subregional networks continue to play a key role in studying the diversity in the collections and evaluating genotypes for adaptation and utility as livestock feed in a wide range of environments.

Distribution

An estimated 138,000 samples have been distributed from the CGIAR collection to 188 countries from the gene banks, in addition to over 55,000 samples made available internally within the centres for forage research and breeding. Opportunities for better alignment of operations and synergies between the CIAT and ILRI forage collections through coordinated curation and harmonization under the CGIAR Genebank Platform were identified in 2018. This is expected to achieve greater efficiencies and lead to greater impact through increased use of the forage genetic resources. The continued long-term safety and availability of the CGIAR forage collections is being ensured by placing a safety duplicate in an alternative location. A second safety duplicate is also being placed in the Svalbard Global Seed Vault and currently 50% of the collections are stored there.

Scientific gaps

Despite substantial effort to characterize and evaluate materials in the collections, there is insufficient information on performance, disease resistance and drought resistance in many species. The gene banks have assigned Digital Objective Identifiers to the accessions to track germplasm use while strengthening characterization work on the collections held in trust.

Development impacts

Uptake summary

The link from distribution from the gene bank to farm use is often undocumented because the accessions are first passed to research programmes and from there are further distributed to farmers. Forages differ from crops in that most common forages are selections from germplasm and not the result of breeding programmes. This direct use should make it easier to track selections, but documentation is still scarce. Some success has been realized with large-scale adoption of *Brachiaria* and *Panicum* in Latin America and the Caribbean, Napier grass in sub-Saharan Africa, and medics and vetch in the dry areas (see Chapter 13, this volume).

Preservation of option value

Conservation of diversity in gene banks is a long-term activity that needs to be resourced to ensure continued availability of germplasm for future use. A return on the investment made can be quantified as the impact from actual and potential use of the germplasm for livestock feed with related increases in on-farm income from sale of livestock products. This can be directly related to the costs of conservation. However, much of the value of the gene bank lies in the future. Option

values are particularly important for germplasm in *ex situ* collections, which are natural resources, and global public goods, which the world community relies on for their existence as a resource for future needs. The option value of having the germplasm available to respond to as-yet-unidentified future needs, such as changing feed needs due to climate change, and the existence value that society derives from knowing that something exists and will be available for future needs, may be more powerful economic drivers of conservation of forage diversity than the cost–benefit analyses that can be done on its actual use.

Germplasm distribution as a proxy for use

Using germplasm distribution data as a proxy for use is complex because many of the samples distributed will not meet user needs or show superior performance in the intended location. Only a small percentage of the materials received will be taken forward from evaluation to adoption and use. Estimates from past variety development in CIAT indicate that about 1% of the grass collection and less than 0.2% of the herbaceous legumes have been released as named varieties.

Development gaps

Barriers to development impacts include: (i) legal restrictions on new collections with new conditions for access to germplasm under the Nagoya Protocol on Access and Benefit-sharing (Nagoya Protocol), which may make reaching agreement on collection and sharing of germplasm a more lengthy process; (ii) costs of maintaining and characterizing collections to make them more accessible to users and prioritizing which species future users are likely to demand; (iii) high uncertainty about options value, even for species that have been well characterized; and (iv) high uncertainty about non-market benefits.

Capacity building and partnerships as development impacts

Improving the capacity of partners in gene bank management and forage research and development will have lasting impact. The CGIAR forage gene bank programmes have provided training to over 1000 scientists and technicians in germplasm management, forage evaluation and forage seed production to build scientific and technical capacities. Much of this training has been done as part of scientific networks to strengthen the capacity of partners to evaluate and select forages for use in smallholder livestock systems. ILRI, CIAT and ICARDA have been working closely together under the System-wide Genetic Resources Programme and have developed training materials and guidelines for gene bank management, including the sections on forages in the Crop Genebank Knowledge Base. ILRI and CIAT, along with the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Department of Primary Industry and Fisheries, Queensland Government, were also founding partners in the development of the online Tropical Forages tool to support forage selection.

The future

Over the past 30 years, the forage programmes and gene banks in CGIAR have focused on building their germplasm collections to cover a broad range of genetic diversity of tropical and subtropical forages to meet user demands, studying the collections to characterize and evaluate diversity and understand the traits in specific accessions, and improving their facilities to securely conserve the germplasm. Going forward, the focus will continue to be on the core operations that are essential to conserve and manage the diversity but with increased emphasis on efficiency and value for money in gene bank operations and on demonstrating the value and impact of that investment. This will include the following:

- Quantifying the diversity within the collections to understand how much of the genetic diversity in key species is already held *ex situ* and how much remains at threat of genetic erosion in the field where attention needs to be given. This will involve working with partners in national forage gene banks to elucidate the geographical origin of populations, identify gaps and determine priorities to fill them.
- Describing the diversity of important forage traits using genomic tools to understand the relationships among traits and identify genes responsible for particularly important plant traits that can be used in forage selection and breeding.

- Making more and better use of the collections by posting information about the collection and traits in specific accessions in global genetic resources web databases such as Genesys, ensuring sufficient disease-free seeds for distribution and sharing knowledge on forages through the online forage selection tool.
- Improving efficiency and effective management of the germplasm by identifying and eliminating genetic duplicates from the collections, using genomic tools and identifying core collections for further focus and study.
- Improving facilities and procedures in laboratories that support more extensive use of genomic tools and increased use of eco-friendly energy. Solar and wind energy can both reduce the environmental footprint of gene banks and can also substantially reduce the costs of conservation and will be used more extensively in improved facilities.
- Continuing a gender-balanced capacity-building effort to support global efforts in forage conservation and sustainable use and make better use of the collections. This will include training, internships and graduate scholarships, mentoring, developing and supporting communities of practice, online training and knowledge sharing.
- Working closely with the CGIAR Research Programme (CRP) on Livestock, information will be collected on user demand for forages and traits, documenting the delivery pathways from the gene bank to forages production and adoption of forages on farm to better document the impact and use of the forage collections. These data will be used to estimate current and option values.

Introduction[1]

Identifying and managing biological diversity is a component of crop improvement to ensure a pool of genetic material for selection and breeding for current and future needs arising from land scarcity, population growth and the increasing demand for food (Hawkes, 1971). Tropical and subtropical forage genetic resources are particularly important because few tropical forage breeding programmes remain in existence,

and they have limited species coverage (Sandhu *et al.*, 2015). With increasing feed demands from livestock intensification, rapid genetic erosion of forage diversity in many regions and the need to select new material, the forage collections held at ILRI (beginning in 1983), CIAT (beginning in 1972) and ICARDA (beginning in 1985) are key to feed development. The knowledge generated from research on forage diversity allows scientists to identify genotypes that have higher feed potential and are adapted to changing environmental conditions, and to support plant breeding programmes in the generation of new material (particularly with tolerance to heat, droughts and flooding, and pests and diseases), which are becoming of increasing importance to respond to climate change.

This chapter outlines the impact of forage diversity conservation, characterization and distribution work under the international network of forage collections in CGIAR.

Coverage of the International Forage Collections in CGIAR

There are three major international forage genetic resources collections held in CGIAR at CIAT (Cali, Colombia, established in 1972), ICARDA (Aleppo, Syria, established in 1985) and ILRI (Addis Ababa, Ethiopia, established in 1983) with an estimated total of 72,000 distinct accessions of 1600 species. These collections are held 'in trust' as international public goods. The largest collection is held by ICARDA with 38,955 accessions of 447 species and includes subtropical and Mediterranean forage legumes adapted to dry areas. The CIAT gene bank conserves more than 23,000 forage accessions of 737 species with a large collection of forage legume germplasm adapted to low-fertility acid soils. ILRI conserves 18,672 accessions representing about 1600 species, including the major collection of African grasses and tropical highland forages, as well as a large collection of tropical herbaceous forage legumes. The World Agroforestry Centre (ICRAF) holds a collection of fodder tree germplasm, which complements the collections held in CIAT and ILRI.

The germplasm of CGIAR is governed under the Multilateral System of access and benefit sharing of the International Treaty on Plant Genetic Resources for Food and Agriculture

(ITPGRFA). Most of the accessions were acquired before the entry into force of the Convention on Biological Diversity (CBD) on 29 December 1993 and are in the public domain. Collections were made with the understanding that all the materials could be made freely available for any agricultural research, breeding and training purposes. The germplasm was placed in trust as a global public good under agreements between the Centres and the Food and Agriculture Organization of the United Nations (FAO) in October 1994. In October 2006, the Centres then signed an agreement to place the germplasm held in trust under the FAO agreement under the Multilateral System of the ITPGRFA. The CGIAR centres claim no ownership and seeks no intellectual property rights over the germplasm and related information. To ensure continued free availability of this germplasm, material is distributed with the Standard Material Transfer Agreement (SMTA) of ITPGRFA and requires all recipients of its germplasm to accept the same conditions.

Germplasm was collected by ILRI and CIAT until 1993 when the CBD came into force and clarity over access and benefit sharing from the use of crop diversity was questioned and collections were halted. Issues of access and benefit sharing were resolved with the Nagoya Protocol to the CBD in 2014, paving the way for future collection and gap filling. Temperate forages continued to be collected by ICARDA because many of them are specifically listed under the Multilateral System of ITPGRFA, making the legal framework for collection clearer. Many tropical forage species are not included in the Multilateral System, which has resulted in reduced collection activities. ILRI, CIAT and ICARDA make the germplasm freely available as part of a global effort to promote genetic resources conservation and use.

Forage germplasm maintained in the ILRI gene bank

ILRI began assembling forage germplasm for use in African farming systems in 1983 as the International Livestock Centre for Africa (ILCA). Since its establishment, the collection had grown to 18,672 accessions in early 2020. Tropical grasses, herbaceous legumes and trees are conserved, representing 426 genera. ILRI collected forage germplasm in sub-Saharan Africa from 1983 to 1993, although the majority of accessions were donated by national partners. A major donor has been CSIRO, Australia, which gave almost 8000 accessions. Most of the collections were made in collaboration with CIAT and Bioversity International (formerly the International Plant Genetic Resources Institute (IPGRI), including 542 accessions of *Brachiaria* spp. that are jointly held by ILRI and CIAT. Forage collections made by Bioversity International in sub-Saharan Africa were also donated to ILRI. ILRI studies the diversity in the collection and promotes knowledge of forage crops with the goal of allowing users to make better-informed choices to select accessions and species best suited to their needs.

ILRI's collection contains germplasm from 160 countries. Much of the collection (43%) is from sub-Saharan Africa, with 17% collected in Ethiopia. In total, 97% of the accessions stored in the ILRI gene bank came from collections made in the wild in rangelands and grasslands, with only 3% represented by cultivars of common forages that are already out of plant variety rights and can be made freely available (Table 12.1).

Forage germplasm maintained in the CIAT gene bank

Forage genetic resources at CIAT have been a continuing activity since the inception of CIAT

Table 12.1. Number of forage accessions conserved at ILRI, by region. (Data from ILRI gene bank, June 2018.)

Forage type	Asia	Australasia and the Pacific	Europe	Latin America and the Caribbean	North America	Sub-Saharan Africa	West Asia and North Africa	Unrecorded regions and cultivars
Browse	492	334	205	1,052	32	974	22	614
Grasses	259	44	20	2,778	159	2,707	53	883
Herbaceous legumes	865	472	264	2,598	116	4,358	238	1,633
Total	1,616	850	489	3,928	307	8,039	313	3,130

in 1972 (Schultze-Kraft *et al.*, 2020). The first phase until 1993 focused on assembling and using the forage germplasm collection for forage-based livestock production on acid, low-fertility soils in tropical American lowlands, particularly savannahs. The objective was to create a germplasm pool that was as diverse as possible for cultivar development via selection for direct use or, if natural variability fails to provide the desired combination of traits, via breeding. With a total of approximately 23,000 accessions (about 21,500 legumes and 1500 grasses) from a total of 75 origin countries, the CIAT collection is the largest tropical forage germplasm collection worldwide (Table 12.2). Its value lies in its focus on plants from, and subsequently adapted to, acid, low-fertility soils, and on legumes. The majority of the legume accessions came from collections made by CIAT, in collaboration with national partners, in South and Central America and South-east Asia, with the remainder acquired from donations from major tropical forage collections. More than 9000 accessions were received as donations, among them, in

2006, a significant part of CSIRO's former Australian Tropical Forages Collection. Over half of the grass accessions in the collection were acquired from donations, with 45% collected by CIAT, mostly in collaboration with ILRI and national partners in sub-Saharan Africa.

Forage germplasm maintained in the ICARDA gene bank

The ICARDA gene banks hold a large and highly diversified collection of temperate/Mediterranean forages including globally important and unique collections of *Lathyrus*, *Medicago*, *Pisum*, *Trifolium* and *Vicia* spp. (Table 12.3). This collection is unique in terms of its geographical coverage, originating from 112 countries, its species coverage with 631 taxa including many neglected but potentially important species, and with 20,831 accessions collected by ICARDA in collaboration with partners. The bulk of the collection is still conserved in the gene bank in Syria. Since 2014, all gene bank core activities

Table 12.2. Number of forage accessions conserved at CIAT, by region. (Data from CIAT gene bank database, June 2018.)

Forage type	Asia	Australasia and the Pacific	Latin America and the Caribbean	North America	Sub-Saharan Africa	West Asia and North Africa	Unrecorded region and cultivars
Trees and shrubs	373	13	336	106	61	–	108
Grasses	12	1	150	1	1,103	3	381
Herbaceous legumes	2,658	152	14,209	1,237	710	1	1,525
Total	3,043	166	14,695	1,344	1,874	4	2,014

Table 12.3. Number of cultivated and wild accessions and taxa of forage germplasm conserved at ICARDA. (Data from the ICARDA germplasm database, March 2020.)

Genus	Cultivated		Wild and Uncertain		Total	
	Accessions	Taxa	Accessions	Taxa	Accessions	Taxa
Lathyrus	2,703	17	1,748	51	4,451	55
Medicago	466	29	9,603	108	10,069	109
Pisum	1,941	11	4,188	13	6,129	15
Trifolium	185	23	5,555	95	5,740	97
Vicia	711	31	5,852	87	6,563	87
Other legume forages	131	15	4,287	193	4,418	198
Other non-legume forages	56	7	1,488	114	1,544	116
Total	6,193	133	32,721	661	38,914	677

have been relocated to Lebanon and Morocco. New facilities are being established, and regeneration and characterization are ongoing to reconstitute the active and base collections and to describe the diversity. ICARDA is also working towards promoting *in situ* conservation and sustainable use of dryland agrobiodiversity including crop wild relatives and forage/range species. The activities include the identification of biodiversity hot spots for protection and recommendation of management plans.

Gaps in the germplasm collections

Although the collections in CGIAR are diverse collections of grasses, legumes and trees in terms of numbers of species and genera, there are still important gaps in the collections, which remain far from representative of the geographical diversity of tropical Poaceae and Leguminosae. Geographically, there are few accessions from Sudan, Somalia and Uganda in East Africa, from Benin, Côte d'Ivoire and Ghana in West Africa, and from Angola and Mozambique in southern Africa in the collections. All these areas are centres of diversity for tropical grasses, and collections from these semi-arid regions may contribute traits of importance for selection of genotypes adapted to drylands. Germplasm of species better adapted to areas with frost and drought are needed for the tropical highlands and subtropical regions. Some important species are still under-represented with relatively small numbers of accessions, such as Napier grass and Guatemala grass. ICARDA and the School of Biological Sciences at the University of Birmingham, UK, undertook ecogeographical surveys and gap analysis for temperate forage genera (*Lathyrus*, *Medicago*, *Pisum*, *Trifolium* and *Vicia*) and identified areas for further collecting, mainly to target threatened wild species with adaptive traits that are needed for developing new varieties that are better adapted to climate change. A complementary analysis showed that the Fertile Crescent region has the highest species richness with the Syrian–Lebanese border deserving efforts for ensuring *in situ* conservation and management.

Important considerations in expanding the germplasm collection include what additional diversity is under threat from genetic erosion in the wild, what additional diversity could be gained from gap filling, whether there are important traits demanded by users that are missing from existing germplasm, and whether the benefits of adding additional collections outweigh the cost of collection and conservation. Additionally, with most of the important tropical forage species outside of the list of Annex 1 crops that are key to food security under the ITPGRFA, reaching bilateral agreements on access and benefit sharing under the Nagoya Protocol will be complicated and, in some cases, may not be possible in the short term. These concerns, together with the limited current use of forage germplasm in breeding programmes (Sandhu *et al.*, 2015), could lead to the conclusion that, until there is more widespread use of forage germplasm and adoption of forages on farm, there is little need to fill the gaps. However, gene banks are also important as sources of genetic diversity for the future, and future needs for traits are uncertain and difficult to predict based on current use, so gene banks remain the most important source of forage diversity that is being rapidly eroded in the wild due to overuse, land degradation and fragmentation. For example, traits such as resistance to a new disease are only sought once the disease spreads and its economic impact is realized. This was the case for stunt disease in Napier grass, which has only been observed over the last 20 years, leading to research to identify resistant genotypes (Asudi *et al.*, 2015; Wamalwa *et al.*, 2017) to protect dairy systems in East Africa that rely on Napier grass as their most important feed (Muyekho *et al.*, 2003).

The question of whether it is better to collect and store in gene banks or to look for diversity on farm or, in the case of forages, in the extensive grasslands where they originated and continue to evolve and adapt must also be considered. Assessments of amounts of genetic erosion, threat levels and the amount of diversity present in the ecosystem are needed to make such decisions. Such assessments have focused on systems and ecosystem scales and not on intraspecific and genotypic variation (West, 1993) or general rangeland degradation (Engler and von Wehrden, 2018). The lack of evidence on the threat of genetic erosion for forage genotypes has led to scientists assuming the worst-case scenario and making *ex situ* collections of forages for gene banks as a precaution to conserve diversity that

could well be lost through overgrazing and poor land management practices were they to be left *in situ*. Given the levels of protection offered to rangelands in national parks in sub-Saharan Africa (Reid *et al.*, 2005), *ex situ* may not have been the best choice for some species that are well protected in the wild. However, having diversity readily available in the gene bank enhances access to a wide range of genotypes for diversity studies and distribution, thereby increasing their use and allowing an assessment of their potential value. In the face of lack of evidence on whether collection is essential, decisions are based on economics and the perceived value of the resources (Evenson *et al.*, 1998).

Describing Forage Traits in Germplasm to Support Use

The value of a gene bank is realized through the use of the genotypes or accessions that are accessed from the collection. The more information available about the diversity and traits in the collections, the higher the probability that accessions will be used, and therefore considerable effort is placed on research to characterize the accessions. ILRI, CIAT and ICARDA's research on forage genetic resources has focused on diversity within the genotypes for their use as feed and for natural resource management. Such research includes assessing variations in phenotype, agronomic traits and nutritional traits, and in resistance to diseases and insects. Diversity within and between populations results from differences in genes and alleles that make up the genotypes represented within the accessions. Each accession can be considered as a representative of diversity within the species.

Genetic diversity can be considered as a proxy for future value of an accession. From the 1990s, calculation of intraspecific diversity has been considered to determine what to conserve and how much to conserve. Diversity is measured on cardinal distances between individuals based on similarity and dissimilarity (Weitzman, 1993). This concept is frequently used in the development of hierarchical diversity trees or phylogenetic trees (dendrograms) that show how one accession relates to another (van Hintum, 1995; Osawaru *et al.*, 2015).

Diversity can be measured through allele frequency in accessions of the same species and genetic distance between accessions, often expressed using Nei's genetic distance (Nei, 1987). Genomic diversity and heterozygosity are estimated over several loci to obtain an estimate of genetic diversity. These studies support functional genomics and association mapping of phenotype and genotype and allow identification of genes or markers influencing specific traits. Information generated from this research is used to develop core collections and subsets for specific use cases and to identify superior accessions for evaluation, distribution and ultimately use in farming systems.

Understanding the diversity and expression of specific traits in each accession allows users to select genotypes to match their environment and production systems and supports increased use of the germplasm. Characterization and selection of traits are very context and species specific, and different traits may be selected when screening germplasm for different purposes. A range of traits have been used to describe and cluster grasses and legumes based on standard descriptors for forage grasses (IBPGR/CEC, 1985) and legumes (IBPGR/CEC, 1984). Standardized observation strategies were tested for morphological characterization of forages at ILRI to ensure that methods used for crops were appropriate for forages (van de Wouw *et al.*, 1999). Characterization of the germplasm is ongoing for minimum morphological descriptors in the forage collections of CGIAR. More extensive characterization has been undertaken to describe the diversity among accessions of species with high economic importance. In ILRI, the focus has been on forage grasses to estimate the diversity in the collections and to select promising accessions for further evaluation of productivity and feed value. In CIAT, the main focus was on the evaluation and introduction of forage legumes until the mid-1990s, after which both legumes and grasses were studied to select promising germplasm to meet livestock producer demands in a range of farming systems. Given their potential for scaling through public–private partnerships, CIAT has concentrated its breeding activities on forage grasses. ILRI has focused mainly on selection of promising genotypes of Napier grass because of its importance in dairy systems in East Africa (Negawo *et al.*,

2017, 2018), while CIAT since the 1990s has focused on *Brachiaria* spp. because of the potential for grazing systems on acid soils in Central and South America (Labarta *et al.*, 2017), and research has been expanded to *Panicum* spp. evaluation to select and breed for specific production niches throughout the tropics.

Genomics has wide application for describing diversity and promoting the use of accessions in gene banks (Kilian and Graner, 2012; Wambugu *et al.*, 2018). Molecular approaches provide useful selection tools to complement morphological characterization. Molecular marker and DNA sequence analysis can identify regions of the genome responsible for the expression of economically important traits, such as improved digestibility and insect and disease resistance, that can be used in marker-assisted breeding. Molecular markers can also be used to confirm the parentage of individuals in a breeding population, for genetic diversity analyses and fingerprinting individual accessions, for taxonomic identification, for finding duplicates within gene bank collections, and for understanding systematic and evolutionary relationships within species.

Diversity studies are also important for differentiating among species and botanical types for taxonomic identification and for understanding the probable geographical origin and evolution of crops and their related species. Molecular approaches have been applied to elucidate taxonomic relationships and genetic distinctness of accessions. While application of genomics is still in the early days for forages, these techniques have been applied to studying diversity among genotypes from the forage gene banks for species in the genera *Lablab* (Maass *et al.*, 2005; Robotham and Chapman, 2017), *Sesbania* (Jamnadass *et al.*, 2005), *Stylosanthes* (Huang *et al.*, 2017), *Pennisetum* (Lowe *et al.*, 2003; Wanjala *et al.*, 2013; Negawo *et al.*, 2017, 2018), *Brachiaria/Urochloa* (Torres, 2005), *Flemingia* (Andersson *et al.*, 2006) and *Cratylia* (Andersson *et al.*, 2007).

Nutritional traits such as protein, fibre, lignin and other chemical components that can limit digestibility are also used to characterize forages and to predict animal performance (Cherney, 2000). Preliminary research on the use of polyphenolic profiles determined by use of high-performance liquid chromatography on a limited number of accessions indicated that there were some distinct profiles that could classify accessions into groups but that they were not sufficiently unique to reliably identify accessions (Heering *et al.*, 1996; Plumb *et al.*, 1996).

Data from morphological, nutritional and genomic characterization can be combined to cluster accessions and to develop core collections from the clusters. Core collections have been described as a limited set of accessions that represents the breadth of genetic diversity contained in the whole collection (Hodgkin *et al.*, 1995; van Hintum *et al.*, 2000). They are useful to rapidly screen a species for potential use from a few accessions in a cost-effective manner, or mini-cores can be created by selecting a subset of the core based on specific characteristics or traits. Clusters were identified in *Lablab* spp., allowing identification of dissimilar accessions to cover maximum diversity for designation as a core collection (Pengelly and Maass, 2001). Users can select either all accessions of a cluster of a specific type of direct interest or take one or two accessions from each cluster to screen a wider range of morphological variation within a limited number of accessions.

Much of the evaluation of forage germplasm has been done by partners through research networks using common protocols to identify broadly adapted accessions as well as genotypes with specific trait adaptation. In Latin America and the Caribbean and in West Africa, forages were screened for adaptation to acid soils, and promising accessions were identified for further promotion as 'best bets'. In East Africa, the focus was on identification of species adapted to the tropical highlands and on disease-resistant Napier grass, while in West Asia and North Africa, the focus was on drought-tolerant forages for the dry areas and cold-tolerant medics for use in Iran. These best bets were later elevated for larger-scale seed production (see Chapter 13, this volume) to provide sufficient seed supply to support forage adoption in the ILRI programme in Kaduna, Nigeria, and the seed units of ILRI, CIAT and ICARDA.

Although emphasis has been placed on characterization and evaluation of the genetic resources, there is still insufficient information on specific traits such as disease and drought resistance in large parts of the collection that limits use. This gap could be partly addressed if users provided more feedback on their research

and on the use of germplasm as forage and feed. The CGIAR gene banks are assigning Digital Objective Identifiers to the accessions to better track use of germplasm in publications and forage release in future.

Value of Forage Germplasm

The primary source of value of germplasm lies in the actual or potential use of the collection. The use value may depend on the extent of uniqueness of a collection and the number of unique traits or traits that are present at low frequencies. This raises the issue of how large a collection is needed and what the chance is of finding rare alleles. The probability of finding a specific trait can be modelled mathematically. For example, if a trait is present with a 0.01 frequency in the population, then there is an 87% chance of finding the trait within 200 accessions. Screening a larger number of accessions increases the probability of finding the trait, but as the number of accessions increases, the likelihood that the trait has already been detected is high and adding more accessions will not greatly increase the chance of finding the trait for added cost (Zohrabian *et al.*, 2003). This theory would indicate that there is little need for large germplasm collections if the focus is only looking for traits. However, selection and breeding are done on whole genotypes and the trait may be in an unsuitable genetic background for the production system. Currently, genotypes provide a short, cost-effective path to cultivar release, but as techniques and costs of gene editing decline and more genomic information is known about accessions, large collections may become redundant.

The value of an individual accession may only be noticed when a new gene or allele that addresses a major production problem, such as disease or climate adaptation, is found in the accession. Information on the traits in an accession increases the chance of use and therefore the value of an accession. This makes use components easier to quantify for the accessions that have been characterized for yield, nutritive value, or insect and disease tolerance. Use value is much more difficult to estimate for the remaining accessions that lack detailed data on their potential for future use but which might have potential for as-yet-undocumented traits or

as a source of genes for adaptive traits. Non-use components are even more difficult to quantify and value because of the difficulty in estimating the existence or bequest value of an accession.

As a result of the germplasm evaluation and selection work at the centres within their respective mandate areas, many accessions from the centres' collections were released by national partners. centre accessions have also been adopted by end users without a formal and documented release, and the real number of such informal distributions is probably much higher than documented. In most cases, there is a lack of accurate information about where released cultivars from centre or other sources have been used, in which areas and with what productivity effects.

Impact of the CGIAR Forage Gene Banks

Forage germplasm distribution

A major focus of any gene bank is to make germplasm available for production use through further evaluation, selection and plant breeding by partners. The Centres' collections supply forage seed to collaborators in addition to their work in collecting, evaluating, conserving and regenerating forage germplasm. Small experimental quantities of seeds or cuttings are provided from the in-trust collection under the terms of the SMTA as part of the CGIAR open-access policy to maximize utilization of germplasm for research, breeding and training. The CGIAR centres have supported the use of forage germplasm through production and distribution of seed or plant materials. Distribution figures have been used as a proxy for use of the collections. While they certainly provide information on the demand for different species and accessions, it is very difficult to link forage germplasm to actual use in livestock systems and to attribute forage use and impact back to the gene bank accessions unless the materials are used in variety development. Many of the samples distributed will not meet user needs or show superior performance in the location. Only a small percentage of the materials received will be taken forward from evaluation to

adoption and use. Estimates from past variety development in CIAT indicate that about 1% of the grass collection and less than 0.2% of the herbaceous legumes have been released as named varieties (see Table 5 in Schultze-Kraft *et al.*, 2020).

Since their establishment, the CGIAR gene banks have provided 137,816 accessions for forage research and development activities in 158 countries. Over 30 countries with a strong livestock sector and demand for feed have received more than 1000 samples each from the gene banks over this period (Fig. 12.1). On average, the Centres freely distribute more than 5000 samples of forage germplasm globally per year for evaluation and selection by partners and for further development and use by smallholder farmers. The majority of samples have been provided to Colombia, Ethiopia and Syria, where the

gene banks were physically located, and partners were aware of and had easy access to the genetic resources available.

In accordance with their role, the gene banks mainly cater to national and international requests to supply a large variety of accessions in small quantities (Fig. 12.2). Most of the samples from the gene bank are supplied to scientists in government agencies, non-governmental organizations, educational institutions, and private farmers and seed producers, with the general purpose of providing germplasm for forage production. In addition, large numbers of samples of forage germplasm have been provided to the Centre's own research and breeding programmes for evaluation and forage development, especially to the breeding programmes of CIAT and ICARDA.
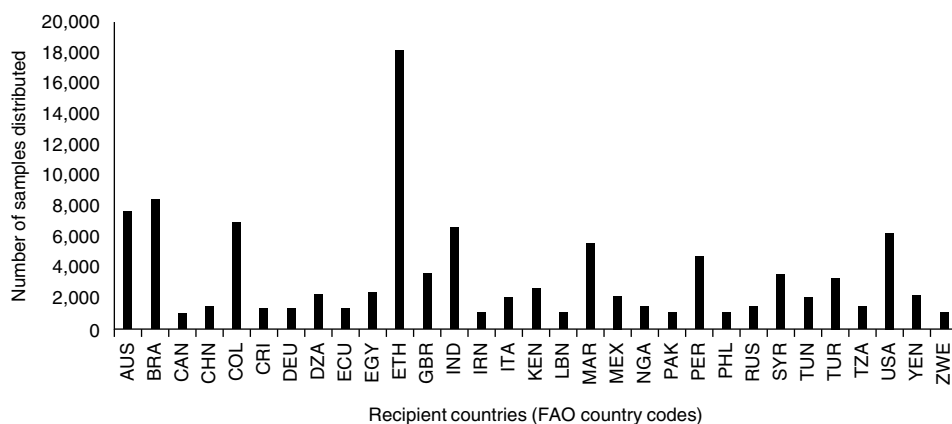
Fig. 12.1. Countries receiving more than 1000 samples from CGIAR forage gene banks.
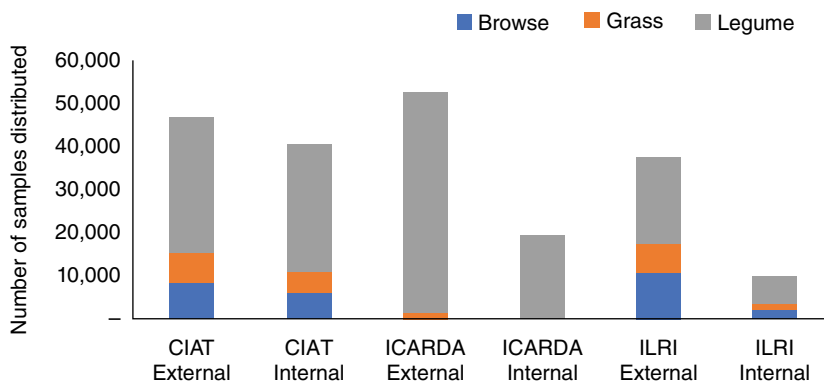
Fig. 12.2. Distribution of samples from CGIAR forage gene banks. (Data from CGIAR gene banks, February, 2019.)

User demand has focused on a limited number of forages that have been perceived to be of high potential for further development as livestock feed. Different species are in demand in the different regions and have been supplied by the CGIAR gene banks based on their respective mandates and locations (Table 12.4) in a complementary way.

Estimating economic benefits of forage gene banks

To estimate the impact of the forage gene bank germplasm, its sources of value must be understood. Forages have some unique features in that they are not directly used as human food but as feed for livestock, which convert the fibre that is inedible for humans into milk, meat and power. Valuation frameworks consider the economic value of plant genetic resources to include both use and non-use components (Smale and Hanson, 2010), both of which can have current and future values. Use values may be derived from the direct use of the product, which for forages could be biomass and feed value of the forage or amount of milk and meat produced when fed to livestock. Use values can also be indirect, including the value of ecosystem or environmental benefits from incorporation of forages into the system. Use values include the option value of having the genetic resources available without knowing whether or not they will ever be used. Non-use values include existence value – the satisfaction that individuals or societies may derive from knowing that something exists and will be available for future needs (Smale and Hanson, 2010). Option value is particularly important for germplasm in *ex situ* collections, which are natural resources and global public goods, and the world community relies on their existence as a resource for future needs.

The discussion of the economic benefits of the forage gene banks is largely limited to showing the number of lines (accessions and hybrids) developed from germplasm maintained in the various collections and subsequently released as cultivars. To estimate economic benefits, field studies are necessary, involving resource economists, to assess areas planted to the new cultivars, crop and livestock production gains, increases in farmers' incomes and non-market benefits (e.g. soil conservation and improvement).

Some attention has been given to estimating the costs and benefits from gene banks (Koo *et al.*, 2003). The costs of conserving accessions in gene banks are easy to calculate, while the expected benefits are quite difficult to estimate.

Costing gene bank operations

The analytical framework used for the cost studies carried out on the CGIAR gene banks in 2008

Table 12.4. Most distributed forage species from the CGIAR gene banks. (Data from CGIAR gene bank databases, February 2019.)

Organization	Species	Class of forage	Number of samples
CIAT	*Desmodium heterocarpon*	Legume	2801
	Centrosema macrocarpum	Legume	2639
	Stylosanthes guianensis	Legume	2455
	Leucaena leucocephala	Browse	2096
	Brachiaria humidicola	Grass	1797
ICARDA	*Pisum sativum*	Legume	13433
	Vicia sativa	Legume	5875
	Medicago polymorpha	Legume	2597
	Lathyrus sativus	Legume	2225
	Vicia narbonensis	Legume	1464
ILRI	*Sesbania sesban*	Browse	2555
	Lablab purpureus	Legume	1982
	Vigna unguiculata	Legume	1457
	Cajanus cajan	Browse	1379
	Stylosanthes guianensis	Legume	1085

and 2009 was the microeconomic theory of production (Pardey *et al.*, 2001). For a gene bank, outputs were considered as numbers of accessions characterized, stored, monitored and regenerated, and inputs were capital, labour, supplies and services. Production decisions involve choosing which outputs to produce in which amounts, with which mix of inputs and input quantities. Optimal resource allocation can be achieved either by minimizing the costs of operation given fixed physical resources and existing technology or by maximizing production subject to a fixed budget and existing technology.

The approach selected by Koo *et al.* (2004) was cost minimization. The costs of running a gene bank vary with target species, type of conservation, location, size of the collection and amount of risk that has to be mitigated in the activities. Most of the benefits of gene bank collections are public goods whose values are both expensive and difficult to estimate and are likely to be unreliably estimated, while the costs of gene bank operations are relatively easy to estimate with a reasonable degree of precision. Pardey *et al.* (2001) reasoned that if the costs of conserving an accession are lower than the lower-bound estimate of the corresponding benefits, it may not be necessary to estimate the actual benefits of each accession.

Koo *et al.* (2003) considered gene bank operations within this production economics framework, looking at the cost of inputs to deliver outputs in terms of stored germplasm and information. Total costs were partitioned into components and each category was then summarized in terms of average and marginal costs. They included variable inputs that are determined by the size of the collection, capital costs that are independent of the size of the collection (up to some limits) and quasi-fixed inputs that are neither fixed nor variable but indivisible large expenses, such as the cost of the gene bank manager and scientific expertise, that are needed independent of the size of the collection (Koo *et al.*, 2003). In this study, costs were calculated for the different gene bank operations and conservation type based on actual annual costs and numbers of accessions for a range of species and locations, taking care to ensure consistency in data collection. This allowed comparisons to be made on operational costs per accession between crops and locations (Koo *et al.*, 2004).

This approach enabled the estimation of possible economies of scale or reduced costs per accession that would come from increases in the size of the collection. The average and marginal costs change with the number of accessions and average fixed or quasi-fixed costs per accession reduce as the number of accessions increases. Marginal costs are the addition to total costs for every accession added to the collection and increase as the number of accessions increases. When inputs are used efficiently and are complementary, the cost of conservation of each accession should decrease.

Management of gene banks based on economics

Management of large collections is based on the science of conservation and economics of different management options. Management decisions based on changes in understanding of seed conservation science, genetic integrity, technology, facilities or staffing affect the costs of inputs. Staff costs, supplies and services increase annually due to inflation, but better use of technology and opportunities for adopting improved operating procedures from better understanding of seed conservation science can reduce the time and supplies needed for routine operations and therefore significantly reduce costs and increase efficiency and cost:benefit ratios (Koo *et al.*, 2004).

These considerations were applied in gene bank costing studies carried out previously on the CGIAR collection in 2009 (Horna and Smale, 2010). Data were compiled by gene bank managers on input use and expenditures and used to estimate average and marginal cost per unit for routine gene bank activities. Data were analysed across all CGIAR gene banks. Gene bank operations are made up of a set of inter-related component activities that occur over the life of the accession. These include acquisition, characterization, safety duplication, medium- and long-term storage, germination and seed health monitoring, regeneration, seed processing, information management, distribution and general management. Gene bank operations are dynamic; some such as storage are incurred annually, while others such as monitoring, regeneration and safety duplication are incurred periodically. In order to estimate annual expenditure,

the overall annual expenditure for the whole operation was used and allocated back over the number of accessions involved in the operation in that year. The study found that the reproductive biology of the species, which determines the type of conservation and regeneration procedures, and level of quality management attained, contributed most to the costs of gene bank operations. Seed crops had the lowest costs of conservation, while vegetatively propagated crops, trees and wild relatives, including forages, had higher costs.

ILRI example of a gene bank costing study

The study on the ILRI data looked at the costs of the different broad categories of forages (annual and perennial grasses, annual and perennial herbaceous legumes, and short- and long-lived fodder tree species) to better understand the costing structure of operational costs (Horna and Smale, 2010). This showed that the quasi-fixed costs accounted for the highest costs in gene bank operations at ILRI (Fig. 12.3). The cost of maintaining an accession varied from US$125 to US$242 per accession per year (Table 12.5), depending on the category of the forage, which was largely determined by the length of life cycle and longevity of the seeds during storage. The study concluded that it was important to take into consideration that the majority of the forages maintained at ILRI are wild species that require special management and have little published information about their breeding systems, seed germination and storage behaviour in gene banks. Regeneration and multiplication of these materials are particularly challenging as the different species have very different behaviours in
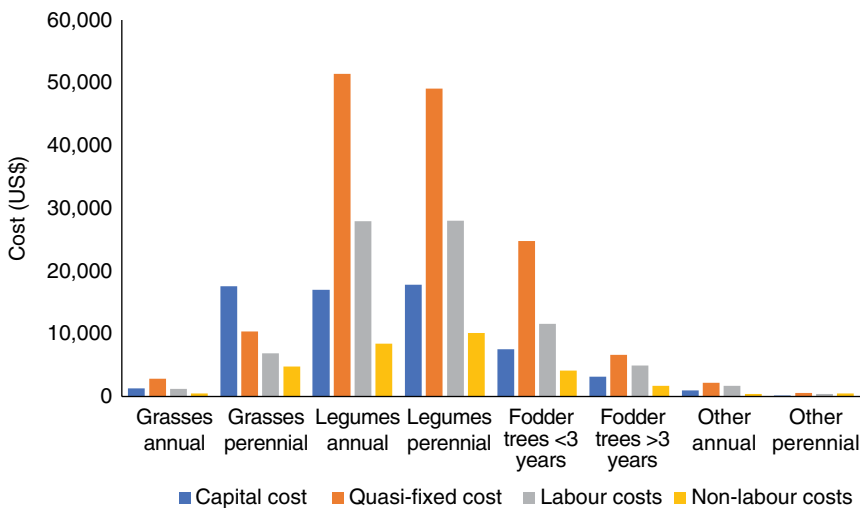
Fig. 12.3. Costs by component and type of forage at ILRI in US$. (From Horna and Smale, 2010.)

Table 12.5. Annual total cost per accession for four forage types, in US$ (*c.*2009). (From Horna and Smale, 2010.)

Forage	Classification	Annual cost per accession
Grasses	Annual	149
	Perennial	171
Herbaceous legumes	Annual	242
	perennial	191
Fodder trees	Short-lived	197
	Long-lived	205
Other forages	Annual	204
	Perennial	125

the field. Therefore, although a small gene bank in terms of number of accessions, the manipulation of a large diversity of materials requires considerable investment in equipment and human capital. Another important cost in using gene bank accessions is the lag between germplasm collection or introduction and cultivar release, which reflects the intensity, and related costs, of research at each step in forage development.

Benefits from use of germplasm

The economic benefits of a specific trait or a specific accession are more difficult to estimate than the value of a species. When different accessions are used in plant breeding the contribution of each accession to the new variety can be estimated from the breeding procedure. Most forage cultivars are selections made directly from accessions, so in forages it is much simpler to estimate the contribution of a specific accession to a cultivar than for crops, where crossing, selection and backcrossing are used in cultivar development. The value of germplasm in use can be measured by the area planted, the yield per unit area and the market price of the crop (or its equivalent when converted into animal products). These data are in short supply for forage production in many countries, making it difficult to come up with good estimates of benefits.

The question remains on how to value the potential benefits from germplasm that is not in use and may not have been fully characterized. Smale and Hanson (2010) concluded that use value is a relatively small component of total value because they have public goods attributes and may not be reaching full market potential in transitional agricultural economies. In some cases, forecasts of future benefits can be estimated based on past benefits and patterns of forage use. The potential benefits from use of an additional accession are usually greater than the marginal cost of conserving it for the long term as seeds in a well-managed gene bank.

Estimating scientific and field benefits of the CGIAR forage gene banks

The scientific benefits of the gene bank are defined as advances in knowledge. The principal form of scientific benefit is the information derived from plant collection and characterization that increases its use value. A second scientific benefit includes the tools for germplasm management in gene banks and in the field.

The field benefits accruing from the use of forages are:

- flows of economic benefits, defined as gains in output or reductions in cost of feed inputs to animal production;
- stocks of economic benefits, defined as gains in asset values, such as soil fertility; and
- environmental benefits, such as carbon sequestration (a stock), soil stabilization (a stock) and water-holding capacity (a stock) or reduced greenhouse gas emissions (a flow).

Estimating these benefits requires data on materials distributed, their use in production and their yield and cost effects.

Success stories in the use of forage germplasm

Forage cultivars have mostly come from selection of more productive types rather than from breeding (Jank *et al.*, 2011). This selection would not have been possible without the sources of germplasm held in the world's forage gene banks. A recent meta-review of global impacts of forage cultivation revealed many data gaps in use of improved forages owing to irregular reporting of forage adoption, with few studies reporting on economic benefits and costs (White *et al.*, 2013).

Most historical success in selection of forage cultivars has been in Australia, which relies heavily on pastures to sustain its lamb and beef industries (Oram, 1990). Some of these selections have been made on germplasm from the CGIAR forage gene banks. For example, in 1994, the University of Queensland registered Mount Cotton, a cultivar of *Sesbania sesban* selected from accession 15036 that is maintained in the ILRI gene bank (Gutteridge and Shelton, 1995). However, despite its identification as very productive and leafy, there is little evidence to suggest that it is widely grown or adopted. Another species of interest currently in Australia is *Lablab purpureus*, because of its fast-growing nature, good protein concentration and the possibility of its use as both food and feed (Pengelly and Maass,

2001). Lablab is already widely grown in the tropics and recently selections have been made from three lablab accessions (13685, 14428 and 14437) provided from the in-trust collection at ILRI to CSIRO in 2004. Five new cultivars were selected from the three accessions and are in the Australian release process (D.S. Loch, personal communication). The original germplasm will continue to be freely available from the ILRI in-trust collection and has also been deposited in the Australian Pastures Genebank.

Documentation of large economic benefits from use of improved forages is rare; a particularly important documented case is in Brazil where improved *Brachiaria* spp. grasses are grown on an estimated 100 million ha (Jank *et al.*, 2014). Except in rare cases, it is even more difficult to attribute any of these benefits to use of accessions from the forage gene banks owing to lack of information. Since 1980, a total of 29 legume and 39 grass cultivars have been released in 17 countries, mostly in Latin America and the Caribbean (Schultze-Kraft *et al.*, 2020). These materials are from the CIAT collection and can be directly attributed to accessions in the CIAT gene bank. However, with some exceptions, the extent of planting and economic impact from use of these cultivars in tropical livestock systems is not well documented.

Although only a few of the registered cultivars came from accessions maintained at the ILRI forage gene bank, ILRI has had a broader impact through the distribution of forage legumes globally to national programmes. The largest number of accessions distributed was in Ethiopia, where a large part of the forage germplasm being evaluated and the old cultivars in use on farm originated from the ILRI gene bank (Hanson and Tedla, 2010; Jorge *et al.*, 2012).

The domestication and evaluation of introduced forage germplasm has allowed some Mediterranean species to play a major role in diversifying the livestock feeding calendars and sustaining the crop–livestock–pasture-based farming systems in Australia, New Zealand, the USA, South Africa and several other regions with Mediterranean-type climates (Cocks and Benett, 1996; Suttie *et al.*, 2005). In Australia alone, more than 50 cultivars of various forage species were released from direct selections from collected genetic resources. Forage breeding started in the 1950s and only a few forage

species are benefiting from hybridization and selection efforts for cultivar development, including lucerne (*Medicago sativa*) and a few temperate legumes and grasses such as *Lolium perenne*. The breeding efforts are mainly by the private sector and their success is tightly linked to efficient seed production, certification and marketing.

The importance of Mediterranean forages is highlighted by several examples:

- Lucerne is among the most important perennial legume forages in the world. Despite extensive breeding efforts, little improvement in potential biomass production has been achieved during the last 60 years, but the use of wild relatives has contributed to enhance resistance to diseases and pests such as leafhopper to maintain high productivity. Most of the perennial *Medicago* spp. can be used for further improvement of *M. sativa* but can also be domesticated as new forage resources. While lucerne breeding is benefiting from genetic transformation efforts for tolerance to herbicides, genetic resources are crucial for further improvement of lucerne and other forage legumes as animal feed, nutritional food and even for pharmaceutical use.

- Annual medics, mainly the self-regenerating species such as *Medicago truncatula*, *M. polymorpha* and *M. littoralis*, have contributed significantly to improving and sustaining cereal and livestock production through their introduction in rotation with cereals within the ley-farming systems developed by Australia and promoted in other regions of the world with Mediterranean climates (Cocks and Bennett, 1996). In Australia, medics occupied 40 million ha, but their importance has decreased since 2005, mostly due to the effects of herbicides used on cereals. However, herbicide tolerance is found in some accessions of *M. littoralis* and *M. truncatula*.

- White clover (*Trifolium repens*) originating from the Mediterranean region forms the basis of the sown pastures covering 9 million ha in New Zealand, 5 million ha in Australia and 5 million ha in USA and spreading to other regions in Europe and Latin America (Mather *et al.*, 1996). New cultivars are being developed in the UK to

replace the old cultivar 'Grassland Huia', released in New Zealand.

- The Dryland Agricultural Research Institute (DARI) in Iran, in collaboration with ICARDA, has tested large numbers of accessions of forage legumes obtained from the ICARDA gene bank for use in the wheat/barley-based livestock systems in the highlands of Iran. Preliminary results showed the good adaptation of some accessions of *Vicia panonica* and *V. ervilia*. Two of the accessions were released in 2010 and in 2013, and now almost 40,000 ha are planted. However, seed multiplication remains a challenge for larger adoption of these species.

- Grass pea (*Lathyrus sativus*) is of economic and ecological significance in South Asia and sub-Saharan Africa and is one of the neglected crops with good tolerance to harsh conditions and with multiple uses. Although it is rich in proteins, when overconsumed, the oxalyldiaminopropionic acid (ODAP) toxin may cause paralysis of the lower limbs. Several accessions of *L. sativus* and *L. cicera* with low ODAP content from ICARDA were selected and used in breeding. More than 20 lines were released by national agricultural research programmes including Wasie in Ethiopia in 2005, Ali-Bar in Kazakhstan in 2004, Tarman for the highlands of Turkey in 2002, and more recently, two varieties (BARI Khesari 3 and 4) with low ODAP content were released in Bangladesh (Kumar *et al.*, 2013).

Example of impact from use of Napier grass germplasm from ILRI

ILRI has focused attention on Napier grass because of its importance as the major forage for East African cut-and-carry dairy systems due to its wide adaptation, high yield, and ease of propagation and management. Napier grass provides more than 50% of the feed for more than 0.6 million smallholder dairy farms in Kenya (Orodho, 2006). More than 80% of milk produced and sold in Kenya comes from smallholder farmers with less than 2 ha of arable land (Thorpe *et al.*, 2000), who feed one or two cross-bred dairy cows on small plots of Napier grass. With fodder in high demand, producing

and selling Napier grass as feed has good potential for improving smallholder livelihoods (ILRI, 2013).

Dairying in Kenya depends on a few Napier grass genotypes, many of them susceptible to two major diseases – head smut, caused by *Ustilago kamerunensis*, and stunt, caused by a 16SrX1 group phytoplasma, both of which are spreading in the country (Jorge *et al.*, 2014). Although other grasses can be introduced into the system, none is as productive, as broadly accepted or as well suited to the system as Napier grass. Losses in feed supply caused by these diseases are serious for smallholders (Mwendia *et al.*, 2006, 2007).

Head smut is spreading across Africa from west to east and in Kenya, where yield losses in Napier grass of up to 46% due to head-smut infection have been reported (Farrell, 1998; Mwendia *et al.*, 2007). The diversity of Napier grass lines held in the forage collection at ILRI was an obvious target to look for tolerance. In 1993, the Kenya Agricultural and Livestock Research Organization (KALRO) evaluated ten accessions from the collection of Napier grass from the ILRI gene bank for tolerance to head-smut disease and identified two accessions (ILRI 16791 and 16798) that showed tolerance. These were released as Kakamega I and II, and in 2007 were reported as being used by 19% of farmers surveyed in smut-affected areas (Mwendia *et al.*, 2007; ILRI/KALRO, 2013). More recently, more germplasm from the ILRI gene bank has been screened, and one additional accession, 16806, was found to be resistant, while three others showed tolerance to smut (Omayio *et al.*, 2015; Kariuki *et al.*, 2016). Accession 16806 was more productive than Kakamega I in the high potential area of Muguga in Kenya producing 51 t dry matter/ha/year compared with Kakamega I, which produced 42 t dry matter/ha/year. This is equivalent to the best-yielding cultivars of Napier grass under farm conditions (Munyasi *et al.*, 2015).

Based on figures from Mwendia *et al.* (2007), production losses due to smut on smallholder farms would be about 0.2 t/ha/year for zero grazing systems, giving an annual loss to a smallholder farmer equivalent to 22 days of feed for a cow, a loss in income of 220–330 L of milk. Considering the cost of Napier grass at US$15/t and an estimated yield under low-input smallholder

conditions of 18 t/ha/year, a reduction of 40% of the yield due to smut would reduce the amount of fodder available for sale and cost a farmer US$108 per year in lost income from Napier grass sales (ILRI/KALRO, 2013). A recent economic analysis of the costs of production and gross margin analysis per year from growing Napier grass in 2017, showed an expected profit of US$245 per acre per year (NAFIS, 2017). This is equivalent to US$605/ha, so a reduction of 40% of the yield would result in losses of about US$242/ha/year at current costs for Napier grass.

Stunt disease is even more devastating in East Africa than smut and is spreading rapidly in Napier grass-growing areas (Khan *et al.*, 2014), causing significant yield loss for smallholder dairy farmers in Kenya, Uganda and Tanzania. Yield losses of 40–90% have been reported due to stunt in western Kenya (Khan *et al.*, 2014), causing reductions of up to 65% in milk yield over the year. Again, the national partners turned to the ILRI forage germplasm collection to look for resistance, and as a result, two different accessions 16789 and 16807, have been identified that have tolerance to stunt (Wamalwa *et al.*, 2017). With yield losses of 40–90% from stunt, a conservative estimate of production loss due to the disease would be similar to head smut for lost feed and lost income from sales of milk or fodder for many smallholders in stunt-affected regions. However, in areas where production is reduced by 90%, losses would be very severe with little production of feed for dairy and potential losses of almost US$550/ha/year.

Use of the two head-smut resistant accessions and two stunt-tolerant accessions from the ILRI gene bank can reduce the economic loss and benefit smallholder farmers in disease-affected areas. Estimating the economic loss requires data on areas cultivated and areas of the resistant accessions that have been planted. Data are scarce because many farmers are not sure of the varieties that they grow with different genotypes being grown under the same name and with the same genotype being grown under different names (Jorge *et al.*, 2014). Using a conservative estimate of 600,000 smallholder dairy farmers in Kenya on farms of about 2 ha and using an average of 4% of their land for growing Napier grass, there are 48,000 ha of Napier in Kenya where use of the tolerant accessions could prevent loss of income of over U$11 million/year. Similar benefits can be projected in Tanzania and Uganda where the diseases are also spreading.

Capacity building

Scientific and technical capacities are a major constraint to forage development. To build this capacity, ILRI, CIAT and ICARDA have provided training for scientists, technicians and farmers in germplasm management and forage seed production. At ILRI, 50% of the 60 beneficiaries taking individual academic training since 1983 were from Ethiopia, plus a wide range of other African, European, Asian and Western countries (Fig. 12.4) with a 50:50 split between males and females. Short courses and workshops were held on demand, and a large number of partners have been trained in both short courses and academic fellowships in ILRI. Earlier courses from 1983 to 1990 focused on forage evaluation and gene bank management; most recent courses have focused on forage seed production and quality management systems for gene bank operations.

At CIAT, the capacity-building-related impact of its forage genetic resources was sought via its entire Tropical Pastures/Forages Program including activities in different subregions of Latin America and the Caribbean, annual training courses, and network-based multilocational germplasm testing within the Red Internacional de Evaluación de Pastos Tropicales (RIEPT, International Tropical Pastures Evaluation Network). During the period 1978–1990, the CIAT Tropical Pastures Program, in its coordinating role in the RIEPT network, held a yearly course, 'Programa de Capacitación Científica en Investigación para la Producción de Pastos Tropicales'. The course was aimed at researchers from Latin America and the Caribbean and consisted of an intensive multidisciplinary phase, in which all participants were exposed to lectures and practical training in all disciplines represented in the programme – thus including the field of genetic resources of forage plants and germplasm handling – and a specialization phase. With an average of 20 participants per course, a total of about 250 researchers were trained during the 13-year period, of which ten specialized in gen-
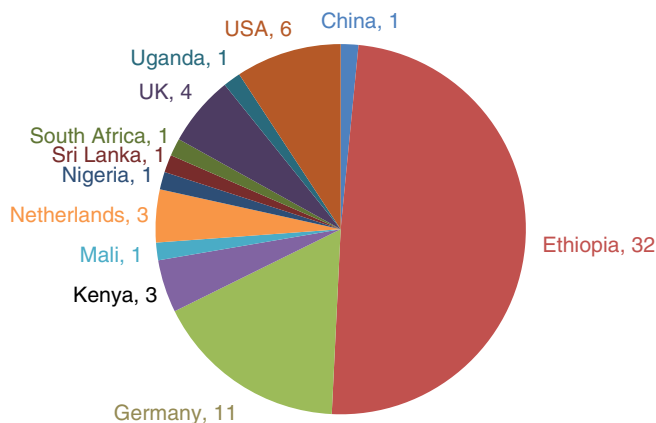
Fig. 12.4. Number of associates working on forage genetic resources by nationality at ILRI from 1986 to 2020. (Data from ILRI databases, March 2020.)

etic resources. In addition, a number of postgraduate students from both Colombian and foreign universities conducted, under the supervision of the programme scientists, field and/or laboratory research for their theses with a focus on genetic diversity. From 1990 onwards, training activities in forage germplasm were mainly in the area of germplasm management and in the form of 'field days' for Colombian university students and technicians, with demonstrations at field, greenhouse and laboratory levels. Several hundred students, technicians and researchers participated in this scheme.

At ICARDA, major training efforts were provided during 1990–2005 to North African and South and Central Asian young researchers through joint projects with Australian partners. In recent years, training on the use of forage germplasm has been provided to Iranian scientists focusing on diversification of cereal-based systems in the highlands. An estimated 750 forage professionals have been trained in forage germplasm activities in the last 30 years, including about 35 carrying out field research for their theses.

A basis of gene bank work is the development and spread of scientific networks. The networks, in which the CIAT Tropical Pastures Program participated, were decisive for the multilocational testing of elite forage germplasm and development of a number of grass and legume cultivars that were eventually released (Schultze-Kraft *et al.*, 2020): RIEPT

(with national research institution partners in Latin America and the Caribbean); Reseau de Recherche en Alimentation du Bétail en Afrique Occidentale et Centrale (RABAOC; with national research institution partners in West and Central Africa, in cooperation with ILRI); and the South East Asian Forage and Feed Resources Network (SEAFRAD; with national research institution partners in South-east Asia; this network developed in the 1990s into the Australian Centre for International Agricultural Research (ACIAR)-funded Forages for Smallholders project). At ILRI, the networks carried out similar activities of forage evaluation, information sharing and capacity building with a focus on sub-Saharan Africa: the Pasture Network for Eastern and Southern Africa (PANESA; with national research institution partners in East and Southern Africa); the African Feeds Research Network (AFRNET; which replaced PANESA with national research institution partners with an Africa-wide focus); and contributions to the Alley Farming Network for Tropical Africa (AFNETA; with national research institution partners in cooperation with the International Institute of Tropical Agriculture (IITA). These networks worked closely with the regional and subregional agricultural research organizations that were established in all regions in the early 2000s, supporting them in their efforts to improve feed resources and nutrition as part of sustainable livestock production systems. Network activities included

the development, publication and use of network-wide common research methodologies, and workshops and meetings with publication of research results.

ILRI, CIAT and ICARDA have collaborated since their establishment on forage genetic resources conservation and use, initially through the Systemwide Genetic Resources Programme and currently through the CGIAR Genebank Platform. Activities have included joint collecting missions for *Brachiaria* spp. germplasm in the early 1980s in East and southern Africa, germplasm exchange, forage evaluation and development of the forage pages of the Crop Genebank Knowledge Base.

ILRI has developed training materials and guidelines for gene bank management (Rao *et al.*, 2006a,b), and with CIAT on regeneration for grasses (Hanson and Schultze-Kraft, 2009) and with ICARDA for legumes (Hanson *et al.*, 2009) and grass pea (Hanson and Street, 2008). ILRI and Bioversity International oversaw the development of the online Crop Genebank Knowledge Base (http://cropgenebank.sgrp.cgiar.org/; accessed 26 February 2020) which was developed to facilitate access to best practices for gene bank management of selected crops, including forages. ILRI, working closely with CIAT and ICARDA gene bank staff, developed the pages on procedures for gene bank management, forage legumes and forage grasses to support more efficient and effective *ex situ* conservation and use of crop genetic resources.

Another form of capacity development is the distribution of germplasm data. ILRI, other centres, and national and international partners compile and develop forage germplasm data and distribute it online and in print. Examples are manuals for forage evaluation (Tarawali *et al.*, 1995) and forage seed production (ILCA, 1994). ILRI and CIAT, together with CSIRO and the Department of Primary Industry and Fisheries, Queensland Government, were founding partners in the development of the online Tropical Forages tool (www.tropicalforages.info; accessed 26 February 2020), an interactive tool for selecting forage species suitable for local climate, soils, production system and management conditions in the tropics and subtropics with comprehensive information on adaptation, uses and management of these forage species (Cook *et al.*, 2005).

Conclusions

Development impact

Despite the recognized value of forages for livestock production and land management, there has been limited use of germplasm in tropical forage development except on larger farms in Latin America (White *et al.*, 2013). The economic impact of the forage germplasm in the ILRI gene bank is relatively low in Africa, except for Napier grass where four accessions with disease tolerance have been selected and released to farmers. The cost of conservation of perennial grasses in ILRI is estimated to be US$170/year/accession, while the benefit to farmers of US$242/ha/year of Napier grass alone, when taking into account the extent of production in Kenya, Tanzania and Uganda, where head smut and stunt disease are spreading, translates into benefits of over US$15 million/year (or US$37.5 million/year when considering that annual profit is expected to be US$605/ha/year).

Potential option values

Much of the value of the gene bank lies in the future. The option value of having the germplasm available to respond to as-yet-unidentified future needs, such as changing feed needs due to climate change, and the existence value that society derives from knowing that something exists and will be available for future needs, may be more powerful economic drivers of conservation of forage diversity than the cost–benefit analyses that can be done on its actual use.

Scientific impact

Environmental benefits

Over the last 20 years, there has been a complementary research focus at the Centres on both feed and environmental benefits (White *et al.*, 2013). This is the study of the contribution of forage plants to ecosystem services such as mitigation of the emissions of nitrous oxide, a potent greenhouse gas, via biological nitrification inhibition.

Basic and applied research

With so many genera and species used as forage, there remains a gap in botanical research to better understand which species have more potential for use as livestock feed and for genetic research to quantify diversity in these species to support forage selection and variety development. Any further diversity research should focus on its relevance for: (i) enhanced germplasm management and utilization (identification of duplicates, establishment of core collections); (ii) relationships between traits and geographical origin of populations; and (iii) identification of genes responsible for particularly important plant traits.

Centres have focused on specific forages that meet the demands of livestock production systems in their mandate areas. The ILRI focus has been on forages for smallholder systems, especially dairy, which provides a steady income for smallholders in East and Southern Africa. Research has focused on three grasses: Napier grass and Rhodes grass for cut-and-carry systems in the subhumid areas, and buffel grass for grazing in dryland areas. Research of forage legumes has focused on lablab and cowpea for supplementation of low-quality diets that are high in fibre.

The CIAT breeding focus is currently on *Brachiaria* spp. and *Panicum maximum*, the most important forage grasses in the subhumid and humid tropics, with goals of developing pest resistance and nutritive value, with appropriate tolerance to drought, excess water, low soil fertility and aluminium toxicity. Seed production, which is key for commercial success, has been added as a criterion. Since 1988, breeding work at CIAT has been using *Brachiaria* germplasm. More than 300 elite hybrid lines had been delivered and seven cultivars have been developed and are being globally commercialized from the start of the programme to date: cvv. Mulato, Mulato II, Cayman, Cobra, Camello, Mestizo (a synthetic variety based on mixtures) and Converse. One hybrid cultivar, Talisman, is in a precommercialization stage. From the *Brachiaria humidicola* collection, intraspecific hybrid lines are developed and are on the path to commercialization in the next 5 years. CIAT's *Panicum maximum* breeding programme is using material from the 560 accessions held at the CIAT gene bank. ILRI and the Biosciences Eastern and central

Africa (BecA)-ILRI Hub have done limited but promising work on *Brachiaria* spp. in sub-Saharan Africa. CIAT's private-sector partner is commercializing hybrids and a selection of *P. maximum* globally in over 40 countries throughout the tropics and subtropics, for example in sub-Saharan Africa, the Mediterranean, tropical Asia, South and Central America, southern USA and southern Europe.

ILRI, CIAT and ICARDA have strong research programmes on forage genetic resources. A promising area is using molecular markers to describe genetic (intraspecific) diversity, clarify species relatedness and elucidate phylogenetics, and to improve gene bank curation by identifying duplicate accessions within collections. Studies on basic floral biology are being done on understudied species of production interest, with the objective of optimizing germplasm management and eventual breeding. As tropical species with forage potential are essentially wild (undomesticated) and not well described botanically, reference herbaria were established at CIAT and ILRI to assist species identification, with the aid of an images database.

The Future

Over the past 30 years, the forage programmes in CGIAR have focused on building their germplasm collections to cover a broad range of genetic diversity of tropical and subtropical forages to meet user demands, studying the collections to characterize and evaluate diversity and understand the traits in specific accessions, and improving their facilities to securely conserve the germplasm. The focus for the future will continue to be on the core operations that are essential to conserve and manage the diversity with increased emphasis on those that will ensure efficiency and value for money in gene bank operations. In addition to these essential activities, there are opportunities to be more forward and outward looking and to link with activities in the Livestock CRP and the Excellence in Breeding Platform, as well as to contribute to the global system of plant genetic resources, support the FAO Global Plan of Action and contribute to the Sustainable Development Goals. These activities will build on the core expertise in the forage gene

banks and will use cutting-edge technologies to add value to ongoing routine activities by increasing the relevance of the collections to climate change, contributing to understanding forage diversity and supporting capacity building in collaboration with partners in the Livestock CRP and national gene banks.

Going forward, the CGIAR forage gene banks need to look at how to respond to future needs to continue to be relevant. Global predictions of climate change indicate that even with a cap of a 2°C increase, new varieties of forage crops will be needed to adapt to climate change. The traits and genes found in the germplasm in the CGIAR collections are essential to realize the genetic gains needed both to adapt to climate change and to produce sufficient livestock feed with limited resources and competition for land to feed a growing population. Additionally, several forages are also wild crop relatives and are an important source of traits and an asset for crop breeding. Wild crop relatives are not well represented in *ex situ* collections, and there is a lack of information on the location of existing collections, optimum storage conditions and efficient management.

New techniques offer many opportunities to understand and make better use of the forage genetic diversity held in the collections. Fingerprinting tools can be applied for improved management, as well as to study diversity and identify traits to support sustainable use in these crops. Sequencing data and DNA markers are essential not only to facilitate use but also for improved management through accession identity and tracking genetic integrity of accessions. Genomic information on gene flow, taxonomy, apomictic status and ploidy levels of the accessions can be used to improve operations and introduce considerable efficiencies in regeneration and multiplication. Research on regeneration methods, breeding systems, seed storage and longevity will provide information that can be used to develop gene bank standards suitable for low-cost operations and conservation of forages and other wild species. This activity will be done through collaboration with national programmes, the Genebank Platform, the Livestock CRP and the Excellence in Breeding Platform for phenotyping and genotyping to support conservation management and use.

Traditional gene banks rely heavily on electricity for cold storage or cryopreservation of seeds or tissues. Advances in renewable sources of energy such as solar and wind can both reduce the environmental footprint of gene banks and can also substantially reduce the costs of conservation. Water will become a major limiting factor, and installation of water-harvesting methods and drip irrigation for regeneration and multiplication can contribute to more sustainable operations and mitigation of the effects of climate change. ILRI and ICARDA have established new gene bank facilities in the last 2 years, and CIAT has embarked on an ambitious initiative called Future Seeds to build a state-of-the-art genetic resources centre that not only ensures the conservation but also encourages the proactive use of the germplasm. The environmentally sustainable facility will use genomics, digital phenotyping and information technologies to gradually build a 'knowledge bank' that enables a more data-driven deployment of crop diversity and serves as a meeting platform for scientists promoting biodiversity as a driving force for innovation in agriculture.

Despite three decades of training in the management and use of forage germplasm, many national gene banks lack the capacity to meet expanding national mandates and to fully participate in the global system. The next generation of forage scientists needs to be able to apply new techniques such as DNA fingerprinting, flow cytometry, bioinformatics and spatial analysis for forage development but need mentoring from experienced genetic resources scientists. The move to using molecular techniques has also resulted in a gap of young scientists with traditional biology skills such as taxonomy, phenology and seed biology. A major gender-balanced capacity-building effort is needed to support global efforts in conservation, make better use of the collections and work efficiently in the genetic resources policy environment. This will include training, internships and graduate scholarships, mentoring, developing and supporting communities of practice, online training and knowledge sharing.

Gene banks are long term and expensive to maintain and have an essential function to support current and future use. Yet questions continue to be asked on the value of the accessions, the efficiency and costs of operations, and the

impact derived from the investments in having three forage gene banks in CGIAR. Future activities will focus on answering some of these questions on the value and use of the collections. Working closely with the Livestock CRP, information will be collected on user demand for forages and traits, documenting the delivery pathways from the gene bank to forage production and adoption of forage on farm to better document the impact and use of the forage collections.

Surveys will follow up with users to provide feedback on their research and the use of germplasm as forage and feed. The CGIAR gene banks are assigning Digital Objective Identifiers to the accessions to better track use of germplasm in publications and forage release in future. These data will be used to estimate current and option values and will lead to a better understanding of the value of the CGIAR *ex situ* forage collections.

Notes

[1] Information for this chapter was compiled by the authors mainly from information accessible at the websites of ILRI, ICARDA and CIAT, from their respective annual reports, unpublished reports on germplasm collecting missions, research papers of national and international partners, and other material published and unpublished. We further note that there have been changes in plant nomenclature for several species of particular interest. As this overview is concerned with the past, we are still referring to the earlier accepted names. It should be noted that according to the USDA Genetic Resources Information Network (GRIN) taxonomy *Brachiaria brizantha*, *B. decumbens* and *B. humidicola* are now accepted as *Urochloa brizantha*, *U. decumbens* and *U. humidicola*, respectively, *Panicum maximum* as *Megathyrsus maximus*, *Pennisetum purpureum* as *Cenchrus purpureus*, and *Desmodium heterocarpon* as *Grona heterocarpa*.

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13 The Impact of CGIAR Centre Research on Use of Planted Forages by Tropical Smallholders

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Executive Summary

The problem

Livestock are an integral component of the smallholder mixed systems that dominate sub-Saharan Africa and South Asia. Availability of sufficient high-quality feed is a major constraint to productivity; livestock are often fed opportunistically and on poor-quality feed resources. A decline in grazing resources in response to the expansion of cultivated land and poor control over grazing rights means ever-increasing proportions of variable-quality cereal and legume crop residues in ruminant livestock diets. Cultivation of green forages specifically for feeding livestock is an important potential means of addressing the feed gap. The prominence of planted forages in smallholder farming systems varies hugely, and the extent of their cultivation in sub-Saharan Africa and to some extent Asia is lower than would be expected given their potential to alleviate the chronic feed gap. This chapter explores the potential and actual impact of planted forages and reviews success cases emerging from CGIAR research.

Potential of planted forages

Planted forages offer a range of benefits, which is at odds with their apparent underuse in many smallholder farming systems. Well-managed cultivated forages provide substantial yields of nutrient-rich biomass. Grasses provide large amounts of moderate-quality feed. Legumes generally yield less, but the vegetative material is of exceptionally high quality and provides an excellent high-quality feed to complement the basal resource of cereal crop residues that often dominate livestock diets across the tropics.

Planted forages have several potential impacts. Use of forages can deliver social benefits including reducing the labour burden associated with feed sourcing, especially on women. Forages can also deliver economic benefits through improved livestock productivity, which often exceeds the opportunity costs of utilizing land for staple crops. Finally, forages can play a strong role in delivering environmental impact through soil stabilization, carbon sequestration and maintenance of habitats which support biodiversity.

Information on the use of planted forages in the tropics is scanty, although there have been recent attempts to synthesize available information. These reviews point to large areas of improved planted forages in Latin America with a few documented successes in high-potential sites in China, India, South-east Asia and East Africa.

Research spending at ILRI

The International Livestock Research Institute (ILRI) and its predecessor, the International Livestock Centre for Africa (ILCA), have made major investments in livestock feed research. ILCA scientists (1974–1994) working on feed research of all types – range ecology, forage diversity, planted forages, multidimensional crops and the nutritional quality of feeds – were about 18.8% of the 1974–1994 number of ILCA staff. These figures imply real spending on various aspects of livestock feeding of some US$70 million (in 2015 US$) in the 20 years of ILCA's existence. ILRI (1995–2017) spending was some US$105 million, for a 1975–2018 commitment of US$175 million, or roughly 10% of the total. Planted forages accounted for the majority of ILRI spending in the area of livestock feeding. We have not been able to estimate research spending on forages at the International Centre for Agricultural Research in Dryland Areas (ICARDA) or at the Centro Internacional de Agricultura Tropical (CIAT, or International Center for Tropical Agriculture now part of the Alliance of Bioversity International and CIAT).

Impacts

Research by the various CGIAR centres with interests in planted forages has yielded a range of success cases where research has led to widespread uptake of specific interventions involving planted forages. For example, the World Agroforestry Centre (ICRAF) has been working on the use of multi-purpose trees as livestock fodder in East Africa for the past three decades. This research effort led to the development of feeding practices especially in support of dairy production. In partnership with a range of development partners, multi-purpose trees were adopted by up to 230,000 farmers according to some estimates. Similar experiences apply to other forage-based technologies including the push–pull system, intensive small-scale grass production for beef fattening in South-east Asia and recent uptake of planted forages – often based on selections by CIAT and ILRI – in South-east Asia and eastern Africa. In Latin America and the Caribbean, planted forages, by spontaneous adoption and selection by the private sector, national agricultural research systems and CIAT have transformed livestock production over the last 60 years and are the main source of animal feed albeit mostly on large farms. More recently, increased attention has been given to bred grass cultivars, with early uptake estimated by extrapolating from seed sales of more than 900,000 ha of CIAT bred hybrids.

Despite these successes, the uptake of planted forages has been much less in sub-Saharan Africa and Asia than, for example, in Latin America. There are different analyses on the basis for this lack of uptake ranging from those who point to lack of awareness of the potential merits of planted forages among farmers through to those who attribute lack of uptake to inherent system characteristics that make them uncompetitive with alternative use of land and labour.

Scientific impacts

Several scientific impacts are clear from CGIAR research on planted forages over the past four decades. First, CGIAR centres and national and international partners have been successful in developing intervention strategies involving planted forages. Examples include the use of multi-purpose trees in East Africa in support of dairy production, the push–pull system with its

multiple production benefits including improved livestock production, and the development of intensive grass production on small plots in South-east Asia in support of beef fattening.

Second, the development of improved planted forage cultivars, especially in Latin America, involving the private sector, the national research system and CIAT has clearly led to extensive uptake by relatively large-scale farmers with clear livestock production dividends.

A third area of scientific impact has been the developing of understanding and methods for prioritization of planted forage options for particular localities. Examples of research outputs that codify the extensive knowledge within the global forage/feed network including CGIAR scientists have been the widely used Tropical Forages tool (www.tropicalforages.info/; accessed 27 February 2020) and recently the Feed Assessment Tool (FEAST). Linked to this, CGIAR research has been important in understanding the systemic constraints on planted forage use in smallholder systems across the tropics.

Development impacts

There has been considerable development impact from planted forage cultivars notably *Brachiaria* spp. in Latin America, especially in Brazil. In Brazil the strong private sector and national research system (Brazilian Agricultural Research Corporation or EMBRAPA) have been instrumental along with CIAT. In other countries in Latin America and the Caribbean, the contributions of CIAT have been more central. Other examples noted in this chapter include *Stylosanthes* spp. in China and Thailand and fodder hedgerows in East Africa.

Several other development impacts can be identified from CGIAR research on planted forages. The forage gene banks of ILRI, ICARDA and CIAT have been the principal sources of germplasm for development as described in Chapter 12 (this volume). The same centres have acted as a knowledge repository on planted forages for example through collation of the Tropical Forages tool.

Studies of the economic impact of planted forages related directly to ILRI's work are rare. An impact assessment in the 1990s in 15 West African countries showed some 27,000 adopters of the fodder bank technology on 19,000 ha. The calculated economic internal rate of return to the fodder bank technology was 38%.

Capacity building and partnerships as development impacts

Capacity development impacts of CGIAR research have been mainly through the development of knowledge products on forages, notably the Tropical Forages tool, which is the main global knowledge repository on tropical forages and is widely used. In addition, the development of technical materials and training manuals on forage development, notably in South-east Asia, is an excellent example of the capacity development work of CGIAR centres. Finally, CGIAR centres have had a strong convening function, for example in convening of international networks on forages through the Tropical Forages Newsletter initiative and the African Feed Research Network (AFRNET) convened by ILCA in the 1990s and the RIEPT network in Latin America and the Caribbean convened by CIAT in the 1980s.

Future directions

Future work on planted forages by CGIAR centres must involve renewed effort in breeding to produce lines that are resilient to stress, particularly in the face of climate change and land pressure and responding to emerging and specific market demands. The promising work on prioritization of feed options including planted forages must be extended to allow better targeting of forage options to reduce effort to promote options that have little prospect of success. Finally, CGIAR research needs to continue the process of stronger partnering with private-sector actors at a range of scales in the feed sector. In the case of planted forages, this could involve the incubation of small-scale seed producers through technical training.

Introduction

The purpose of this chapter is to answer the question of what the scientific and economic value of research and development work by CGIAR centres and partners has been in planted forages for smallholders in tropical and subtropical livestock systems in Africa, Asia and the Americas. By planted forages, we mean the whole range of plants used for feeding livestock and specifically cultivated for livestock nutrition. This includes forage grasses, herbaceous forage legumes and forage shrubs/trees, the latter often legumes; in addition, some non-legumes and non-grasses such as *Tithonia diversifolia*, *Morus alba* and *Trichanthera gigantea* are planted and used for animal feeding.

Forage-based livestock production is significant in temperate systems. In some cases, planted forages are the main source of nutrition (e.g. Williams *et al.*, 2007, for New Zealand). In the tropics and subtropics, cultivation of forage dominates livestock production in Latin America and the Caribbean (Jank *et al.*, 2014) but is much less prominent in Asia and Africa. In the latter regions, livestock are fed on crop residues and natural forage either grazed *in situ* or cut and carried to confined animals (Renard, 1997). In a recent study of 12 global locations in sub-Saharan Africa and South Asia, forage crops contributed no more than 10% of cattle diets, with crop residues accounting for a much larger share (Valbuena *et al.*, 2015). Research in India has found that crop residues were the single most important feed resource, supplying around 70% of intake, with planted forages contributing 15% (Blummel *et al.*, 2014). There are pockets of intensive forage use; for example, Napier grass (*Pennisetum purpureum*[1]) in East Africa is a base feed of choice in dairy systems (Staal *et al.*, 2002). Moreover, recent work and case studies have identified the potential benefits of planted forages in eastern Africa (González *et al.*, 2016; N. Teufel *et al.*, unpublished data) and tropical Asia (Stür *et al.*, 2013) with an increasing – although as yet limited – uptake of tropical forages beyond Latin America and the Caribbean, as shown later in this chapter.

The work of CGIAR on forages commenced in the early 1970s with research in CIAT as part of the Beef Production Systems Program. This programme later shifted its focus entirely to tropical forages and became the Tropical Forages Program in 1979 (Lynam and Byerlee, 2017b). In ILCA (and later ILRI), planted forages research began in the late 1970s with evaluations of grass, forage legume and forage tree species in Nigeria and later in Ethiopia. The work of ICARDA started at a similar time, focusing on testing and disseminating cereal/legume rotations with farmers in several countries in the West Asia and North Africa region, including Algeria, Iraq, Jordan, Lebanon, Morocco, Syria and Tunisia.

The empirical basis of the impact of planted forages on tropical and subtropical livestock production in Africa and Asia is not as strong as it should be. Some argue that there has been little to show for this effort in CGIAR institutions (Squires *et al.*, 1992; Thomas and Sumberg, 1995) beyond Latin America and the Caribbean, where there are documented large-scale impacts (Lynam and Byerlee, 2017b).

In this chapter, we first consider the technical merits of planted forages. We then review what is known about the extent of cultivation of planted forages in selected locations before summarizing various successes in different tropical regions. Last, we reflect on lessons from these experiences and present ideas for future research.

The Role of Planted Forages in Tropical Farming Systems

Livestock are ubiquitous in the mixed crop–livestock systems of the tropics. They are often poorly fed, subsisting on poor-quality crop residues, scavenged grasses and leaves, and a limited ration of agro-industrial by-products. Planted forages have long been promoted as a way of improving feed supply. However, the place of planted forages in smallholder livestock production outside of perhaps East Africa, especially Kenya, is often limited[2]. Planted forages are widely used in Latin America, although the definition of smallholder there does not compare with the much smaller scale in sub-Saharan Africa. Some have argued that they are not used because of systemic and economic constraints (McIntire and Debrah, 1986), although analysis often focuses on forage legumes (Thomas and Sumberg, 1995; Sumberg, 2002). There are, however, recent success reports such as from Asia (Stür *et al.*, 2013) with more than 10,000 farmers adopting intensive grass production, eastern Africa (Maass *et al.*, 2015) with stated adoption of *Brachiaria* hybrids by at least 20,000 farmers, eastern Africa (Franzel and Wambugu, 2007) on the uptake of fodder shrubs (mostly *Calliandra calothyrsus*) by more than 200,000 farmers, the adoption of the push–pull system of the International Centre of Insect Physiology and Ecology (ICIPE) by more than 30,000 farmers (Khan *et al.*, 2011), the recent

work on *Brachiaria* coordinated by ILRI and CIAT in East Africa with scaling of up to 25,000 households adopting *Brachiaria* germplasm selections (S. Ghimire, personal communication) and the adoption of *P. purpureum* in eastern and Central Africa (Negawo *et al.*, 2017; Staal *et al.*, 2002).

The work of Peters *et al.* (2001) is a forceful argument for planted forages as instruments for higher productivity and better natural resource management. They reviewed '...the role of forage crops in improving the productivity of smallholder farming systems and breaking the cycle of poverty and resource degradation [by presenting] the contributions of forage crops to increasing farm incomes, intensifying farm production, and contributing to better human nutrition.'

Planted forages offer strong technical benefits in mixed crop–livestock systems. For example, Peters *et al.* (2001) gave the agronomic arguments for planted forages in the tropics: (i) they provide higher crop yields per unit of land compared with alternatives, such as crop residues, natural pastures and browse; (ii) they provide higher forage quality in terms of nutrients per unit of dry matter (DM); (iii) there is improvement of soil quality by fixing nitrogen and retaining water; and (iv) they may fill seasonal feed shortages, in terms of providing feed when alternatives are scarcest (e.g. natural pastures in the dry season). Similar arguments were advanced by Shelton *et al.* (2005). Rao *et al.* (2015) outlined the importance of planted forages for ecosystem services.

White *et al.* (2013) give the technical benefits of forages in three domains. First, planted forages can improve labour productivity given that they can reduce work to collect natural vegetation. Second, forages can allow savings in input use, such as water and fertilizer. Cultivation of forages can lead to improved productivity in terms of biomass yield, energy or protein per unit area. Finally, forages can also have environmental benefits. Such benefits include improved soil cover, reduced erosion and less weed infestation.

Table 13.1 lists the top 15 forage species requested from the ILRI forage gene bank since the early 1980s. Of the top ten grasses, *P. purpureum* (commonly known as Napier or elephant grass) has been reported to produce a DM yield of

Table 13.1. Indicative yield and nutritive value of the forage species most commonly requested from the ILRI gene bank (1984–2016). (Data on number of requests extracted from ILRI gene bank database. Yield and protein data from Cook *et al.*, 2005; nutritive value data from Feedipedia, 2013.)

Forage	Type	Number of requests	Indicative yield (t DM/ha/year)	Crude protein (% DM)	Metabolizable energy (MJ/kg DM)	Observations
Chloris gayana	Grass	833	10–25	3–17	8.5	
Cenchrus ciliaris	Grass	699	2–9	6–16	8.0	
Pennisetum purpureum	Grass	564	10–30	Leaf: 9.5–19.7	8.2	
Lablab purpureus	Legume	1,874	4	Leaf: 21–38; stem: 7–20	9.2	Yield is per season
Vigna unguiculata	Legume	1,412	3–10	Green foliage: 14–21; crop residue: 6–8	9.8	Yields refer to 8–12 weeks
Cajanus cajan	Legume	1,354	~2	Leaf: 10–15	9.6	DM yields can be much higher under optimal conditions
Stylosanthes guianensis	Legume	1,210	5–10	12–20	8.0	
Medicago sativa	Legume	1,078	8–27[a]	18.3	8.5	No crude protein data in Cook *et al.* (2005)
Neonotonia wightii	Legume	828	3–8	17.1	9.1	No crude protein data in Cook *et al.* (2005)
Stylosanthes hamata	Legume	785	1–7	Leaf: 17–24; stem: 6–12	8.8	
Stylosanthes scabra	Legume	763	1–10	Leaf: 10–20	n/a	
Trifolium tembense	Legume	590	3–6	10–24	10.9	
Sesbania sesban	Tree	2,581	6–12	25–30	11.5	
Leucaena leucocephala	Tree	780	1–15	19–24	11.0	
Gliricidia sepium	Tree	604	2–20	18–30	11.5	

[a]The yield of *M. sativa* is under irrigation.

between 12 and 90 t/ha/year and crude protein concentrations of between 5 and 16% (Negawo *et al.*, 2017, and references therein). The data overall show the very high yield potential of planted forages, particularly forage grasses, when compared with natural pasture DM yields in, for example, Ethiopia, which range from 1 t/ha/year in the lowlands to 4–6 t/ha/year on seasonally waterlogged fertile areas (Alemayehu, 1998). The data also illustrate the high nutritive value of forages, especially forage legumes, many of which have crude protein concentrations of around 20%. Comparing these with the other major sources of nutrition for livestock in developing-world smallholder systems, crop residues, under normal agronomic practices, cereal straw yields in sub-Saharan Africa would be in the order of 1.5–7.0 t/ha with crude protein concentrations of 5–10% and metabolizable energy concentrations of 6–8 MJ/kg DM (Zaidi *et al.*, 2013).

Forage legumes, through their ability to form a symbiotic relationship with nitrogen-fixing rhizobia hosted in their root nodules, also offer improvements in soil quality and reductions in greenhouse gas (GHG) emissions and nitrogen fertilizer application. After harvesting the aerial portion of the plants, the remains are degraded to produce organic matter and the nitrogen component is mineralized to form ammonia, which is released into the soil and can be utilized by other plants in close proximity or planted subsequently. In addition, unlike in the above-ground portion of the plant where nitrogen concentrations do not vary significantly, nitrogen concentrations in below-ground legume tissues have been shown to vary considerably (Carranca *et al.*, 2015).

Results by Muhr *et al.* (1999) showed the positive effects of nitrogen contribution in the order of 80 kg/ha to the succeeding crop, even when removing the above-ground biomass, of *Stylosanthes guianensis*. Depending on the way in which livestock are managed, some nitrogen from legumes may be deposited on arable land as excreta returns but usually only a fraction (Rufino *et al.*, 2007). Finally, there is the case that some forages provide feed at times of general feed scarcity. For example, some fodder trees provide green feed during the dry season when other feeds are scarce (Franzel *et al.*, 2014). Seasonal livestock exclosures, where livestock are excluded for a time to allow biomass accumulation, can also provide dry-season feed by reserving biomass for periods of scarcity (Tarawali and Pamo, 1992; Mekuria and Veldkamp, 2012) although practical uptake of such practices has generally been limited (Tarawali *et al.*, 1999).

As well as biological nitrogen fixation by forage legumes, some tropical grass roots have recently been shown to exude chemical inhibitors of biological nitrification, which suppress soil-nitrifying bacteria, reducing the rate of leakage of nitrogen from the system, by blocking the conversion of ammonium to nitrate. Inhibitors have been identified in root exudates from a number of legume and grass species including sorghum and rice, but by far the most intense activity was detected in *Brachiaria humidicola* (Subbarao *et al.*, 2007). Subsequently, the cyclic diterpene 'brachialactone' was demonstrated to contribute between 60% and 90% of the biological nitrification inhibition activity in *Brachiaria* root exudate (Subbarao *et al.*, 2009). A further benefit of these soil-nitrifying bacteria is reductions in emissions of the GHG nitrous oxide.

The paradox is that despite the positive nitrogen-fixing properties of legumes, which offer benefits to plant production and soil health when grown in nitrogen-constrained environments, in general the uptake of forage legumes in smallholder systems has been limited (Sumberg, 2002; Shelton *et al.*, 2005).

The extent of planted forages in tropical farming systems

Global estimates of the area planted to forages are not readily available. There are, however, countries where forage data are readily available. Data from the Indian Council for Agricultural Research (ICAR) indicate the area planted to 'improved' forages in India is around 8 million ha with the dominant species being Egyptian clover (*Trifolium alexandrinum*) and forage sorghum (ICAR, 2011). In Brazil, another hotspot of planted forage production, EMBRAPA estimates that the total area planted to forages is 115 million ha with *Brachiaria* spp. accounting for 80% of the area and *Panicum maximum* accounting for 10% (Sluszz, 2012).

Planted forages have been promoted for many years in eastern Africa (Abate *et al.*, 1985). A survey of areas with commercial dairy

production was carried out in Ethiopia and Kenya in 2015 to determine the levels of forage adoption, production practices and importance as a feed source (N. Teufel *et al.*, unpublished data), in which 180 communities were selected across the major regions in each country. In Ethiopia, 20 woredas were purposively selected from Tigray (three), Amhara (six), Oromiya (seven) and Southern Nations Nationalities and Peoples (four) for intensity of dairy production. Within these woredas, nine kebeles[3] were randomly selected. In Kenya, 12 counties were selected from Nyanza (three), western (two), Upper Rift (three), central (three) and coast (one) regions, based on the density of dairy animals and information about forages. Random selection identified 15 sublocations, the lowest formal administrative level, within each selected county and one village within each selected sublocation for the survey. During the survey, focus groups responded to quantitative and qualitative questions on farming characteristics and forage production practices regarding the whole village, such as the total number of farming households and cultivated area, the number of households growing a specific forage and the area of this forage planted. Most forages were differentiated by species only. Because of its importance, Napier grass (*P. purpureum*) was differentiated into four variety types at data collection: 'Kakamega I', 'Kakamega II', 'other improved varieties' and 'local varieties'. The share of households growing forages among farming households and the forage share of cultivated land, where forage extent was expressed in area units, were calculated for comparison.

Results of this study indicate that in Ethiopia, forage grasses are grown by 10–35% of households, while in Kenya 10–85% of households grow grasses. Forage legumes are grown by fewer households overall; in Ethiopia, their occurrence (up to 12% of households) is higher than in Kenya (up to 2% of households). Forage trees occur reasonably widely with up to 40% of households growing trees in Ethiopia and up to 20% in Kenya. The areas devoted to planted forages are small. However, forage trees are often planted singly or in rows, for which area measures were not recorded.

Sesbania was the most common planted forage in Ethiopia, with 34% of households growing it and 0.5% of cultivated area allocated to it. Local

varieties of Napier grass also figure highly. In Kenya, local Napier varieties were the most common forage and were grown by over 90% of households in the surveyed areas, although they accounted for only around 5% of total cultivated area. Improved varieties of Napier grass ranked second in frequency of occurrence. Measuring adoption by area favours crops that are grown on larger farms, such as fodder oats in Ethiopia or Rhodes grass and the Kakamega Napier grass varieties in Kenya. In summary, the area shares of fodder crops are generally low in both countries, with Napier grass in Kenya being the most widespread, grown on around 6% of cultivated land (combining all varieties). Because many of these crops are harvested multiple times per year, their biomass shares are higher than their area shares.

Adoption of planted forages in sub-Saharan Africa

In this and the following sections we review current knowledge on adoption of planted forages related to CGIAR research efforts. We do this by focusing on a series of significant bodies of work in different regions that have led to at least moderate success.

Fodder banks in West Africa

The fodder bank concept was developed by ILCA (now ILRI) and partners in the late 1970s in Nigeria to help crop–livestock farmers in the dry to subhumid zone to: (i) overcome dry-season feed constraints; and (ii) improve soil fertility. It consisted of establishing small (typically 4 ha) fenced paddocks with a prolifically seeding, self-regenerating forage legume (mainly *Stylosanthes hamata*) for strategic supplementation of livestock grazing natural pastures (Mohamed-Saleem and Suleiman, 1986). Such supplementation led to significant increases in livestock productivity under experimental conditions. After 2–3 years, the legume fodder bank was replaced by an unfertilized sorghum or maize crop that provided yields equivalent to fertilization with up to 45 kg nitrogen/ha (Tarawali, 1991). After the crop phase, the area was reconverted to a fodder bank via hard-seeded soil seed reserves. Research and promotional activities related to this technology came to an end in the early 1990s.

An impact assessment, conducted by Elbasha *et al.* (1999) in 15 West African countries showed that, until 1995, there were about 27,000 adopters of the fodder bank technology covering about 19,000 ha. Given the estimated US$7 million research expenditure to develop this technology, an internal rate of return of 38% was calculated. Elbasha *et al.* (1999) stressed the finding that a considerable time lag (at least 15 years) was necessary for diffusion of the technology. The second part of their statement, '… the impact of adopted fodder banks has paid for the research that went into their development at least three times over, and this will increase substantially in the next few years, given current adoption trends' remains to be confirmed.

Multi-purpose trees

ICRAF and partners have been active in developing multi-purpose trees and shrubs as fodder in East Africa over the past three decades[4]. Multi-purpose trees have been defined as 'all woody perennials that are purposefully grown to provide more than one significant contribution to the production and/or service functions of a land-use system. They are so classified according to the attributes of the plant species as well as to the plant's functional role in the agroforestry technology under consideration' (Huxley, 1984). Functions include livestock feed, construction, fuel, improved soil fertility, erosion control and shelter, among others.

Initial research in the early 1990s estimated the potential of *C. calothyrsus*, *Sesbania sesban* and *Leucaena leucocephala* to provide feed for smallholder dairy cows in the central highlands of Kenya (Franzel and Wambugu, 2007). *C. calothyrsus* proved most suitable, and much of the research effort has focused on understanding how it fits into small farms. Multi-purpose trees and forage trees in general have the advantage that they require minimal inputs and can be planted along field margins and on soil bunds. They have the disadvantage of slow growth (first harvests in much of East Africa are 12 months after transplanting) and the need for stable land tenure to justify investment in a multi-season crop.

ICRAF published a comprehensive review of the impact of multi-purpose trees (Place *et al.*, 2009). This review gave data on the production impact of intake of tree forage by livestock as well as a synthesis of the various adoption studies. The best estimate was that milk yield increased by 0.6–0.8 kg/kg intake of *Calliandra* leaf. Scaling this production impact up using estimates of adopters in East Africa, the authors estimated the economic impact of forage tree adoption in Kenya in 15 years to be in the order of US$20–30 million. The report also assembled adoption data from various sources to arrive at a total of 206,000 farmers having adopted multi-purpose trees in East Africa by 2005. By the authors' own admission, the farmer numbers are 'rough guesses', often partly based on data from reports of non-governmental organizations promoting multi-purpose trees with associated uncertainties. Nevertheless, it is clear that the number of farmers growing multi-purpose trees in East Africa is notable.

The 'project focus' of the reported adoption of multi-purpose trees was highlighted in a recent paper by Brockington *et al.* (2016) in which a previous agroforestry intervention was revisited 5 years after the project end. While the primary focus was on fruit trees, multi-purpose trees also formed part of the study, and the issues around 'adoption' are generic. Assessment of fodder tree adoption must be done over several years, whereas conventional project cycles are usually too short to allow this. The result is that most assessments track the very early stages of adoption focusing on counting numbers of farmers receiving extension support and materials while neglecting evaluation of longer-term diffusion of tree technologies. Abandonment of fodder tree interventions following the end of projects is relatively common (Francis and Atta-Krah, 1989; Mekoya *et al.*, 2008). Not all farmers who test fodder trees go on to adopt them (Kiptot *et al.*, 2007). However, there are also cases of spontaneous diffusion of fodder tree technologies without researcher involvement (Kiptot *et al.*, 2006; Wambugu *et al.*, 2011) so the story is not clear. What is needed for this and other planted forage initiatives are some independent evaluations involving medium-term revisits to project sites to assess the extent of sustained use of fodder trees beyond the project life. Further studies like that of Brockington *et al.* (2016) would be welcome.

Successful use of multi-purpose trees for fodder is 'knowledge intensive', and much of ICRAF's recent work has been around suitable

dissemination pathways to enhance adoption (Kiptot *et al.*, 2006; Lukuyu *et al.*, 2012). At the current stage of smallholder system development, it may therefore be some while before we see spontaneous uptake of multi-purpose trees without project intervention.

Napier grass in East Africa and beyond

Napier grass (*P. purpureum*, sometimes called elephant grass) is a perennial species originating in sub-Saharan Africa that is known for its high biomass production and rapid regeneration capabilities, good palatability and nutritional qualities. These features have made it highly popular, mainly as a 'cut-and-carry' feed in livestock production systems across the tropics and subtropics. The popularity of Napier grass is not attributable to CGIAR research as it was introduced from southern Africa in the colonial, pre-CGIAR era. However, because of its importance, especially in East Africa, it has featured strongly in CGIAR research as outlined below. Napier grass is highly adaptable to a broad range of production systems and environments. Although it is known to grow best in regions where annual rainfall exceeds 750 mm and in locations below 2100 m above sea level, it has been reported to grow at up to 3000 m above sea level in tropical regions and to contain similar concentrations of crude protein to lucerne, and has been used to replace lucerne hay in livestock production systems (Criscioni *et al.*, 2016). It can be chopped and fed directly and can also be grazed or conserved and made into hay, silage or pellets (Figueira *et al.*, 2015; Mapato and Wanapat, 2018). There are approximately 25 Napier grass varieties or cultivars, and an additional 16 sterile hybrids formed with pearl millet (*Pennisetum glaucum*) currently being grown around the world (Cunha *et al.*, 2011). In addition, the species is open pollinated and therefore highly heterozygous with significant variability for both nutritional and agronomic traits, which indicates that there are significant opportunities for the development of new and improved varieties (Negawo *et al.*, 2017). The current varieties come in two main forms: there are the standard 'tall' varieties, which are renowned for their biomass production and are most popular in the cut-and-carry systems and there are the dwarf or 'short' varieties, which do not produce as much biomass but have shorter internodes (i.e. increased leaf:stem ratio) and are considered to be of higher quality and to have greater resilience to abiotic stresses (Sollenberger *et al.*, 1987).

Napier grass is most prevalent in the cut-and-carry systems that dominate livestock production systems, particularly dairy, in East and Central Africa. It is considered the most popular perennial fodder for the smallholder crop–livestock farming systems in Kenya (Nyambati *et al.*, 2010), and has been reported to represent approximately 80% of planted forages in this country (Staal *et al.*, 1997). Recent estimates by authors of this chapter based on the survey reported in Tables 13.2 and 13.3 indicated that Napier grass is an important feed resource for at least 1.3 million households in Kenya and Ethiopia. The variety Bana is currently the most commonly grown in Kenya, although, as indicated elsewhere in this chapter, other selected varieties are growing in importance. This is mainly because, while considered resilient in the face of many pests and diseases, the impact of some specific diseases (namely head smut and stunt) have had a negative impact on the further growth and distribution of this species. However, new material such as the smut-resistant Kakamega I and Kakamega II, which are accessions from the ILRI gene bank, are alternatives where smut is a threat (Mwendia *et al.*, 2008). More recently, other gene bank accessions have been identified as a source of tolerance, or resistance, to stunt disease (Wamalwa *et al.*, 2017). The potential of Napier grass with respect to yield, disease resistance and ease of harvest has been assessed in Ethiopia (Kebede *et al.*, 2017) and Tanzania (Sikumba *et al.*, 2015).

Napier grass has also had a significant impact in production systems outside Africa and has been readily adopted in South and Southeast Asia. For example, Pakchong 1 (or 'Super Napier'), a tall hybrid cultivar recently developed in Thailand and distributed in other countries including the Philippines, Malaysia and India, is being widely promoted for cultivation in smallholder systems (Halim *et al.*, 2013; Wangchuk *et al.*, 2015). In India, the standard Bajra-Napier hybrid (also known as king grass) variety has been identified as an option for sustained fodder yields, particularly for cattle and buffalo production systems (Kadam *et al.*, 2017). Napier grass is also a popular cut-and-carry forage in the trop-

Table 13.2. Distribution of fodder grasses, legumes and trees in areas with dairy production in Ethiopia and Kenya. (Data from N. Teufel. *et al.*, unpublished survey.)

Country	Region	No. villages	Forage grasses			Forage legumes			Forage trees		
			No. villages[a]	Hh (%)[b]	Area (%)[c]	No. villages[a]	Hh (%)[b]	Area (%)[c]	No. villages[a]	Hh (%)[b]	Area (%)[c]
Ethiopia	Amhara	54	40	10.9	0.6	25	5.6	0.4	53	40.6	2.4
	Oromiya	63	54	12.2	0.6	30	3.3	0.1	40	15.2	3.1
	SNNP	36	34	34.5	1.3	23	12	0.4	21	6.1	0.3
	Tigray	27	25	14.8	1.3	23	8.5	1.1	27	24.3	3.4
Kenya	Central	45	45	82.7	12.9	13	2	0.2	11	0.7	0.1
	Coast	15	6	9.2	0.5				1	0.1	0
	Nyanza	45	39	67.1	6.7	3	0.8	0.1	16	20.3	0.7
	Upper Rift	45	45	42.2	7.6	3	0.3	0.2	11	6.3	0.1
	Western	30	30	68.3	6.8	4	0.8	0	12	4.2	0.1

SNNP, Southern Nations, Nationalities, and Peoples' Region.

[a]Number of villages in which fodder was grown.

[b]Share of households (Hh) growing forages among farming households.

[c]Area share of cultivated area devoted to forage, considering only forages for which extent of adoption was recorded by area units.

Table 13.3. The most important fodder crops by households in Ethiopia and Kenya. (Data from N. Teufel *et al.*, unpublished survey.)

Country	Rank	Species	No. villages[a]	Hh (%)[b]	Area (%)[c]
Ethiopia	1	Sesbania (*Sesbania sesban*)	136	34	0.5
	2	Napier, local (*Pennisetum purpureum*)	141	16	0.3
	3	Rhodes grass (*Chloris gayana*)	50	7	0.2
	4	Desho grass (*Pennisetum pedicellatum*)	44	6	0.1
	5	Lucerne (*Medicago sativa*)	43	5	0.1
Kenya	1	Napier, local (*Pennisetum purpureum*)	162	93	5.2
	2	Napier, other improved (*Pennisetum purpureum*)	11	10	0.2
	3	Rhodes grass (*Chloris gayana*)	41	8	0.8
	4	Calliandra (*Calliandra calothyrsus*)	43	7	0
	5	Fodder sorghum (*Sorghum* spp.)	3	6	0

[a]Number of villages in which fodder was grown.
[b]Share of households (Hh) growing forages among farming households.
[c]Area share of cultivated area devoted to forage, considering only forages for which extent of adoption was recorded by area units.

ical southern states of China where king grass is also an option. Here, new varieties that have been developed include Guimu and Guimin Yin, which are mainly considered for use as feed for cattle and other livestock (Shilin *et al.*, 2007). In the grazed systems of Japan, the dwarf varieties, commonly grown in combination with Italian ryegrass (*Lolium multiflorum*), are growing in popularity (Ishii *et al.*, 2005; Fukagawa and Ishii, 2018).

In South America, one of the few active breeding programmes for Napier grass exists at EMBRAPA in Brazil (Gomide *et al.*, 2015). There is a history of exchange of material between the ILRI gene bank and EMBRAPA, which enhanced the diversity in each of the collections in support of the development of new cultivars (Negawo *et al.*, 2018). Some of the most recent cultivars from EMBRAPA produced include Pioneiro, a standard variety for cut-and-carry systems (Figueira *et al.*, 2016), and BRS Kurumi, a dwarf variety mainly targeted for grazing but also considered suitable for cut-and-carry systems (Gomide *et al.*, 2015; Pereira *et al.*, 2017).

Push–pull technology

The so-called push–pull system developed by ICIPE and the Rothamsted Research Institute is a biological intervention to control maize stem borer (Khan *et al.*, 2006, 2008a, 2014; ICIPE, 2015). The basis of the technology is that stem borer moths are repelled by phytochemicals in the legume *Desmodium* spp. (*D. intortum, D. uncinatum*) but are attracted by the green biomass provided by Napier grass. Planting patterns for *Desmodium*, Napier grass and maize that take account of these effects can lead to reduced stem borer infestation. The planting pattern usually involves maize intercropped with *Desmodium* as a repelling plant (push) with the intercropped area surrounded by Napier as an attractant for pests (pull). A further benefit is reduced infestation by *Striga* spp. (*S. hermonthica* and *S. asiatica*), an obligate parasitic weed that can greatly reduce host crop yields. The technology has potential environmental and economic benefits in that it does not require expensive and damaging pesticides. The technology also provides feed in the form of Napier grass and *Desmodium* fodder, as well as reducing pests.

Assessments by the originating institutions suggest that tens of thousands of farmers have adopted the practice in East Africa. For example, a 2011 study put the number of adopters at 30,000 in East Africa, with the technology covering 15,000 ha (Khan *et al.*, 2011). More recent promotional materials estimate the number of

adopters to be closer to 100,000 (ICIPE, 2015). In common with fodder trees, push–pull is a knowledge-intensive technology that has been heavily promoted by the originating institutions. Definitions of 'adoption' in the literature around push–pull tend to be vague and often relate to the numbers of farmers 'reached' with the technology rather than those accepting and adopting the practice over the long term. Adoption estimates are usually presented without a clear definition of adoption and without supporting evidence against which to judge their reliability. As with fodder trees, there is a need for independent evaluations to assess the true extent of adoption of the push–pull technology.

The assumed strength of push–pull is its multiple benefits, which include reduced pest damage, fewer weeds, more feed and improved soil fertility using legumes (*Desmodium* spp.). However, in the context of assessing forage successes, push–pull is not necessarily the strongest example because the potential benefits accrue from both improved cereal yields and improved forage production. In some economic assessments of the benefits of push–pull, the extra milk from improved livestock feeding does not feature in cost–benefit calculations (Khan *et al.*, 2008b). Other studies have factored in economic benefits from forages based on prevailing market prices for forages and found them to be important in the overall profitability of the technology (de Groote *et al.*, 2010).

Adoption of planted forages in Asia

CIAT has stimulated adoption of intensive grass production linked to beef cattle fattening and cow–calf breeding systems in South-east Asia (Stür *et al.*, 2007). The technology involves cut-and-carry grass plots with the species being mainly *Panicum maximum*, *B. humidicola* and *Brachiaria* hybrids. The areas planted to grasses are small, averaging around 0.25 ha, but plots as small as 0.1 ha are viable because production is intensive and grass yields can be very high. The success of the planted forages initiative depended on the participatory nature of the intervention coupled with improved planting materials (Ayele *et al.*, 2012).

The planted forage initiative in South-east Asia evolved over two decades through multiple projects with estimated numbers of farmers adopting it in excess of 10,000 in Vietnam alone among those directly involved in project areas (Stür *et al.*, 2013). Although assessments of the extent of adoption are conducted by the originating institutions and are thus not independent, the counts are based on surveys of random samples of households in the study districts and thus have some credibility. The technology has now been taken up by local government structures (Millar and Connell, 2010), and the reach is likely to be much larger although, again, independent assessments are needed.

Other examples are the adoption of the legume *Stylosanthes guianensis*, based on accession CIAT 184, as a cover crop and for leaf meal production in tropical China, reaching about 300,000 farmers to feed poultry and pigs (Guodao and Chakraborty, 2005) and the use of various *Stylosanthes* spp. in India by 250,000 farmers (Shelton *et al.*, 2005).

Adoption of planted forages in Latin America and the Caribbean

In terms of area, adoption of tropical forages in Latin America and the Caribbean is widespread and the role of the CGIAR centres has been important (Lynam and Byerlee, 2017a) although the beneficiaries have generally been larger farmers.

In 2002, a *Brachiaria decumbens* × *brizantha* × *ruziziensis* cultivar coming out of CIAT's breeding programme (Miles, 2001, 2007) was released (Lynam and Byerlee, 2017b) as the first bred *Brachiaria* cultivar to be documented. *Brachiaria* hybrids have since been commercialized through interaction with the private sector, namely the Papalotla Group and Dow AgroSciences. Uptake based on documented commercial seed sales to the end of 2018 was estimated to be some 960,000 ha mostly sown in the past decade. According to CGIAR reports, more than 100,000 ha are planted on an annual basis, with numbers still below the potential as seed production and commercialization channels are still evolving (CGIAR, 2018). Most adopters appear to be small and medium-sized livestock producers (Papalotla, personal communication),

although not equivalent to 'smallholders' as used in the African context. Recently, Papalotla registered advanced cultivars in Kenya and is commercializing these through licensing agreements (Government of Kenya, 2016). The original cultivar Mulato had limited commercial success due to low seed production and was quickly replaced by Mulato 2 when higher seed production was included as an additional breeding objective. In subsequent years, a series of *Brachiaria decumbens × brizantha × ruziziensis* hybrid cultivars and a synthetic mixture were released, namely Cayman (tolerant to water logging), Cobra (more erect growth habit), Camello (better drought tolerance), Mestizo (synthetic mixture of three hybrids for better establishment and pasture utilization) (Papalotla: www.grupo-papalotla.com/productos.html and Tropical Seeds: www.tropseeds.com/varieties/, both accessed 27 March 2020) and Converse (Dow Agrosciences). Additional materials for increased tolerance to drought and shade (e.g. for silvopastoral systems) and additional synthetic mixtures are to be commercialized in the next 2–4 years (Papalotla, personal communication). CIAT is also advancing the development and commercialization of *B. humidicola* and *Panicum maximum* breeding lines.

Some of the most widespread adoption of planted forages is in Brazil where it is estimated that about 120 million ha have been planted, of which 99 million are *Brachiaria* spp. and about 17 million ha are *P. maximum* (Jank *et al.*, 2014). This has largely been driven by the private sector and EMBRAPA, which are valuable partners, and involves large farms that are only peripherally within the mandate of the CGIAR system.

Similar production increases have been achieved in the Eastern Plains of Colombia as part of the collaboration of the Corporacion Colombiana de Investigacion Agropecuaria (CORPOICA) and CIAT, with inclusion of *Brachiaria* spp. in crop/pasture rotations leading to a doubling of carrying capacity compared with degraded pasture and a tenfold increase over native savannah (Rincón and Ligarreto, 2008; Rincón *et al.*, 2010).

Better documented is the uptake of *Brachiaria* grasses in Mexico and Central America where by the early 2000s over 3 million ha were reported based on extrapolation from seed sales

(Holmann *et al.*, 2004). Surveys in Colombia's Eastern Plains carried out in 2017 suggested that about one-third (about 3 million ha) of improved pastures are sown using *Brachiaria* cultivars selected by CORPOICA and CIAT or bred by CIAT; across a set of five countries, an estimated 59.2% of all pastures were found to be planted with *Brachiaria* grasses, with about half being CIAT-selected *Brachiaria* (ISPC, 2018). Through the work of EMBRAPA, with contributions from CIAT, Rivas (2002) estimated that 1.5 million ha had been sown to *Andropogon gayanus* by 2000.

The documented success of forage legumes so far is less visible. However, for *Arachis pintoi*, cv. Amarillo developed in Australia and selected by EMBRAPA and CIAT for tropical America, around 65,000 ha have been reported to be adopted in Acre in Brazil (Valentim and de Andrade, 2005). A *Stylosanthes* spp. mixture ('Estilosantes Campo Grande'), co-developed by B. Grof (EMBRAPA, ex-CIAT), has been sown on 150,000 ha in the southern Cerrados of Brazil (Fernandes *et al.*, 2005).

These South American examples point to possible future growth in use of planted forages in Africa once livestock production becomes more commercial, farm sizes increase, private-sector actors have stronger engagement and the institutional environment is more conducive to growth of the forage sector.

Knowledge products on planted forages

As well as research on planted forages, CGIAR centres have generated a range of 'knowledge products', which collect internal and published knowledge and present it in a form that is useful for scientists and the wider livestock development community. Examples of such knowledge products are the Tropical Forages tool, the *Tropical Grasslands-Forrajes Tropicales* journal and the Feed Assessment Tool (FEAST).

Tropical Forages tool

A wide array of plant species is used as feed for livestock and these differ in both their suitability as livestock feed and in the biophysical conditions

that support their growth. In 2005, the international planted forages community initiated the Tropical Forages tool to collate the tacit knowledge of forage experts as well as published data on forage characteristics to develop an online tool to support selection of appropriate forages for specific purposes and locations. The Tropical Forages tool (www.tropicalforages.info; accessed 28 February 2020) has been available since 2005 and is currently receiving approximately 500,000 annual hits with visitors coming from universities, development agencies, seed companies and (informed) farmers. It is open access and easy to use, providing detailed information on more than 170 major forage species and the environments they are adapted to. The tool was developed by the Commonwealth Scientific and Industrial Research Organisation (CSIRO), the Queensland Department of Agriculture and Fisheries, CIAT and ILRI, and capitalized on the inputs on more than 50 forage experts, with widespread knowledge and experience in tropical and subtropical forages. An updated version of the tool was launched in 2021.

Tropical Grasslands-Forrajes Tropicales

The online journal *Tropical Grasslands-Forrajes Tropicales* was established in 2012 as a successor to the former journals, *Tropical Grasslands*, published during 1967–2010 by the Tropical Grassland Society of Australia, and *Pasturas Tropicales*, published during 1979–2007 by CIAT.

The main features of *Tropical Grasslands-Forrajes Tropicales* are that the journal is international, published online only, open access (no charges for subscription or publication fees), bilingual (English and Spanish), peer reviewed and guided by a 23-member Editorial Board, which is composed of the world's leading tropical pasture scientists. Further information on the journal is available at its website (www.tropicalgrasslands.info; accessed 28 February 2020). Back issues of the predecessor journals, *Tropical Grasslands* and *Pasturas Tropicales*, can also be accessed at this site. The journal is indexed in the major abstract and citation databases of peer-reviewed literature and is widely used; as of December 2019, there had been more than 492,000 abstract views and more than 669,000 PDF/eBook downloads; currently the journal receives 229,000 annual visits.

Feed Assessment Tool (FEAST)

FEAST (Duncan *et al.*, 2012) is a systematic, participatory approach to supporting design of livestock feed interventions at the village/community level. It was originally developed in 2008 by ILRI in collaboration with CIAT. FEAST involves a structured conversation with farmers at the village level to characterize the local farming system, the role of livestock in the farming system and the way in which livestock are currently fed. This is followed by application of a short household survey among selected farmers. Data from the survey are used to develop a series of standardized graphical outputs, which support decision making on appropriate feed interventions. A further feature is an intervention-ranking module, which generates a prioritized list of candidate interventions derived from automatic analysis of survey data. The FEAST data application itself has been downloaded by 1400 individuals and has been applied in over a dozen countries. Over 70 FEAST reports have been published online. Published outputs in the FEAST collection in the CGIAR publication repository have had over 15,000 views and downloads per year in the past 5 years.

Forage seed technical support and distribution

CGIAR has been active in the provision of advice and technical training in forage production as well as production and sale of seeds for establishment of tropical forages to address these constraints. The seed production units of CIAT and ILRI provide a source of tropical forage seeds and planting material of selected best-bet species at cost for use in establishing national forage seed production. CIAT provides seeds of 25 herbaceous legumes, nine grasses and seven fodder trees. ILRI currently can supply seeds of 33 species of herbaceous legumes, ten species of grass and five species of fodder trees. Provision of seeds from the two sources is complementary, mostly handling different species and distributing in different regions, primarily within the regions where the centres are located (Table 13.4). CIAT has shipped seeds of over 20,000 samples to 88 different countries, while ILRI has provided over 8500 samples in response to over 1500 orders

since the establishment of their forage seed activities. Seed distribution has supported the forage evaluation networks of CIAT and ILRI in Asia, Latin America and the Caribbean, and sub-Saharan Africa, and has strengthened forage research and development activities globally.

Tropical forage seed production is a specialist market because many species are perennial and annual reseeding is not required. This leads to uncertain demand, which causes a high degree of risk to both seed producers and sellers and has reduced investment in a more formal distribution seed system for forage seeds in many developing countries (Hanson and Peters, 2003). This has also contributed to fewer new varieties and species being released in recent years and promotion of an informal integrated community-based seed supply system to fill the gap. A recent survey in Ethiopia showed that many smallholders are willing to pay for forage seeds and to use land for planted forages where alternative feed is scarce and where market opportunities for milk and meat exist (Negassa *et al.*, 2016).

Both centres have supported alternative suppliers in the tropical forage seed agribusiness. CIAT has partnered with the Papalotla Group from the private sector to achieve a wide dissemination of hybrid pasture seeds developed by CIAT that will be distributed by Papalotla. Both CIAT and ILRI have supported entrepreneur- or farmer-led seed supply systems to complement large-scale private seed production. Collaboration with government institutions and non-governmental organizations has ensured training of farmers in seed production, seed quality control and certification. A farmer-led seed enterprise, PRASEFOR (Artisanal Forage Seed Production), was formed in Honduras as an association of 12 smallholder farmers to produce grass seeds. In contrast to many other farmer-led seed enterprises, this was business oriented and formed with very limited financial support, making the approach easily replicable (Hanson and Peters, 2003). Farmers were able to obtain a return of more than US$600/ha on forage seed production compared with an estimated US$60/ha for maize production. A similar approach was recently piloted in Ethiopia through the Deutsche Gesellschaft für Internationale Zusammenarbeit GmbH (GIZ)-funded FeedSeed project by mentoring individuals and forage seed businesses representing smallholder farmers, cooperatives and commercial seed companies, thereby helping to stimulate the availability of more and better-quality forage seed and forage use by smallholder livestock producers. The pilot project

Table 13.4. Major countries of recipients of forage seeds from CIAT and ILRI. (Data from ILRI and CIAT databases, February 2019.)

CGIAR centre	Country	Number of seed samples	Amount distributed (kg)
CIAT	Bolivia	492	306
	Brazil	837	535
	Colombia	16,202	55,912
	Costa Rica	570	993
	Ecuador	618	189
	Honduras	476	95
	Mexico	597	110
	Nicaragua	522	162
	Peru	1,024	1,295
	Venezuela	605	1,723
ILRI	Burundi	42	54
	Cameroon	98	74
	Ethiopia	6,989	34,591
	Ghana	81	33
	Kenya	159	199
	Pakistan	51	44
	Rwanda	47	29
	Tanzania	130	136
	Uganda	69	77
	Zambia	58	43

incubated 30 profitable private companies whose annual seed sales reportedly started at US$20,000 and increased to US$400,000 by the end of the 2-year project. With seed prices at US$5–20/kg in early 2019, forage seed production does seem to be economically attractive.

Environmental benefits of planted forages

The potential impact of tropical forages on GHG emissions has been well documented. Mitigation approaches include direct reduction of emissions, enhancing of carbon sequestration, higher productivity per land area and/or livestock unit and of feed efficiency (Peters *et al.*, 2013; Searchinger *et al.*, 2013; Rao *et al.*, 2015) and avoiding detrimental land conversion. By applying suitable practices, land can be freed for reforestation or for landscape restoration while livestock output grows. Genetic solutions to curb nitrous gas emissions and nitrate leaching – while reducing the amount of nitrogen fertilizers in crop–livestock rotations – have been demonstrated as a proof of concept for biological nitrification inhibition (Subbarao *et al.*, 2017). The environmental role of symbiotic nitrogen fixation by tropical legumes is recognized, as is the potential of tannin-rich legumes for reduction of methane emissions by livestock (Schultze-Kraft *et al.*, 2018). Less information is currently available on the water footprint of forage-based feed production, with fodder production being a major driver of water use in livestock systems (Herrero *et al.*, 2012).

The main potential environmental impact of tropical and subtropical planted forages will be through intensification of livestock production and accompanying reductions in emissions assuming livestock numbers decrease as production intensifies. The situation may change when the role of tropical forages in providing ecosystem services is further recognized and economic incentives for increased adoption of planted forages are in place (such as Payment for Ecosystem Services schemes). Because pasture-based systems, which are the largest single land-use category globally (Erb *et al.*, 2007), are changing from extensive grasslands to more intensive mixed crop–livestock farming, there is the opportunity that this transition could reduce GHG emissions without negative effects on food security (Havlík *et al.*,

2013). Moreover, the high-risk sites, or 'hotspots', for GHG emissions are located in areas of low livestock productivity – extensively managed areas in eastern Africa, Latin America and the Caribbean, and South Asia (Gerber *et al.*, 2013; Herrero *et al.*, 2013). These are also the areas with the greatest potential for increased forage use, although as argued elsewhere in this chapter increased forage use would depend heavily on the economics of land and labour use.

As examples of the potential importance of forages in climate-change scenarios, the governments of Brazil and Colombia have identified the intensification of livestock production, using planted forages and proper management, as key strategies to mitigate GHG emissions in agriculture. The strategies are outlined in the Plano ABC (Ministério da Agricultura, Pecuária e Abastecimento, 2012) and the NINO (Ministerio de Ambiente y Desarrollo Sostenible, 2015) for Brazil and Colombia, respectively, as a combination of increased productivity per livestock unit and land area and favouring environmentally sound land-use changes. Thornton and Herrero (2010) has illustrated the possibility of specific technologies such as improved *Brachiaria* and *Leucaena* spp. to reduce GHG emissions through increased per-animal productivity and assumed reductions in livestock numbers. Lal (2010) has stated that 29% of the overall carbon mitigation potential will be from pastureland. The biggest potentials for carbon sequestration (i.e. through restoring degraded grasslands) are in South America and Africa (Conant, 2002; Conant *et al.*, 2011).

In a review of the potential of forages to mitigate emissions, Peters *et al.* (2013) concluded that forage-based systems have a lower ecological footprint than feedlots. Better management of crops and grasslands, and restoration of degraded lands, can result in a mitigation potential as high as 3.5 billion t CO_2-eq/year or 75% of the biophysical mitigation potential stated by Smith *et al.* (2008). Thornton and Herrero (2010) calculated that a modest 30% adoption rate of improved deep-rooted *Brachiaria* pastures could yield a mitigation potential of 29.8 million t CO_2-eq/year in the Cerrados of Brazil alone, an amount equivalent to 2% of the total mitigation potential of agriculture. According to Fisher *et al.* (2007) and Blanfort *et al.* (2012), the mitigation potential of planted forages to accumulate carbon under adequate pasture and animal

management is second only to forests. To refine these estimates, further research in a variety of contexts is required.

What has limited the impact of planted forages in tropical Africa and Asia?

Despite the technical potential of planted forages, a common research finding is that they are rarely adopted beyond project-led initiatives in Africa and Asia. Evidence for spontaneous widespread adoption is rare, except, for example, Australia and Brazil where the context is very different and smallholders are not the main beneficiary. The reasons for lack of adoption are complex. Promoters of planted forages are convinced of their technical merits and advocate greater 'promotion and dissemination' to convince smallholders of their advantages. In the terminology of Sumberg (2002) forage legumes have taken on a 'mantle of absolute goodness'. The realists view lack of adoption as being related to inherent system properties, which make them unattractive for farmers given the prevailing economic environment. To quote Sumberg (2002): 'Particular attention is placed on the idea that the biophysical and socio-economic factors that have previously been constraints to legume adoption should now be viewed as system properties and incorporated into the design specification of technology.'

This idea that system properties are what constrain the uptake of planted legumes and planted forages in general is compelling and was also proposed by McIntire and Debrah (1986) as long ago as the mid-1980s. McIntire and Debrah (1986) laid out a series of propositions regarding the suitability of forage legumes for smallholder systems. Among their propositions were that at different population densities competition for land and labour will tend to disadvantage forage legumes as a viable part of the farm enterprise. At low population densities (e.g. pastoral systems), competition for labour is an issue. In such systems, crops and animals are managed as separate enterprises, as mobility of livestock is a necessary property of the system. Devoting labour to tending of forage crops becomes impractical. At high population densities (e.g. mixed intensive systems), competition for land becomes the issue. In such systems, land is scarce and use of land for production of staple and cash crops takes priority over the production of livestock feeds for reasons of economics.

The barrier of system properties is also apparent in the arguments of Ruthenberg (1980) in his consideration of the scarcity of medium- to long-term grass cultivation in the tropics ('ley farming'). Ruthenberg pointed out various characteristics of tropical farming systems that make ley farming unattractive. Among the reasons offered by Ruthenberg were the poor nutritive quality of tropical grasses, the advanced animal husbandry needed to make such systems work and the relative (un)profitability of use of land for livestock production compared with arable options such as maize, sorghum and cassava.

A more recent line of argument in the debate about adoption success of planted forages frames the problem as one of 'innovation capacity failure' (Hall et al., 2007). The application of innovation systems theory to the question of feed development follows a trend across the CGIAR system to think about technical change in the context of innovation systems – the network of agents and their interactions that are necessary to foster change. In ILRI and CIAT, projects around the time, including the Fodder Adoption Project and Fodder Innovation Project, attempted to move beyond technical feed research to investigate institutional barriers to technical change in the feed sector (Ayele et al., 2012; Reddy et al., 2013). In the logic of these projects, there was a recognition that Sumberg's (2002) 'system properties' were indeed impediments to progress but that focusing on the institutional issues could overcome some of these barriers including difficulties of seed supply, access to markets and the need to deal with policy constraints to bring about improvements in livestock feeding. While these projects did not fully achieve their ambitions, they did bring in new thinking about innovation in the livestock feed sector and helped to broaden research perspectives beyond a narrow focus on forage management. In South-east Asia in particular, application of such thinking did lead to adoption of forages at a reasonable scale (Stür et al., 2013). Such innovation systems thinking is now routinely embedded in CGIAR-led projects and programmes focused on feed and forage

improvement in the CGIAR Research Programme on Livestock and Fish (Puskur *et al.*, 2011).

Global impacts from planted tropical forages

Early research on tropical planted forages focused on collection and characterization of forage species with economic potential to improve livestock productivity. This involved collections in sub-Saharan Africa organized mainly from Australia. Promising accessions are now stored in the various gene banks of CGIAR, notably those at ILRI, CIAT and ICARDA. Despite extensive forage research activity in the CGIAR and other centres, forage adoption among smallholders has generally been disappointing. Pengelly *et al.* (2003) concluded that 'despite 50 years of investment in forage research in the tropics, forage adoption has been relatively poor across all tropical farming systems'. Sumberg (2002) argued that forage legumes had not achieved their potential in sub-Saharan Africa, despite 70 years of research to promote them. Shelton *et al.* (2005) in their review of forage legume successes found that none of the 14 legume cultivars released in Latin America and the Caribbean between 1980 and 2000 was well adopted.

In reaction to these disappointing findings about the impact of tropical forages research, there have been attempts to re-evaluate the impact. The most recent example is the meta-analysis of White *et al.* (2013), which built upon the study by Shelton *et al.* (2005). The Shelton study presented 19 case studies and estimated areas planted to various tropical legumes around the world, along with numbers of farmers and gross economic benefits. Notable successes were cowpea in West Africa accounting for 1.4 million ha (*ex ante* impact estimate), fodder trees in East Africa totalling 4 million m of hedgerows, *Stylosanthes* spp. in southern China (more than 200,000 ha), Thailand (more than 300,000 ha) and India (less than 250,000 ha), *Pueraria phaseoloides* as grazed pastures in Brazil (480,000 ha) and *A. pintoi* also in Brazil (more than 65,000 ha). The authors identified factors favouring adoption as meeting the needs of farmers, building partnerships, understanding the resources and skills of farmers, engagement with rural communities, and long-term involvement of champions (Shelton *et al.*, 2005).

The study by White *et al.* (2013) sought to quantify the impact of planted tropical forages in general (and not just legumes, as in the study by Shelton *et al.*, 2005). They defined the impacts in three main domains: economic, social and environmental. Positive impacts can include improved soil cover and hence reduced erosion, nitrogen fixation by legumes leading to improved soil health, and deeper rooting leading to improved water-use efficiency and soil carbon storage. Negative impacts can include the introduction of invasive characteristics and loss of local biodiversity.

The authors set out a series of nine methodological shortcomings of the studies reviewed as a caution to the conclusions about economic impact. Despite shortcomings in the methods and data in the evidence reviewed, the analysis yielded some interesting insights. White *et al.* (2013) identified a total of 118 million ha planted to 'improved' tropical forages from the studies they compiled. They estimated that Brazil accounted for 86% of the known planted area of improved forages. The area under *Brachiaria* spp. dominated. The farm-size characteristics of this adoption were not fully defined and included large commercial operations.

Emphasizing the methodological shortcomings of the sample studies, fewer than 20% of the studies directly attempted to quantify economic impacts. Furthermore, the lack of a common methodology to quantify economic impacts (mixture of net present value approaches and annual estimates) meant that it was difficult to come up with an estimate of total economic benefit. Environmental and social impacts were even less frequently quantified, with 7% and 2% of the studies quoting environment and social impacts, respectively. The authors recognized a trend for greater emphasis on longer-term impacts in later studies, suggesting that the research for development community is increasingly aware of the need to quantify large-scale impacts. Of all the studies analysed, fewer than 15% were conducted independently of the personnel affiliated with the programme or project. This may have led to exaggeration bias, as those closely involved would be under pressure to justify their research through impact. As previously noted,

this lack of independent assessment is also an issue with the various success cases outlined earlier in this chapter.

New adoption potential

Given the advances in the quality and coverage of databases, scientists can target forage research to sites of highest probable adoption. Several factors affect adoption potential. One is population density. Forage cultivation can be expected to occur at intermediate population densities where there is sufficient land but where labour does not become a limiting constraint, or in areas of high population density that are highly productive. A second factor is profitability in the situations where high demand and prices can provide the incentive to invest in forages (e.g. instead of or as well as vegetable production). A third factor is rainfall distribution: given that forage is a year-round enterprise especially for dairy production, forages are more likely to succeed where rainfall is well distributed. If this is not the case, forages can work but the capacity to conserve, especially through hay-making, may be crucial for adoption.

We outline an example for Napier grass (*P. purpureum*) and its potential as a cut-and-carry forage. We utilized the model EcoCrop as implemented in DIVA-GIS (Hijmans *et al.*, 2012). To generate suitability surfaces for Napier grass, EcoCrop estimates a suitability index from 0 to 100 for a crop, based on monthly precipitation and temperature surfaces and on a small number of crop-specific parameters. We evaluated Napier grass suitability for current climatic conditions using the WorldClim dataset (distributed as part of DIVA-GIS). For possible future climatic conditions, we downscaled spatially coarse output from

several climate models in relation to a high GHG emissions scenario for periods centred on 2050 and 2090 (Jones and Thornton, 2015). Aggregate differences in both projected temperature and rainfall for the climate models selected are shown in Table 13.5.

To identify areas with 'moderate' population densities, following Kruska *et al.* (2003) we used a lower limit of 20 people/km², above which increasing proportions of land are cultivated (Reid *et al.*, 1995, 2000). Goddard *et al.* (1975) and McIntire *et al.* (1992) showed that fallowing disappears (and agricultural fields coalesce) at densities above 85 people/km² across the semi-arid to humid zones in Africa. We thus set the moderate population density to be between 20 and 85 people/km², and we used the dataset GPW v4 (CIESIN, 2016).

As a proxy for market pull, we used the accessibility dataset of Nelson (2008), which gives the travel time in minutes to the nearest city with a population in excess of 50,000, based on the estimated travel time to cross each pixel in relation to land cover, slope, elevation, the roads network, and any railways, rivers and water bodies. As a threshold, following Jones and Thornton (2009), we selected a value of 200 min, allowing the possibility for a smallholder to take produce to market and return home on the same day.

The results are shown in Table 13.6 and Fig. 13.1. These 'high-potential' sites are defined as the areas having at least moderate suitability for Napier grass and having a moderate human population density (20–85 people/km²) *and* are within 200 min travel time of large population centres. In all regions, suitability increases to the 2050s but then declines to the 2090s, presumably in response to ever-higher temperatures and increased plant

Table 13.5. General Circulation Model (GCM) responses for the land areas between latitudes 30°N and 30°S. Values shown are for 'future minus current'. (From Jones and Thornton, 2015.)

	2050s		2090s	
GCM	Annual rainfall (mm)	Average annual temperature (°C)	Annual rainfall (mm)	Average annual temperature (°C)
GISS-E2-R (NASA Goddard Institute for Space Studies)	−53	+1.96	−56	+3.63
Ensemble mean (17 GCMs)	+12	+2.36	+32	+4.68
HadGEM2-ES (UK Met Office, Hadley Centre)	−2	+2.93	−10	+5.83

Table 13.6. High-potential sites for Napier grass as a cut-and-carry forage by region, period and climate model (km²). (Unpublished data from K. Kekae, G. Brychkova, P.C. Mckeown, J. Hanson, C.S. Jones, P.K. Thornton and C. Spillane, 2018.)

Region	Current conditions (2000)		Ensemble mean (17 GCMs) (2050s)		Ensemble mean (17 GCMs) (2090s)	
	Moderate suitability	Excellent suitability	Moderate suitability	Excellent suitability	Moderate suitability	Excellent suitability
Global	600,847	1,355,312	516,552	2,169,758	652,472	1,668,437
Latin America	174,039	363,101	97,149	560,998	162,458	394,257
Sub-Saharan Africa	201,548	712,057	109,829	920,105	186,875	725,251
Asia	149,343	257,897	89,741	436,231	125,500	304,854

	Current conditions (2000)		GIS2 GCM, 2050s		GIS2 GCM, 2090s	
	Moderate suitability	Excellent suitability	Moderate suitability	Excellent suitability	Moderate suitability	Excellent suitability
Global	600,847	1,355,312	546,007	1,981,659	524,104	2,044,916
Latin America	174,039	363,101	115,716	522,540	88,633	504,335
Sub-Saharan Africa	201,548	712,057	117,360	766,692	120,844	689,778
Asia	149,343	257,897	94,726	467,864	82,912	483,741

	Current conditions (2000)		HADG GCM (2050s)		HADG GCM (2090s)	
	Moderate suitability	Excellent suitability	Moderate suitability	Excellent suitability	Moderate suitability	Excellent suitability
Global	600,847	1,355,312	557,462	2,212,979	571,497	2,365,266
Latin America	174,039	363,101	114,498	557,242	131,724	491,588
Sub-Saharan Africa	201,548	712,057	116,960	876,141	109,760	848,881
Asia	149,343	257,897	87,816	446,145	94,043	441,943

Top, mean of 17 General Circulation Models (GCMs); middle, a 'cool' GCM (GISS-E2-R, see Table 13.5); bottom, a 'warm' GCM (HadGEM2-ES, see Table 13.5).

evapotranspiration. Nevertheless, the proportion of area that is of high suitability increases over time compared with the area of moderate suitability, and the proportion of highly suitable hotspot land outside the tropics is increasing over time. The trends for the cooler General Circulation Model (GCM; Table 13.6, middle panel) are similar, although Asia sees an increasing area of highly suitable high-potential sites up to the 2090s. The hotter GCM results (Table 13.6, lower panel) indicate that the tropics are in general becoming rather warm for Napier grass, and there are large areas in the northern temperate zones that are projected to be highly suitable high-potential sites.

Changing human population dynamics in the coming decades can be expected to affect suitability by increasing pressure on land,

particularly in peri-urban areas. These effects are difficult to estimate, however. For example, increasing population densities to the middle of the current century are likely to decrease the range of tsetse-transmitted trypanosomiasis in parts of Africa through habitat destruction (McDermott *et al.*, 2002). However, evaluating possible future changes in land use and land competition due to population growth and urban migration is more challenging, mostly because of the difficulty in projecting future development of road and other transport infrastructure, which is often the forerunner of highly localized increases in population density

This simple illustrative analysis suggests that the potential high-potential sites for Napier grass adoption as a cut-and-carry forage are relatively
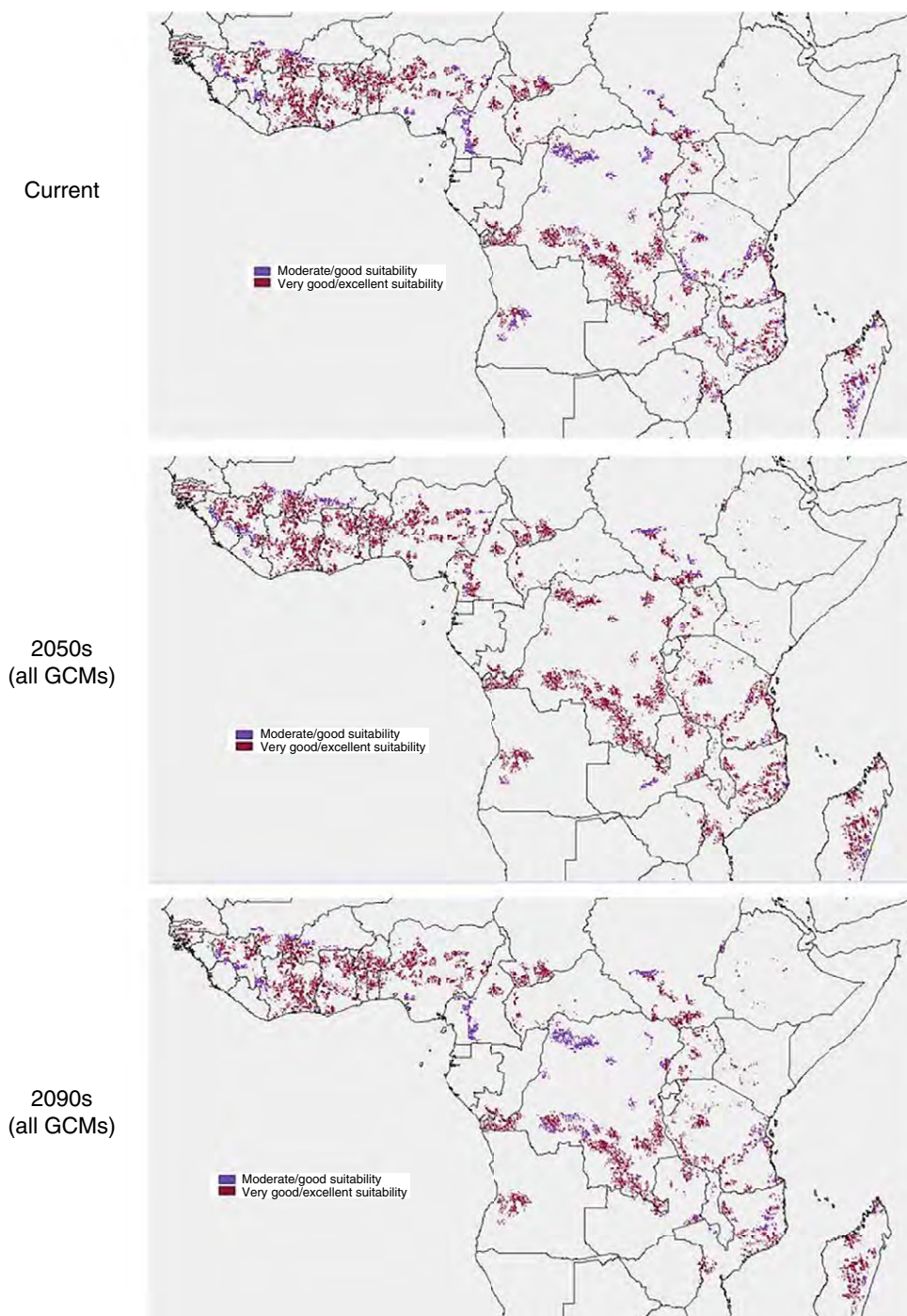
Fig. 13.1. High-potential Napier adoption sites in sub-Saharan Africa.

limited in the global tropics. A more robust analysis could be done that takes rainfall distribution into account, as well as by using a more sophisticated niche and suitability model than EcoCrop, such as MaxEnt (Warren and Seifert, 2011). Another missing element is information on possible changes in forage quality under a changing climate. Nevertheless, there is considerable potential to exploit new datasets for more appropriate targeting. Local evaluation, coupled with information on where particular forages are actually being utilized, has considerable potential to guide future forage targeting and adoption.

The Future

Planted forages have the potential to fuel growth in the smallholder crop and livestock sector in Africa and Asia by providing high-quality feed and by filling seasonal gaps. In addition to productivity benefits, planted forages can reduce the environmental footprint of livestock.

Adoption of planted forages has been below its potential in nearly all of sub-Saharan Africa and South Asia. Adoption in Latin America has been better, notably in Brazil and in parts of Central America. Such success is rare in Asia and sub-Saharan Africa (with the possible exception of Napier grass in East Africa), but as mixed crop–livestock systems continue to expand, so will planted forage use.

To conclude, we offer some lessons for the future:

- Apply lessons from Latin America and the Caribbean to sub-Saharan Africa and South-

east Asia about the systemic conditions needed for successful planted forage development among smallholders. These South American examples point to possible future growth in use of planted forages in Africa once livestock production becomes more commercial, farm sizes increase, private-sector actors have stronger engagement and the institutional environment is more conducive to growth of the forage sector.

- To exploit the full potential of environmental benefits, it is evident that work on forages (and other feeds) needs to be integrated with animal health and animal genetics.
- We need to better define system constraints to forage use and to target solutions for system constraints along with a continuing focus on farm-level experimentation and on forage breeding. Understanding system constraints will facilitate better forage targeting using spatial forecasting of global high-potential sites.
- Create markets for public and private agents by: (i) building germplasm supply arrangements (public or private, depending on location); and (ii) identifying value chain constraints and resolving them through novel business arrangements.

Notes

[1] The nomenclature of several tropical forage species has changed recently. Because this review considers past research, we use the earlier accepted names throughout. It should be noted, however, that according to the taxonomy proposed by the USDA Germplasm Resources Information Network (GRIN), *Brachiaria brizantha*, *B. decumbens* and *B. humidicola* are now accepted as *Urochloa brizantha*, *U. decumbens* and *U. humidicola*, respectively; *Pennisetum glaucum*, *P. pedicellatum* and *P. purpureum* as *Cenchrus americanus*, *C. pedicellatus* and *C. purpureus*, respectively; and *Panicum maximum* as *Megathyrsus maximus* and *Pueraria phaseoloides* as *Neustanthus phaseoloides*.

[2] Older accounts from East Africa show Napier grass in the early 20th century (Boonman, 1993).

[3] A kebele is the smallest administrative unit in Ethiopia. A 'woreda' is the second smallest admininstrative unit in Ethiopia.

[4] Fodder tree research has been pursued in East Africa for decades, as shown in the archives of the *East African Agricultural and Forest Journal*: (www.tandfonline.com/toc/teaf20/current).

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14 Multidimensional Crop Improvement by ILRI and Partners: Drivers, Approaches, Achievements and Impact

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Contents

Executive Summary

The problem

Livestock provides food and income for almost 1.3 billion people across the world. Grazing has long been a principal source of feed in much of South Asia and in sub-Saharan Africa. Due to population pressure, land degradation and conversion from grazing to arable land, grazing areas have contracted, resulting in feed shortages. The conversion of grazing land is likely to be aggravated by climate change (Blümmel *et al.*, 2015b). The increasing demand for animal-sourced food is another factor in putting pressure on feed from all sources (Blümmel *et al.*, 2017).

Feed supply and demand scenarios for South Asia and sub-Saharan Africa have shown that crop residues (CRs) such as straws, stover and haulms commonly provide 50–70% of the feed resources in smallholder systems (Blümmel *et al.*, 2014b; Duncan *et al.*, 2016). In the highlands of Ethiopia, cereal CRs have emerged as the main components of the livestock diet but are generally poor in their nutritive value with a low crude protein content (4%) and digestible organic matter (less than 50%).

Lignocellulosic biomass from forest, agricultural waste and CRs is the most abundant renewable biomass on earth with a total production estimated to range from about 10 billion to 50 billion t (Sanchez and Cardena, 2008). About 3.8 billion t are contributed by CRs, with cereals contributing 74%, sugar crops 10%, legumes 8%, tubers 5% and oil crops 3% (Lal, 2005). Considering the quantities of CRs available and the high nutritive quality of its basic constituents – hexose and pentose sugars – attempts to improve CR biomass for fodder began a century ago (Fingerling and Schmidt, 1919; Beckmann, 1921).

These and later attempts to improve CR biomass included chemical, physical and biological treatments. Chemical treatments, particularly the use of hydrolytic agents such as sodium hydroxide and ammonia (Jackson, 1977; Owen and Jayasuriya, 1989), received significant research attention. However, little uptake of chemical treatments was observed, despite efforts by the international research and development communities, and investments into chemical straw treatments have declined since (Owen and Jayasuriya, 1989).

The lack of adoption of postharvest treatments of CRs gave way to a new model of improving the fodder value of CRs by selection and plant breeding (Reed *et al.*, 1988a) and by identifying anti-nutritive factors in crop biomass (Reed *et al.*, 1988b, 1990). In the mid-1990s, the International Livestock Research Institute (ILRI) and International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) began a joint programme on improvement of grain and CR traits, focusing on sorghum (*Sorghum bicolor*) and pearl millet (*Pennisetum glaucum* (L.) R. Br.) in the semi-arid tropics of India. *Ex ante* estimates of potential productivity gains from genetic improvement of the digestibility of multidimensional food and fodder crops would produce high rates of economic return in the form of incremental meat, milk and draught power (e.g. Kristjanson and Zerbini, 1999, for pearl millet and sorghum in semi-arid India). Similar work started in West Africa in the 1990s among the International Institute of Tropical Agriculture (IITA), ICRISAT and ILRI, targeting cowpea.

This chapter therefore addresses the following questions. What is the extent of cultivar-dependent variation in CR fodder quality? Can these variations be exploited without detriment to grain yield? Have quality improvements in CRs from plant selection and breeding been achieved? Have such improvements made a field impact on crop and animal productivity?

Scientific impacts

The principal scientific achievement was to force a reconsideration of the single-trait (i.e. grain) model in favour of the multi-trait and whole-plant (i.e. food and fodder) model. While there are as yet few public-sector decisions to include stover traits as cultivar release criteria – sorghum and pearl millet are recent examples – public and private

crop-improvement programmes have reoriented their efforts towards whole-plant improvement. Crop-improvement paradigms are changing to whole-plant optimization, as, for example, reflected in the new CGIAR Research Program (CRP) on Grain Legumes and Dryland Cereals.

Under this principal achievement, scientific impacts are the findings that: (i) there is significant variation in CR quality; (ii) such variation does not compromise grain yield; (iii) near-infrared spectroscopy (NIRS) methods are accurate for rapid screening of quality traits; and (iv) recent molecular analyses can detect variations in fodder quality early in breeding material.

NIRS equations were also developed for grains of key crops, including routine quality traits such as protein, starch and fat but also amino and fatty acids.

The fodder quality of CRs can be increased by targeted genetic enhancement using conventional or molecular crop-improvement approaches such as marker-assisted breeding, use of quantitative trait loci (QTLs) or genome-wide association studies (GWAS). Nepolean *et al.* (2009) used QTL to map the genomic regions controlling stover quality and yield traits in pearl millet, while Blümmel *et al.* (2015a), used stay-green QTLs in sorghum. GWAS was used to unravel favourable native genetic variations for traits of agronomic and economic importance across many cereal crops (Vinayan *et al.*, 2013).

Genomic selection (GS) or marker-enabled predictions can predict untested phenotypes from whole-genome information. Blümmel *et al.* (2014b) developed a GS model of fodder quality traits to predict superior lines from a collection of doubled-haploid lines from the maize work of the International Maize and Wheat Improvement Centre (CIMMYT) in Asia.

Apparently, small differences in CR fodder quality result in substantial differences in livestock productivity because of the additive effects of higher diet quality and higher feed intake.

Mapping recommendation domains has allowed spatial stratification of farming systems to better assess the potential of multidimensional cereals (Kristjanson and Zerbini, 1999).

Development impacts

Market studies in India and West Africa have identified significant differences in CR prices attributable to CR quality in India and West Africa. This information is valuable to crop extension programmes.

Adoption studies have shown that materials with higher straw digestibility improve livestock productivity, which is again valuable to extension work.

Plant breeding and selection have led to the availability of crop cultivars with higher-quality CRs in sorghum, pearl millet, groundnut, rice and maize in India, and in cowpea in West Africa.

Higher productivity and income come from sales of CRs and from livestock production. Salient examples are as follows:

- An ILRI-CIMMYT collaboration identified a multidimensional maize hybrid (NK 6240), which is now a very popular hybrid in India (Anandan *et al.*, 2013). ILRI, CIMMYT and Syngenta are now exploring branding for CR fodder quality traits.
- Adoption of improved multidimensional cultivars based on seed production has been difficult and at times contradictory to estimate. Randomized adoption studies by household surveys show generally less adoption than estimates based on seed production.
- Adoption of hybrids is much faster because seed availability is less of a problem than with open-pollinated varieties. Thus, a new dual-purpose maize hybrid (MHM4070 or Lall-454) specifically bred by CIMMYT and ILRI for high temperatures in India reached more than 23,000 ha within 3 years.
- Concomitant increases of about 10% each of pod yield, haulm yield and haulm fodder quality in some new cultivars has provided sufficient incentives for their fast and large-scale adoption.

Policy impacts through the provision of information

Fodder market studies in South Asia and West Africa have shown that: (i) market prices reflect fodder quality differences within and between crops; (ii) customers are willing to pay price premiums for apparently small differences in fodder quality traits; (iii) the price of CRs relative to grain has increased during recent decades (Kelley *et al.*, 1993; Sharma *et al.*, 2010); and (iv) in some Indian markets, income from CR sales exceeded that from grain sales (Samireddypalle *et al.*, 2017).

*Capacity building and partnerships
on multidimensional crop
improvement as outcomes*

ILRI has established scientific partnerships in the CGIAR system with ICRISAT, CIMMYT, IITA, national agricultural research and extension systems (NARES) in Ethiopia (Ethiopian Institute of Agricultural Research, EIAR) and India (National Research Centre for Sorghum, now the Indian Institute for Millet Research, IIMR), and the private sector (SeedCo, Syngenta and Advanta).

Affordable and comprehensive phenotyping for food–feed and fodder traits in all key cereal and legume crops is feasible. The ILRI-crop-centre collaboration developed and validated NIRS equations for nitrogen (N), neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL), *in vitro* organic matter digestibility (IVOMD) and metabolizable energy (ME) of CRs of sorghum, pearl millet, groundnut, pigeon pea, chickpea, cowpea, rice, wheat and maize. ILRI NIRS specialists have trained hundreds of laboratory technicians from public and private sectors in South Asia and East and West Africa on NIRS operations. NIRS hubs exist in India and Ethiopia, and NIRS hubs in Nigeria, Mali and Burkina Faso are being established. These hubs are based on NIRS equations developed by ILRI and partners and on extensive training given by ILRI NIRS specialists.

Introduction

The growth in demand for animal-source food in low- and middle-income countries provides challenges and opportunities. A principal challenge is to raise fodder and animal yields per unit of land in a situation where the shrinking natural resource base in terms of land and water makes feed production harder.

In addition, feed resourcing and feeding are at the very interface where positive and negative effects from livestock occur (Blümmel *et al.*, 2013b). Feeds are the single most important input cost into livestock production and largely determine its profitability (Swanepoel *et al.*, 2010). Feed production accounts for the bulk of water required in livestock production (Singh *et al.*, 2004), as well as direct (enteric

methane production) and indirect (land use and conversion) greenhouse gas emissions (Steinfeld *et al.*, 2006).

Previous work by the ILRI and partners has identified feed shortage as a major constraint to higher livestock yields; this feed constraint will worsen with the increasing demand for animal-sourced food (Blümmel *et al.*, 2017). Opportunities for improving feed resources are constrained by shortages of arable land and, increasingly, water, and these constraints are likely to become aggravated by climate change (Blümmel *et al.*, 2015b). Feed supply–demand scenarios for South Asia and East and West Africa have shown that CRs such as straws, stover and haulms are already the most important feed resources, commonly providing 50–70% of the feed resources in smallholder mixed crop–livestock systems (Blümmel *et al.*, 2014b; Duncan *et al.*, 2016).

Generally, lignocellulosic biomass from forest, agricultural waste and CRs is the most abundant renewable biomass on earth, with a total production estimated ranging from about 10 billion to 50 billion t (Sanchez and Cardena, 2008). About 3.8 billion t are contributed by CRs, with cereals contributing 74%, sugar crops 10%, legumes 8%, tubers 5% and oil crops 3% (Lal, 2005). Considering the huge quantities of CRs available from agricultural production and the high nutritive quality of their basic constituents – hexose and pentose sugars – it comes as no surprise that attempts to upgrade CR biomass for livestock fodder reach back to the beginning of the 20th century (Fingerling and Schmidt, 1919; Beckmann, 1921). These and later attempts included chemical, physical and biological treatments, but chemical treatments received the maximum attention of researchers, particularly the use of hydrolytic agents such as sodium hydroxide and ammonia (reviewed by Jackson, 1977; Owen and Jayasuriya, 1989). However, comparatively little uptake of these technologies was observed, even though considerable effort was made by the international research and development community (Owen and Jayasuriya, 1989). For example, Owen and Jayasuriya (1989) listed and reviewed 12 major international conferences addressing the improved use of CR biomass for livestock feed from 1981 to 1988 and concluded that large-scale adoption of treatment interventions was very

rare and did not continue once project activities ceased, despite efforts to simplify treatment technologies and to use local inputs.

The lack of adoption of postharvest approaches to improving CRs gave way to a new research paradigm of targeted improvement of CR fodder value by plant breeding and selection. This was discussed at an international conference by the International Livestock Centre for Africa (ILCA) in 1987 (Reed *et al.*, 1988a). At that time, research on improving CR fodder value at source was largely restricted to barley because of the importance of green barley in the mixed systems of the eastern Mediterranean (Capper *et al.*, 1988). The ILCA proceedings (Reed *et al.*, 1988a) contained 12 papers: three addressed the use of CRs as livestock feed in smallholder crop–livestock farming systems (globally: McDowell, 1988, and Kossila, 1988; West Asia and North Africa: Nordblom, 1988) and three focused on the limited nutritive quality and characteristics of CRs but exclusively on cereal CRs (Mueller-Harvey *et al.*, 1988; Owen and Aboud, 1988; van Soest, 1988). The excellent fodder quality of many of the legume residues was not addressed. Crop and cultivar variations in CR fodder traits were explored by Ørskov (1988) and Capper *et al.* (1988) in some depth with regard to the number of cultivars investigated, while the remaining papers focused more on types of cultivars, such as bird-resistant versus non-bird-resistant cultivars (McIntire *et al.*, 1988; Reed *et al.*, 1988b), or on very few cultivars (Khush *et al.*, 1988; Pearce *et al.*, 1988). Both Ørskov (1988) and Capper *et al.* (1988) reported highly significant cultivar-dependent variations in CR fodder quality traits with limited trade-offs with grain yields.

Kelley *et al.* (1993) at ICRISAT surveyed fodder trading of cereal straws and farmer perceptions of grain and straw value in India from a more demand-side perspective. These authors found that farmers paid attention to stover quantity and fodder quality in new sorghum cultivars and that new cultivars could be rejected if found lacking in these traits. The authors furthermore reported that the monetary value of sorghum grain relative to stover decreased from about 6:1 to 3:1 within two decades (1970–1990) and concluded and recommended that crop improvement consider CR fodder traits in future crop improvement work. It was in the

mid-1990s that ILRI, a successor of ILCA, and ICRISAT concluded a memorandum of understanding to jointly attempt concomitant improvement of grain and CR traits.

The present chapter reviews the findings, outputs and outcomes of research on multidimensional crops in the tropics, focusing mainly on cereals and grain legumes. Specifically, the chapter addresses the following:

- Establishment of CRs as traded commodities and their changing valuation as the impetus for multidimensional crop improvement.
- Trait identification and development of infrastructure for quick and affordable phenotyping for CR fodder quality.
- Exploitation of existing cultivar-dependent variations in CR fodder quality.
- Targeted genetic enhancement for multi-trait food–feed–fodder cultivars.
- Trade-offs between CR fodder traits and primary traits, notably grain and pod or straw yields.
- Outcomes of multidimensional crop improvement and future work.

Future work on multi-trait crop improvement.

Fodder markets

Increasing the feeding value of CRs by multidimensional crop improvement depends on the inherent variation among cultivars of the same crop in the nutritive value of their residues fed to livestock. Practical evidence of such variation has been observed in fodder markets in India for many years, as reviewed by Kelley *et al.* (1993, 1996).

While the fodder quality of CRs was largely ignored in historical crop-improvement programmes, farmers and fodder traders long recognized differences in the fodder quality of CRs, even within the same species. At the farm level, new pearl millet cultivars that had been improved only for grain yields had sometimes been rejected by farmers because of low CR quantity and quality (Kelley *et al.*, 1996), and similar findings were reported by Traxler and Byerlee (1993) for wheat. Kelley *et al.* (1993) reported from surveys of sorghum stover trading from 1985 to 1989 in four districts of Maharashtra, India, that stover from landraces realized on

average 41% (range 24–61%) higher prices than modern cultivars. These surveys provided early evidence that CR fodder quality differences are reflected in livestock production responses of some magnitude. In addition, the collaboration between ILRI and ICRISAT starting in the mid-1990s was preceded by an *ex ante* assessment of the impact of improving the quality of sorghum and pearl millet stover on livestock performance (Kristjanson and Zerbini, 1999). These authors calculated that a 1% increase in digestibility in sorghum and pearl millet stover would increase milk, meat and draught power outputs by 6–8%. These estimates appeared very high and were questioned by Thornton *et al.* (2003), who argued that a mere increase in only digestible energy, for example, without regard for protein would not result in a significant improvement in livestock productivity.

One support for a higher productivity impact is market prices of sorghum stover where a difference in digestibility of 5% was associated with price premiums of 25% and higher. Blümmel and Rao (2006) surveyed six major sorghum stover traders in Hyderabad, India, monthly from 2004 to 2005 and observed that six different stover types were usually traded. Customers usually had the choice of two or three sorghum stover types offered by the same trader. The poorest and best-quality stover (perceived in terms of colour, softness, sweetness, etc.) were sold on average for INR 3 and INR 4 per kg of dry matter, respectively. Blümmel and Rao (2006) investigated these traded stovers for laboratory fodder quality traits, such as crude protein and IVOMD, and related these laboratory traits to stover prices. While stover crude protein content was not related to stover prices, IVOMD accounted for 75% of the price variation. In rice straw, trading differences in IVOMD as low as 2–3 percentage points were associated with similar price premiums (Teufel *et al.*, 2010). Incidentally, these findings were in accord with the above-reported observations of Kelley *et al.* (1993) that stover from sorghum landraces achieved on average mean prices 41% higher than modern cultivars. Customers would not pay such price premiums if feeding of stover from landraces would not result in significantly higher livestock productivity. Findings from the surveys of sorghum stover (Blümmel and Rao, 2006) and rice straw (Teufel *et al.*, 2010) trading are combined in Fig. 14.1.

ILRI-ICRISAT work on fodder trading in India was followed by research in Mali, Niger and Nigeria by ILRI, ICRISAT and IITA. Price premiums related to fodder quality differences were also observed in West African markets (Jarial *et al.*, 2016a,b). Livestock producer preferences for haulms from groundnut or cowpea varied with haulm quality between groundnut and cowpea. Thus, cowpea haulms were costlier than groundnut haulms in fodder markets in Mali and Niger, but they also had superior N content and IVOMD than groundnut haulms, while the reverse was true in Nigeria (Table 14.1).

Price differences between cowpea haulm and groundnut haulm reflected quality differences. There was also consistency in pricing of cowpea haulm, groundnut haulm, sorghum stover and pearl millet stover over 2 years at four fodder markets in Niger (Table 14.2). The average price per kg of legume haulms was about five times that of the cereal stover; the average price per unit of N was about 2.7 times as high. Sorghum stover received about 30% higher prices than pearl millet stover, probably because of a 5% unit difference in IVOMD. Across the four CRs, N accounted for 98% ($p = 0.008$) of the variation in price and IVOMD for 91% ($p = 0.04$), respectively. While Jarial *et al.* (2016b) did not report price differences for CRs within crops related to cultivar differences, observations at a fodder market in Kano in September 2016 found cultivar differences in price in sorghum stover and in groundnut haulms (M. Blümmel, personal observation, September 2016).

A further point is the relative monetary value of grains and CRs. In legume haulms, the monetary value of grain and CRs can reach parity (Samireddypalle *et al.*, 2017), and grains can occasionally (e.g. when there is high demand for mutton during Muslim festivals) even be cheaper than haulms (Ayantunde *et al.*, 2014). In sorghum stover trading in India during the past decade, stover prices were about 50–60% that of sorghum grain value (Sharma *et al.*, 2010).

In summary, CR fodder market studies in South Asia and West Africa showed that: (i) traders and customers are aware of CR fodder quality differences within and across crops; (ii) customers are willing to pay considerable price premiums for apparently small differences in fodder quality traits; and (iii) the monetary value of CRs relative
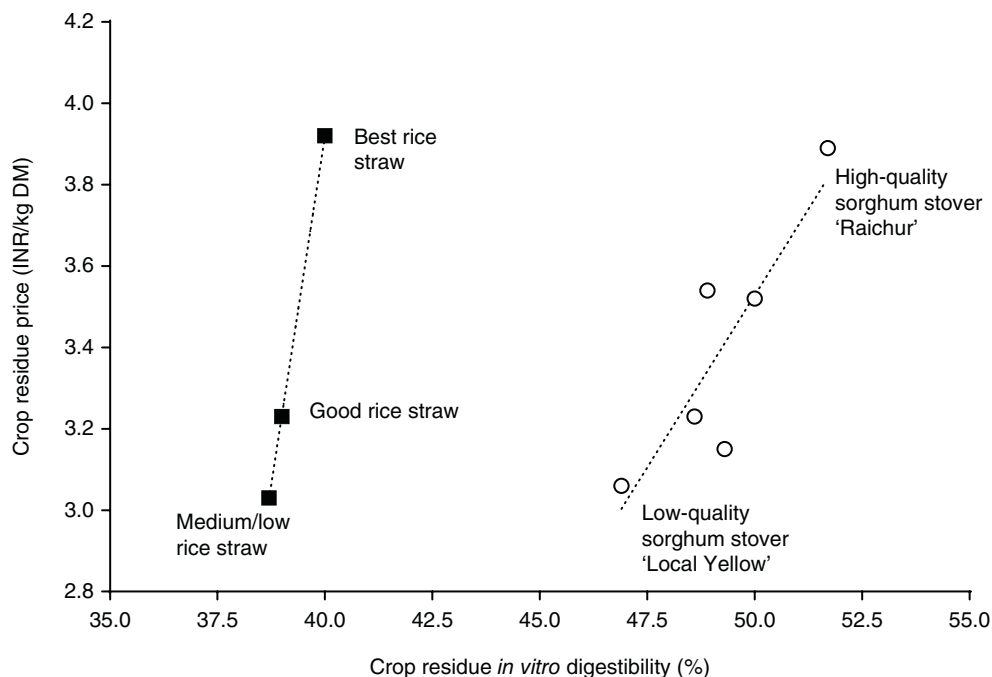
Fig. 14.1. Relationship between cost of sorghum stover and cost of rice straw and their *in vivo* digestibility. DM, dry matter. (Data from Blümmel and Rao, 2006, and Teufel *et al.*, 2010.)

Table 14.1. Prices, relative value and fodder quality traits of cowpea haulm (CPH) and groundnut haulm (GNH) traded in Niger, Mali and Nigeria.

Variable	Niger[a]		Mali[b]		Nigeria[c]	
	CPH	GNH	CPH	GNH	CPH	GNH
Price (US cents/kg)	28	20	95	86	19	72
Price grain:haulm	2.4:1	4:1	1:1.7	1:1.5	3.5:1	1.1:1
Haulm nitrogen (%)	2.2	1.7	2.9	2.4	2.0	2.4
Haulm IVOMD (%)	61.3	58.4	65.4	64.2	55.6	57.1

[a]Jarial *et al*. (2016a) for four fodder markets, over 2 years, bimonthly.
[b]Ayantunde *et al*. (2014) for five fodder markets, over 1 year, monthly.
[c]Samireddypalle *et al*. (2017) for five fodder markets, over 2 years, monthly.

Table 14.2. Average N content, IVOMD and prices (CFA franc) of cowpea haulm, groundnut haulm, sorghum stover and pearl millet stover traded over 2 years at four fodder markets in Niger. (Modified from Jarial *et al.*, 2016b.)

Fodder	N (%)	IVOMD	Price (CFA franc/kg)	Price (CFA franc/N)
Cowpea haulm	2.22	61.3	164	73.9
Groundnut haulm	1.60	58.4	119	74.4
Sorghum stover	1.03	52.2	31	30.1
Pearl millet stover	0.98	47.2	24	24.5

to grain values is considerable and has been increasing over recent decades (Kelley *et al.*, 1993; Sharma *et al.*, 2010). In fact, depending on harvest indices and/or CR fodder quality, more money can be earned from CRs than from the primary product (Samireddypalle *et al.*, 2017). The findings from fodder markets as far apart as West Africa and South Asia send strong signals that both fodder quantity and fodder quality of straws, stovers and haulms do matter.

CR fodder quality and livestock productivity

Livestock productivity trials conducted with the private sector confirmed information from fodder market studies. In India, Miracle Fodder and Feeds Pvt Ltd designed so-called densified total mixed ration (DTMR) feed blocks that consist largely of by-products such as sorghum stover (about 50%), bran, oilcakes and husks (about 36%), with the rest contributed by molasses (8%), maize grain, urea, minerals, vitamins, etc. (Shah, 2007). In a series of experiments with Miracle Fodder and Feeds Pvt Ltd, the authors tested these feed blocks with two objectives: (i) to estimate probable maximum productivity levels on cereal CR-based diets; and (ii) to estimate the importance of the quality of the basic CR going into the blocks on overall livestock performance. In an experiment with a large private Indian buffalo dairy (Anandan *et al.*, 2010), two experimental DTMR feed blocks were produced from low-quality (47% IVOMD) and premium-quality (52% IVOMD) sorghum stover traded in the fodder markets (Blümmel and Rao, 2006).

The results from these trials are reported in Table 14.3. Using premium sorghum stover ('Raichur' in Fig. 14.1) resulted in more than 5 kg higher daily milk potential than using the lower-quality stover ('Local Yellow' in Fig. 14.1). This differential yield potential was due to higher ME content/kg DTMR and also higher feed intake in the ration containing the premium stover. These accumulating effects of higher ME content and higher feed intake are the reason that apparently small difference in feed quality can have considerable effects on animal performance. The increase in milk potential of 5 kg compared with the ration containing the lower-quality stover explains the decisions of customers to

invest in higher-quality stover. However, only part of the incremental increase in milk potential was due to the higher-quality stover, as this group also consumed more concentrate (0.85 kg/day), which contributed about half to the DTMR. The increased milk potential attributable to higher stover quality is estimated to be 2.4 kg/day (increase from 4.4 to 6.8 kg/day; Table 14.3). This would be an increase of about 24% relative to the milk potential of the DTMR with the lower-quality stover of 9.9 kg/day. This increase appears to agree with the price premiums paid for the higher-quality sorghum stover at the fodder markets in India. It also seems to align with the price differences observed between sorghum and pearl millet stover traded at fodder markets in Niger (Table 14.2).

The effect of CR quality on livestock productivity is clearer in cases where the residues are fed as sole diets rather than as basal diets, as is generally the case with cereal CRs. Table 14.4 summarizes work where legume haulms were fed as sole diets to small ruminants. Cultivar-dependent variations in haulm fodder quality were considerable. In the case of groundnut haulms harvested from six different cultivars in Nigeria, sheep could lose weight on haulms from one cultivar while gaining 46 g/day on haulms from another cultivar. In India, weight gains in sheep could differ by more than twofold (from 65 to 137 g/day) depending on haulm fodder quality difference among groundnut cultivars. Similar proportional genotypic variations have been reported for faba bean haulms in Ethiopia (Table 14.4). For unsupplemented barley straw from eight different cultivars, Capper *et al.* (1988) reported daily weight changes from 150 g to little above live weight maintenance. Protein supplementation resulted in cultivar-dependent variations in weight gain from 100 to 250 g/day.

These examples show that the effect of cultivar variations on fodder quality of CRs on livestock productivity can be substantial. The high response in livestock performance to apparently small differences in CR fodder quality is the result of two cumulative effects: higher diet quality and higher feed intake. However, this effect can only be effective where feed is offered *ad libitum*, which is not always the case, and often CRs are in short supply and fed in a restricted fashion (Mayberry *et al.*, 2017). It is also worth pointing out that higher productivity can be achieved on mostly, or even completely, by-product-based

Table 14.3. Milk potential in Indian dairy buffalo fed two DTM feed blocks based on premium-quality (52% digestibility, 7.39 MJ ME/kg) and low-quality (47% digestibility, 6.52 MJ ME/kg) sorghum stover with total by-product proportion of feed blocks greater than 90%. (Data from Blümmel *et al*., 2017, based on the actual milk fat contents of buffalo milk.)

	Low-quality stover	Premium-quality stover
Protein (%)	17.1	17.2
ME (MJ/kg)	7.37	8.46
Voluntary intake of feed block (kg/day)	18.0	19.7
Voluntary intake of feed block (% /kg LW[a])	3.6	3.8
ME intake (MJ/day)	132.7	166.7
ME intake stover (MJ/day)	58.7	72.7
Milk fat (%)[b]	7.4	7.6
Milk potential (kg/day)	9.9	15.5
Milk potential from stover[c]	4.4	6.8
Milk potential from cross-bred cattle (kg/day)	14.0	21.0
Milk potential from stover[c]	6.2	9.2

[a]Live weight (LW) of buffalo was calculated by body measurements and estimated to be on average 506 and 525 kg in the low-quality and premium-quality feed block, respectively.
[b]Milk fat in cattle was assumed to be 4% with a cross-energy content of 3.13 MJ/kg.
[c]Estimated based on ME contribution of stover to ME of DTMR as: ME stover/ME DTMR × milk potential.

Table 14.4. Effect of groundnut and faba bean cultivars on live-weight changes in sheep fed exclusively with haulms offered *ad libitum*.

Experiment	Average (g/day)	Lowest (g/day)	Highest (g/day)
Haulms of ten groundnut cultivars fed to Indian Deccan sheep[a]	94.1	65	137
Haulms of six groundnut cultivars fed to West African Dwarf sheep[b]	26.5	–6	46
Haulms of five faba bean cultivars fed to Ethiopian Arsi sheep[c]	49.2	37.5	64.6

[a]Prasad *et al*. (2010).
[b]Etela and Dung (2011).
[c]Wegi (2016).

feeding systems. In the case of DTMR, milk yields in cross-bred cattle of more than 20 kg/day seem achievable (Table 14.3) and these DTMR consist of more than 90% by-products. Feeding legume haulms as the sole feed to sheep can result in daily weight gains of well over 100 g/day (Table 14.4). These are productivity levels more commonly associated with concentrates than with CR diets. Findings from the livestock productivity trials are consistent with price premiums paid for fodder quality differences (Fig. 14.1, Tables 14.1 and 14.2). It is important to point out that the variations seen in the fodder markets and livestock productivity trials came about largely by chance and that those differences in fodder quality were not the intentional results of crop breeding or selection. We will see

in a later section that the fodder quality of CRs can be increased further by targeted genetic enhancement using conventional or molecular breeding crop-improvement approaches.

Trait Identification and Tools for Affordable Phenotyping for Crop Residue Fodder Quality

Validation of laboratory fodder quality traits

Fodder quality is ultimately determined only by livestock production and productivity, but livestock performance trials are unsuitable for routine

feed and fodder quality analysis. This is particularly valid in crop improvement, where many samples must be analysed and where initially the biomass availability is low. Simple laboratory fodder quality traits are needed, but these traits must be well correlated with actual livestock performance measurements. 'Simple' here refers not only to logistical and economical laboratory demand but also to the need for the traits to be comprehensible to, and usable by, crop scientists, seed producers, fodder traders and development practitioners with no or little training in livestock nutrition. When the ILRI-ICRISAT collaboration on multidimensional crop improvement started, a wide range of potential morphological, chemical and *in vitro* traits were investigated and related to livestock performance measurements usually obtained with sheep (Sharma *et al.*, 2010).

Ravi *et al.* (2010) investigated morphological, chemical and *in vitro* traits in pearl millet stover and related these traits to organic matter digestibility, organic matter intake, digestible organic matter and N balances in sheep. Generally, fibre components and *in vitro* laboratory traits were more closely related to *in vivo* measurements than morphological traits, even though plant height and stem diameter were both consistently and statistically significantly inversely related to the *in vivo* measurements of 40 pearl millet stovers. In contrast, traits such as leafiness, including estimates of residual green leaf area, which are often employed for sensory phenotyping by crop-improvement programmes and farmers, were less well related to *in vivo* measurements. It is important to realize that all stovers were offered chopped (which is increasingly the practice or the trend, at least for stover utilization in India and elsewhere), which might reduce the importance of leafiness and other morphological traits on intake responses.

Bearing in mind the above considerations about the simplicity and meaningfulness of fodder quality traits, NDF (a cell wall estimate), ADF (an estimate of cellulose) and *in vitro* digestibility seem to be good indicators for ranking fodder quality in pearl millet, sorghum (Ramakrishna *et al.*, 2010) and maize (Ravi *et al.*, 2013) stover, while ADL (an estimate of lignin) seems to predict fodder quality in groundnut haulms better than any of the aforementioned traits (Prasad *et al.*, 2010). Combining different laboratory traits using stepwise multiple regressions improved predictions of *in vivo* measurements in most cases in pearl millet, sorghum stover and groundnut haulms. In all three cases, laboratory traits related to available feed energy (*in vitro* digestibility, ME and fibre constituents) were found to exhibit more consistent relationships with *in vivo* measurements than CR N content (Prasad *et al.*, 2010; Ramakrishna *et al.*, 2010).

Calibration and validation of NIRS tools

Conventional laboratory analysis cannot efficiently cope with the large set of sample entries from multidimensional crop-improvement programmes. NIRS is a non-invasive technique routinely used since the 1960s in the food industry, forage breeding and pharmaceutical industry. Most instruments used are manufactured by FOSS (Forage Analyser 500 and 6500), which has the advantage that NIRS equations developed in one laboratory can be transferred to other laboratories using FOSS. The ILRI-crop-centre collaboration developed and validated NIRS equations for N, NDF, ADF, ADL, IVOMD and ME of CRs of sorghum, pearl millet, groundnut, pigeon pea, chickpea, cowpea, rice, wheat and maize. We generally expected an R^2 value of at least 0.90 between conventionally analysed laboratory traits and blind predictions by NIRS (see also Sharma *et al.*, 2010). With new global interest in monogastric and fish feed, NIRS equations were also developed for grains of key crops, including routine quality traits such as protein, starch and fat (Choudhary *et al.*, 2010) but also amino and fatty acids (Prasad *et al.*, 2015), which still mostly rely on costly high-performance liquid chromatography analysis.

NIRS equations can be transferred across FOSS-type instruments with little spectra standardization to account for instrument-to-instrument variation. Over the past one and a half decades, ILRI NIRS specialists have trained hundreds of laboratory technicians from CGIAR and the national public and private sectors in South Asia and East and West Africa on NIRS operations, including NIRS networking and the generation of NIRS equations. Fully functioning NIRS hubs exist now in India and Ethiopia, and NIRS hubs in Nigeria and Mali are being set up.

Thus, quick, affordable and comprehensive phenotyping for food–feed and fodder traits in all key cereal and legume crops is feasible, but sample processing (drying, grinding and shipping) limit experimental efficiency. Mobile NIRS applications can potentially overcome this constraint. Two new mobile hand-held systems manufactured by Phazir and Brimstone have been explored during the past 2 years to remove, or at least mitigate, the sample processing constraint (Prasad *et al*., 2015). Phazir and Brimstone currently cost about US$40,000 each, but recently an extremely cheap (about US$450–500) and small pocket NIRS system called Scio came on the market and is currently being tested at ILRI in India and Ethiopia.

Exploitation of Existing Cultivar-dependent Variation in CR Fodder Quality

Phenotype pipeline and releases for variations in CR fodder quality

A widespread misconception about how superior CRs can be generated is that targeted crop breeding is invariably required. However, phenotyping for fodder quality to detect genetic differences in food–feed–fodder traits in advanced cultivars and exploiting them often suffices. Exploiting existing variations in traits and targeting genetic enhancement towards specific traits are separate approaches, and the first is possible without the second. The first approach does not require much investment besides phenotyping for CR traits and has short delivery pathways. The second approach requires more investment and time but promises greater impact.

This timespan of crop improvement can be shortened by phenotyping CRs of released cultivars for fodder quality and by promoting superior dual-purpose cultivars with farmers, traders and processors. This approach is particularly promising where the private sector is involved, usually in the promotion and marketing of hybrids. A collaboration between ILRI and CIMMYT identified such a superior dual-purpose maize hybrid (Anandan *et al*., 2013), which is now a very popular hybrid in

Asia, and its producer, Syngenta, has recently approached ILRI and CIMMYT for ways of advertising the high fodder quality on the seed packets of the hybrid. ILRI, CIMMYT and Syngenta are now exploring processes to bring about such branding and seed bag labelling for CR fodder quality traits. Work is ongoing in the use of check cultivars analogous to current methods of comparing grain yields of yet-to-be-released cultivars with yields of selected check cultivars; in addition to grain yields, CR quality traits could also be compared. Another option is comparing CR quality of yet-to-be-released cultivars with longer-term average qualities of CRs traded at fodder markets or with the average values of CR qualities given in nutritional textbook/feeding tables for a given country. In any event, getting the private sector interested in dual-purpose traits is of great strategic importance for mainstreaming Multi-dimensional crop improvement and for scaling of new cultivars, as public-sector crop improvement groups are watching the private sector closely.

Phenotyping pipeline hybrids that are close to release is also cost-effective and has short delivery pathways. This was implemented with a private-sector maize programme in India; examples of this work from 2014 onwards are presented in Fig. 14.2, where 24 pipeline hybrids were tested at four locations in India. The hybrids with the highest average grain yield also had highest stover N and second highest stover IVOMD (Fig. 14.2a,b). The variation in stover IVOMD among the top grain yielders of 9–10 t/ha was like the variation between the best and poorest sorghum stover in fodder trading in India (Fig. 14.1) or between the average sorghum and pearl millet stover traded in Niger (Table 14.1), which resulted in appreciable price premiums for the better-quality stover in both cases. The implication for promoting the maize hybrid with the highest IVOMD rather than the lowest IVOMD among the top yielders in dairy productivity can be extrapolated from the findings in Table 14.3. However, while combination of highest grain yields and highest stover traits such as N and IVOMD are entirely feasible, these trait combinations seem to be associated only with intermediate stover yields (Fig. 14.2c,d).
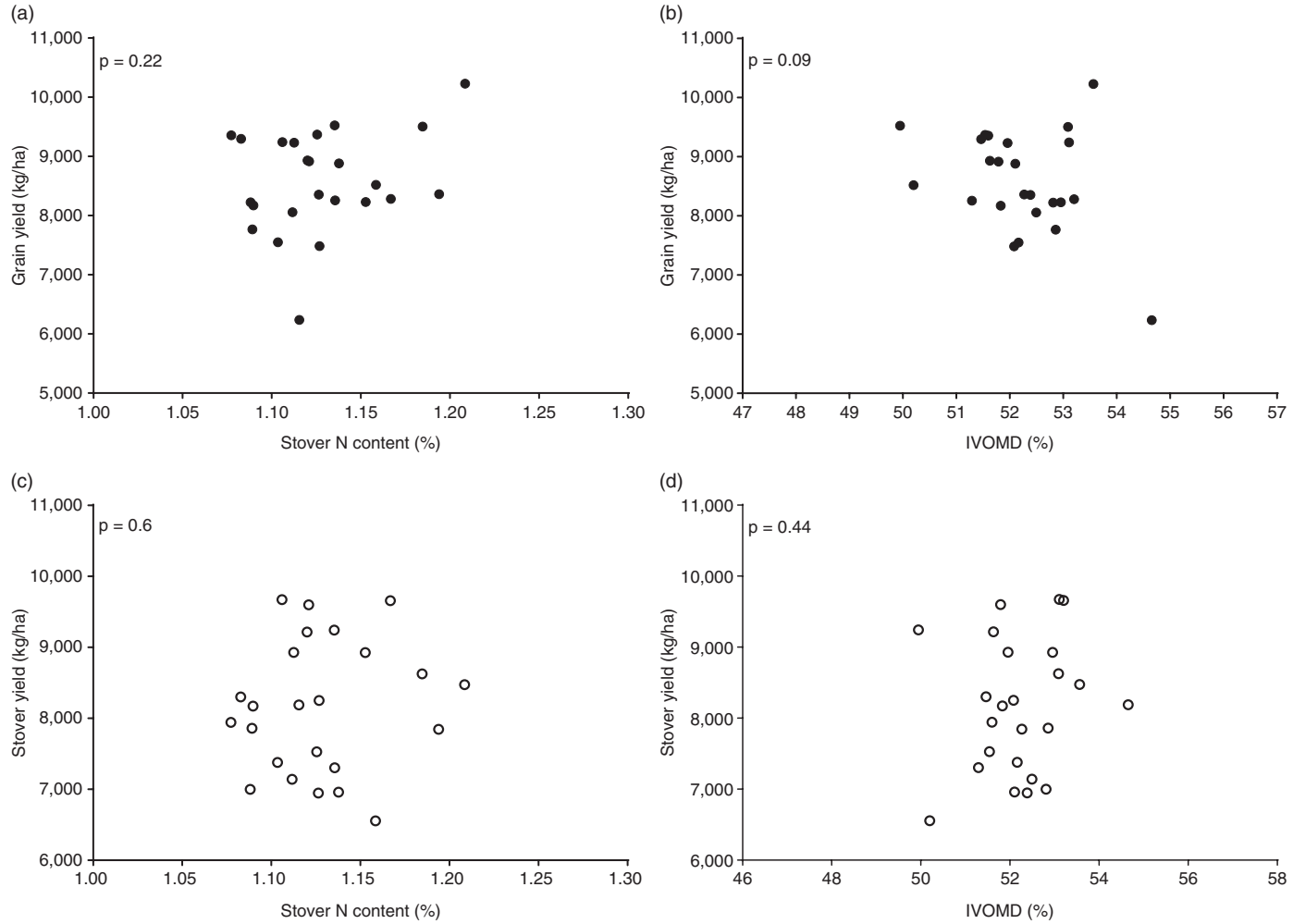
Fig. 14.2. Relationship between stover N and grain yield (a), between stover IVOMD and grain yield (b), between stover N and stover yield (c) and between stover IVOMD and stover yield (d) in 24 pipeline maize hybrids grown at four locations in India.

Institutionalized Multidimensional crop improvement has advanced only slowly. In 2002, the National Research Centre for Sorghum (NRCS) decided to include sorghum stover traits as release criteria for new sorghum cultivars. Interestingly, this was influenced by a visit of the then Director of the NRCS to the sorghum fodder markets in Hyderabad described earlier. This involved seconding NRCS technicians to the ILRI NIRS Hub hosted by ICRISAT to analyse stover of all new sorghum cultivars submitted for release under the All-India Coordinated Research Project (AICRP) on Sorghum (Venkatesh *et al.*, 2006). This work continues and is now being explored for minor millets by IIMR. Stover traits have now also been included as release criteria for pearl millet, although this crop is, paradoxically, currently not under the mandate of IIMR. Less formalized pilot studies have been undertaken with the Indian Directorate for Maize, where the modification of cultivar release criteria to include maize stover traits was discussed during recent annual maize meetings, although without a formal decision yet being taken. The situation is similar in Ethiopia, where the International Centre for Agricultural Research in the Dry Areas (ICARDA) prepared the ground with EIAR by phenotyping lentils, chickpeas and faba beans for haulm fodder quality traits during release processes (Alkhtib *et al.*, 2016, 2017).

Targeted genetic enhancement towards food–feed crop cultivars

The targeted concomitant improvement of grain and CR traits requires more investment and time than the mere detection and exploitation of already existing variations but promises greater impact. In ILRI-ICRISAT-CIMMYT collaborations, both conventional and molecular breeding approaches were applied for targeted genetic enhancement of CR fodder traits within the paradigm of simultaneous improvement of grain and fodder traits.

Recurrent selection

Bidinger *et al.* (2010) showed that within two recurrent selection cycles, digestible organic matter intake of pearl millet stover measured in sheep increased from 12.9 to 15.1 g/kg live weight (LW), an increase of 17%, and the N balance changed from negative (−0.016 g/kg LW/day) to positive (0.05 g/kg LW/day). The improvement in stover quality did not come at any penalty for grain or stover yield. Choudhary *et al.* (2012) investigated the mode of inheritance of stover N and IVOMD. From a full-sibling (FS) base population of pearl millet variety ICMV 221, three high and low N and three high and low IVOMD FSs were selected. Crosses were made for high × high (H × H), low × low (L × L), and high × low (H × L) FS trait contrasts and evaluated at Patancheru, in India, in the rainy seasons of 2007 and 2008. The high- and low-N (HN and LN, respectively) FS parents were 0.85% and 0.72% N, respectively. In the crosses, stover N contents were: HN × HN = 0.85%, LN × LN = 0.73% and HN ×LN = 0.80% ($p < 0.05$). The high- and low-digestibility (HD and LD, respectively) FS parents were 43.3% and 40.3% IVOMD, respectively. In the crosses, stover IVOMD were: HD × HD = 43.7%, LD × LD = 40.3% and HD × LD = 42.2% ($p < 0.05$). The intermediate results of H × L crosses strongly indicated the additive nature of the stover quality traits of N and IVOMD and suggest the application of cyclic breeding methods for increasing stover N content and IVOMD in pearl millet.

A further pilot study was conducted to increase the key fodder quality traits of N content and IVOMD through two cycles of FS recurrent selection of open-pollinated pearl millet cultivar ICMV 221 (base population, C_0). Six experimental varieties were selected from the first cycle (C_1) and second cycle (C_2) of selection for: (i) high grain yield; (ii) high grain and stover yield; (iii) high stover IVOMD, (iv) low stover IVOMD; (v) high stover N content; and (vi) low stover N content. Stover N and IVOMD increased by 9.5% and 2%, respectively, in the C_1 bulk, and by 21% and 5%, respectively, in the C_2 bulk over the base population C_0. The high-N experimental varieties showed the highest N percentage and stover N yield, while the high-digestibility experimental varieties showed the highest ME and IVOMD values from both selection cycles. The findings suggest that stover N and IVOMD can be improved without significant detriment to grain and stover yield.

Hybrid breeding for dual-purpose maize

In South Asia, dual-purpose maize breeding was supported by the CRP on Maize through a competitive grant scheme to ILRI. Zaidi *et al.* (2013) reported substantial variability for stover quality in maize working with germplasm available from CIMMYT-Asia with no negative effect of the stover quality traits (IVOMD and ME) on grain yield, indicating the possibility for simultaneous improvement of both stover quality and grain yield. In addition, substantial progress has been made in identifying trait-specific genomic regions for use in targeted breeding programmes to improve stover quality and grain yield (Vinayan *et al.*, 2013). This breeding initiative for improving stover quality has led to the development of advanced lines with high digestibility (over 50%) and energy (greater than 8.0 MJ/g) for use as parents of new hybrid combinations. Results from evaluation of these experimental hybrids under optimal growing conditions have shown promise in terms of their yield performance (roughly 8.0 t/ha) and *in vitro* digestibility (over 50%). Studies of the performance of

commercial hybrids within India also led to identification of promising hybrids such as NK6240 (Syngenta) with high digestibility (over 50%) (Anandan *et al.*, 2013) and high grain yields (over 9.0 t/ha) during the rainy season.

Maize is fast replacing some of the major cereal crops grown widely in these regions and currently ranks first followed by rice and wheat in terms of production and growth. One of the emerging seasons for maize cultivation in India is spring, particularly in South India (usually a rice–fallow system), where adverse weather conditions prevail (high temperature and low rainfall). Several pipeline hybrids and breeding lines have been tested to suit this environment, and preliminary investigations led to identification of potential hybrids that have good grain yield and high stover quality. The progress of this maize hybridization programme to simultaneously improve food and fodder traits is exemplified in Fig. 14.3 using data from sorghum stover trading as reference values; the perceptions of farmers and traders in India are that sorghum stover is nutritionally superior to maize stover (Blümmel *et al.*, 2014b).
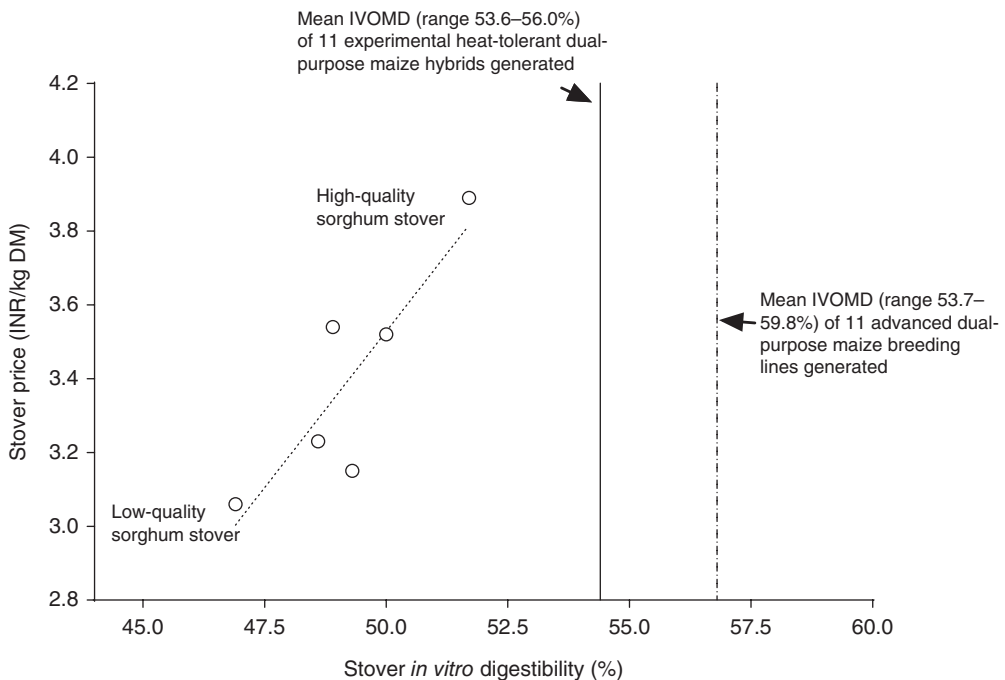
Fig. 14.3. Breeding advances in dual-purpose maize stover quality relative to different sorghum stovers traded in rainfed India in the past decade. (Data from Blummel *et al.*, 2014b).

Fig. 14.3 shows that maize stover is not inferior to sorghum stover, which was also confirmed in trials with dairy animals (Blümmel *et al.*, 2014b). Furthermore, the average IVOMD (54.4%) of the new hybrids targeting areas with adverse weather conditions is about 2.5% higher than that of the highest-quality traded sorghum stover (Fig. 14.3). This was one of the sorghum stovers used for the dairy experiments described in Table 14.3. It is very likely that dairy productivity would be substantially further enhanced if the sorghum stover were replaced by a maize stover with 56% IVOMD as available in the new hybrids, and even more so by a maize stover with an IVOMD of close to 60% now available in the new dual-purpose breeding lines (Fig. 14.3).

Similar findings were reported from CIMMYT-ILRI dual-purpose maize breeding research in East Africa (Ethiopia, Tanzania and Kenya). Ertiro *et al.* (2013) produced 60 experimental dual-purpose hybrids from 16 parental lines, yielding 10 t of grain with an IVOMD of up to 62% (range 53.1–62.3%). Mid-parental key stover traits such as IVOMD were well related ($r = 0.78$; $p < 0.0001$) to the IVOMD of the hybrids produced from them, also strongly suggesting the opportunity for dual-purpose hybrid breeding.

QTL identification and backcrossing

Nepolean *et al.* (2009) used QTLs to map the genomic regions controlling stover quality and yield traits in pearl millet. Marker-assisted breeding would be an effective tool to exploit these genomic regions and to choose breeding lines having combinations of better stover quality and high grain yield without linkage drag between these traits. With these objectives in mind, QTLs for stover IVOMD and ME content were identified and introgressed into four parental lines of existing hybrids showing good agronomic performance. Three generations of marker-assisted backcrossing and subsequent selfing of backcrossed progenies having target QTLs was carried out with the help of QTL-flanking microsatellite simple-sequence-repeat markers. Single QTL introgression lines that were homozygous for target regions were identified. Improved hybrids were synthesized from these QTL homozygous lines and were evaluated in multi-location field trials. The results from the laboratory analysis of stover samples showed that one of the improved hybrids was at least 8.5% higher in ME and 6.3% higher in IVOMD than the control hybrid. The new hybrid also produced a 10% increase in grain yield and a 4% increase in stover yield. These results suggest that new hybrids can be developed, concomitantly improving grain and stover traits using QTLs (Nepolean *et al.*, 2009).

Blümmel *et al.* (2015a) introgressed stay-green QTLs into the sorghum genetic backgrounds S-35 and R-16, generating 52 and 39 lines, respectively, to investigate the effects of stay-green introgression on stover traits and grain–stover relationships. The stover quality traits analysed were N, IVOMD, ADF, ADL and neutral detergent solubles (= $100 - NDF$) using a combination of conventional nutritional laboratory analysis with NIRS. Field trials were conducted under treatments of unlimited (control) and limited water supply. Significant ($p < 0.0001$) differences were found among lines for grain and stover yield and all stover quality traits under both water treatments. Water treatment had greater effects on grain and stover yields, which decreased by between 20% and 32% under water stress, than on stover quality traits, which varied at most by 8% between treatments. Year had the greatest effect among treatments, followed by water treatment and cultivar. Trade-offs between stover quality traits and grain yields were largely absent in both backgrounds. However, the effect of QTLs on selected stover quality traits was background dependent. In S-35, one stay-green QTL (stgB) significantly increased stover IVOMD and grain and stover yield, while no concomitant trait improvement was observed in the background R-16. The QTL in S-35 also increased the water-use efficiency of the whole plant in terms of grain yield, stover yield and stover ME (Blümmel *et al.*, 2014a).

GWAS and GS

GWAS have the potential to unravel favourable native genetic variations for traits of agronomic and economic importance across a wide range of cereal crops. Vinayan *et al.* (2013) studied a panel of 276 inbred lines from CIMMYT's

Drought Tolerant Maize for Africa (DTMA) project using their test-cross hybrids with the maize line CML312, and the single crosses were evaluated for grain and stover yields, plant height, days to 50% anthesis and silking, stover N, NDF, ADF, ADL, IVOMD and ME content. GWAS analysis was carried out using genotyping by sequencing, and 55K single-nucleotide polymorphism arrays revealed several regions of significant association for N, ADF and IVOMD, each explaining from 3% to 9% of the phenotypic variance for these fodder quality traits. GWAS was helpful in uncovering genomic regions of interest for target traits.

GS or marker-enabled predictions can predict untested phenotypes from whole-genome information. In one study, GS models were developed for fodder quality traits to predict superior lines from the collection of doubled-haploid lines generated by the Global Maize Program of CIMMYT in Asia. Using high-density genotypic information as well as fodder quality phenotypes of approximately 700 lines from two association panels – DTMA and the CIMMYT-Asia Association Panel (CAAM) – marker effects were obtained for fodder quality traits using GS models. The results indicated significant relationships between genotyping-by-sequencing-derived values and the phenotypes, with r values ranging from $r = 0.44$ to $r = 0.45$ across IVOMD and ME, respectively (Blümmel *et al.*, 2014b). These predictions of fodder quality phenotypes in biparental populations indicated that genomic selection can be used to: (i) improve fodder quality in maize breeding populations; and (ii) select parents in breeding for fodder quality from maize repositories without phenotyping the lines.

Trade-offs Among Crop Residue Fodder Traits and Primary Traits

Primary and secondary traits

The increasing importance and demand for CRs as fodder is reflected in four major trends: (i) increasing labour investment in collecting and storing CRs in more extensive systems (Valbuena *et al.*, 2015); (ii) farmer preferences for dual-purpose crop varieties; (iii) higher market price for CRs with a higher feed quality;

and (iv) higher livestock productivity with CRs with a higher feed quality. Evidence for cultivar preferences based on feed traits comes from farmer rejection of new sorghum and pearl millet cultivars that had been improved only for grain yields and had low stover quantity and quality (Kelley *et al.*, 1996). Recently, farmers ranked maize stover traits highly when assessing cultivars in East Africa (de Groote *et al.*, 2013). Trading of CRs is expanding in volume and distances, and CR:grain price ratios during the past two decades have decreased (Kelley *et al.*, 1993; Blümmel and Rao, 2006; Berhanu *et al.*, 2009). Nevertheless, grain yields remain the primary trait that most crop-improvement programmes focus on. When multidimensional crop-improvement programmes target CR traits, they need to address potential trade-offs between grain and CR traits.

It is important to understand what causes trade-offs between grain and CR traits. In its simplest form, a nutrient limited by soil fertility and/or fertilizer application, such as N, is partitioned between grain and the CR. A more complex example is in the partitioning of photosynthetic products (which are not finite quantities such as soil and fertilizer N), notably soluble carbohydrates, which contribute significantly to CR digestibility and therefore to fodder quality. Trade-offs can also arise from more indirect mechanisms of ensuring grain yields and efficient harvest, such as lodging resistance, which can affect fodder quality of CRs through increased stem lignification.

On the most basic level of trade-offs, grain and CR yields were only moderately correlated in sorghum (Blümmel *et al.*, 2010), groundnut (Nigam and Blümmel, 2010), pearl millet (Bidinger and Blümmel, 2007), cowpea (Samireddypalle *et al.*, 2017), maize (Blümmel *et al.*, 2013a) and wheat (Blümmel *et al.*, 2012a). Grain yields rarely accounted for more than 50% of the variation in CR yields. In other words, variation in harvest indices were considerable and grain yield is an insufficient predictor of CR yield. Breeding for increases in grain yield was often accompanied by shortening of stems to prevent lodging, resulting in the longer term in increasing harvest indices (Hay, 1995). While this relationship has been shown in temperate cereals, it is less clear in pulses and tropical cereals such as rice and maize (Hay, 1995). In recent

years, investments in second-generation biofuel technologies have resulted in renewed interest in variations in harvest indices, as CRs provide valuable feedstock for ethanol production (e.g. Dai *et al*., 2016). These authors also reported considerable cultivar- and management-dependent variations in harvest indices, suggesting that CR yields cannot be satisfactorily calculated from grain yields. Grain yield and total biomass yield should therefore be recorded in Multidimensional crop-improvement efforts. These considerations are also relevant for conservation agriculture, as higher biomass yield would make the partitioning of CRs between livestock feeding and soil improvement perhaps less contentious (Baudron *et al*., 2014).

CR N content and grain and CR yield

Relationships between the N content of CRs and grain and CR yields vary. Under balanced crop management, when no restrictions were imposed on fertilizer or water, trade-offs between the N content of CRs and grain and CR yield were largely absent (Fig. 14.4). (The data in Fig. 14.4 were derived from a collaboration between the National Research Center for Sorghum, later renamed the Directorate for Sorghum Research, and Indian Institute for Millet Research). No relationship was observed between the protein content of sorghum stover (which is calculated as stover N × 6.25) and grain yield (Fig. 14.4a). Under high Kharif (sorghum grown in the rainy season in semi-arid India) grain yielders of 5 t/ha, stover protein content could vary from 4% to 7%, the latter being adequate

to provide minimum microbial N requirements in the rumen (van Soest, 1994). Sorghum stover protein and stover yield were significantly positively correlated, but the correlation coefficients were low (Fig. 14.4b).

Bidinger and Blümmel (2007) and Blümmel *et al*. (2007a) imposed N restrictions by limiting fertilizer application while increasing pressure on partitioning of N and adjusting planting densities on different cultivars (landraces, open-pollinated varieties (OPVs) and hybrids) of pearl millet. Even under these imposed restrictions, the authors found no inverse relationship between the stover N of pearl millet and grain yields (Fig. 14.5a). However, stover N and straw yield could be significantly inversely associated under low fertility and high population density (Fig. 14.5b).

Water restriction reinforces trade-offs under normal management and growing conditions. For example, in chickpea cultivars, haulm, N and grain yield were inversely correlated ($r = -0.41$) under normal growing conditions but this association became closer ($r = -0.62$) under water restriction (Fig. 14.6a). Associations were positive between haulm N and grain yield and again the association was stronger under water restriction (Fig. 14.6b). Similar relationships have been observed for groundnut (Blümmel *et al*., 2012b).

CR digestibility and grain and CR yield

As with CR N content, relationships between CR digestibility and grain and CR yield are affected by water stress. No relationship was observed
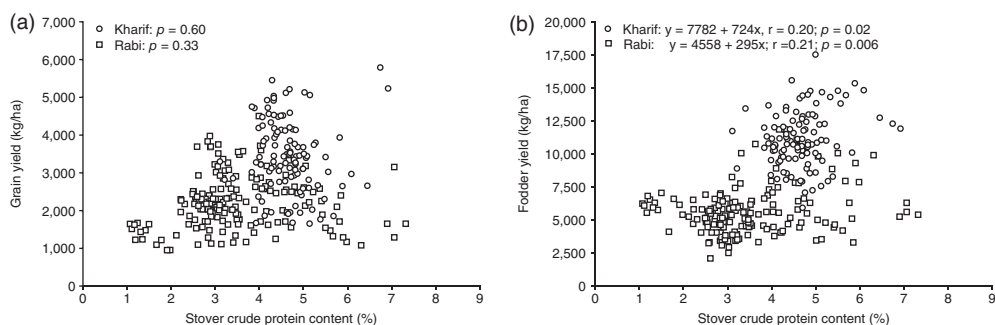
Fig. 14.4. Relationships between mean stover crude protein and grain yield (a) and between mean stover crude protein and stover yield (b) in Kharif and Rabi sorghums submitted for cultivar release from 2002 to 2008. (Unpublished data, Michael Blümmel).
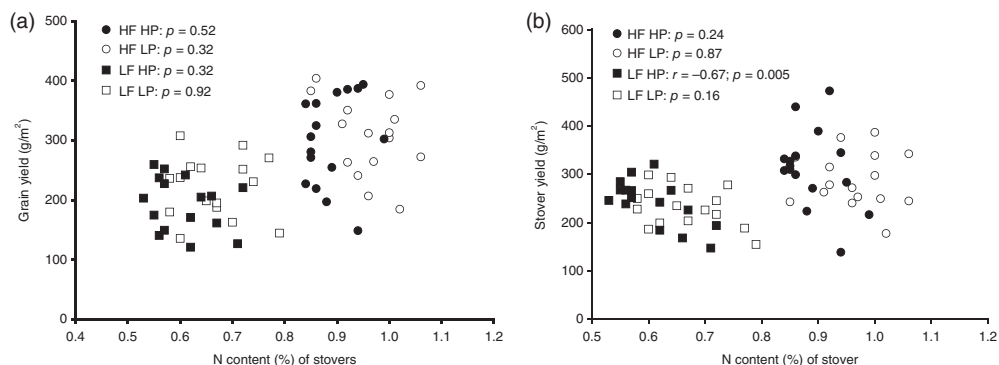
Fig. 14.5. Relationships between N content of pearl millet stover and grain yields (a) and between N content of pearl millet stover and stover yields (b) under high (HF) and low (LF) fertility and high (HP) and low (LP) population density. (Data from Bidinger and Blümmel, 2007).
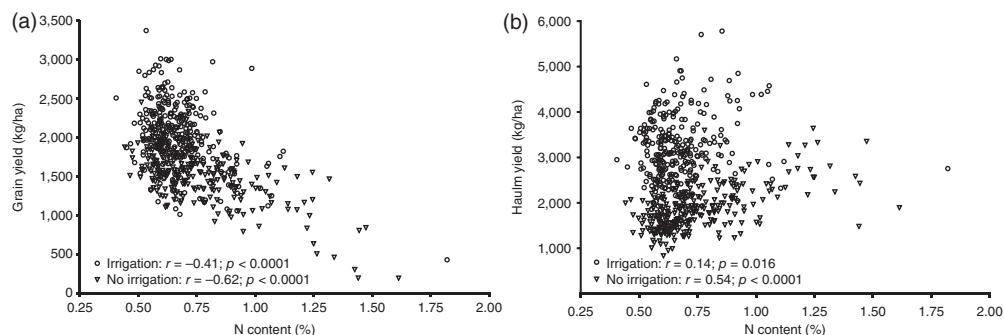
Fig. 14.6. Relationship between haulm N content and grain yield (a) and between haulm N content and haulm yield (b) in 280 chickpea cultivars. (Data from Blümmel *et al.*, 2012b).

between stover digestibility and grain yield in Kharif sorghum, while this relationship was significantly inverse in Rabi sorghum (grown in the dry season) (Fig. 14.7a). The variation in stover digestibility in high Kharif grain yielders of about 5 t/ha was close to 10% (Fig. 14.7a), which is twice the difference observed in sorghum stover trading situations (Fig. 14.1). Even in Rabi sorghum, with the overall negative association between stover digestibility and grain yield, stover digestibility among Rabi high grain yields of about 3.5 t/ha could vary by a similar magnitude.

In pearl millets, stover digestibility and grain yield were unrelated, regardless of N fertilizer level and population density (Fig. 14.8a). In chickpea haulm, digestibility and grain yield were weakly although significantly ($r = -0.13$, $p < 0.03$) associated under irrigation, but the

trade-offs became more pronounced ($r = -0.50$, $p < 0.0001$) under water restriction (Fig. 14.9a). In all three crops, stover and haulm digestibility and stover and haulm yields were significantly positively associated (Figs 14.7b and 14.8).

The relationships between stover and haulm digestibility and grain yield would be affected, for example, by arrested translocation of soluble carbohydrate from the stem to the grain or from lignification of stems to prevent or counteract lodging. While these mechanisms might be real, they were expressed only mildly in the relationships of CR digestibility and grain yields in rice (Blümmel *et al.*, 2007b), groundnut (Nigam and Blümmel, 2010), cowpea (Samireddypalle *et al.*, 2017), maize (Blümmel *et al.*, 2013a) and wheat (Blümmel *et al.*, 2012a).

Considerable elasticity exists between biomass yield (grain and CR) and CR fodder quality.
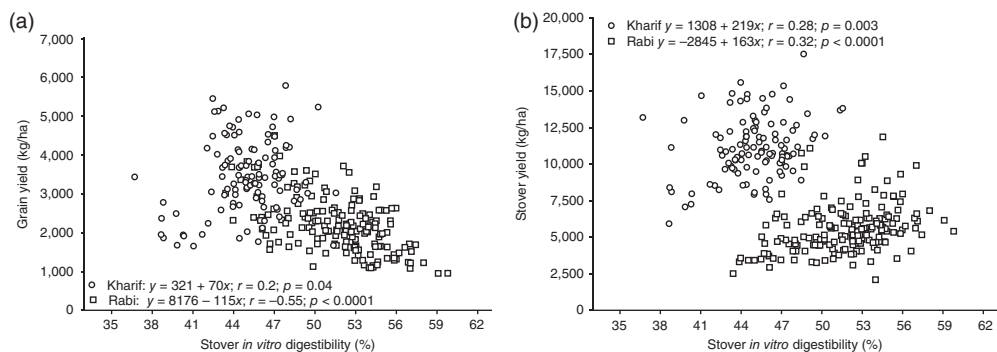
Fig. 14.7. (a) Relationships between mean stover *in vitro* digestibility and grain yield in Kharif and Rabi sorghum cultivars submitted for release from 2002 to 2008. (b) Relationships between mean stover *in vitro* digestibility and stover yield in Kharif and Rabi sorghum cultivars submitted for release from 2002 to 2008. (Data from Blümmel *et al*., 2010).
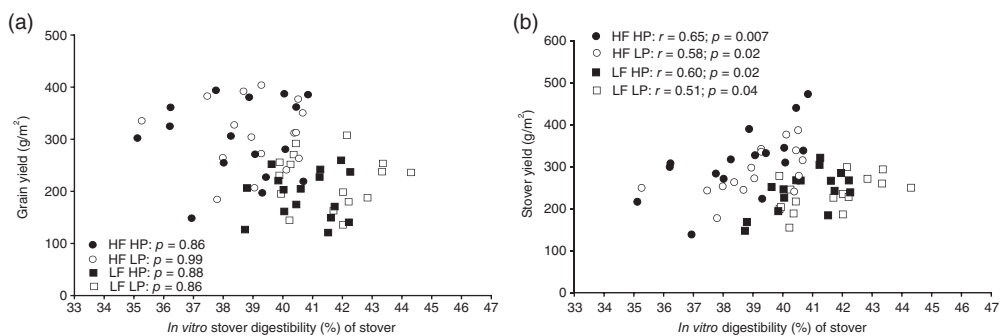
Fig. 14.8. (a) Relationships between *in vitro* digestibility of pearl millet stover and grain yield (a) and between *in vitro* digestibility of pearl millet stover and stover yield under high (HF) and low (LF) fertility and high (HP) and low (LP) population density. (Data from Bidinger and Blümmel, 2007).
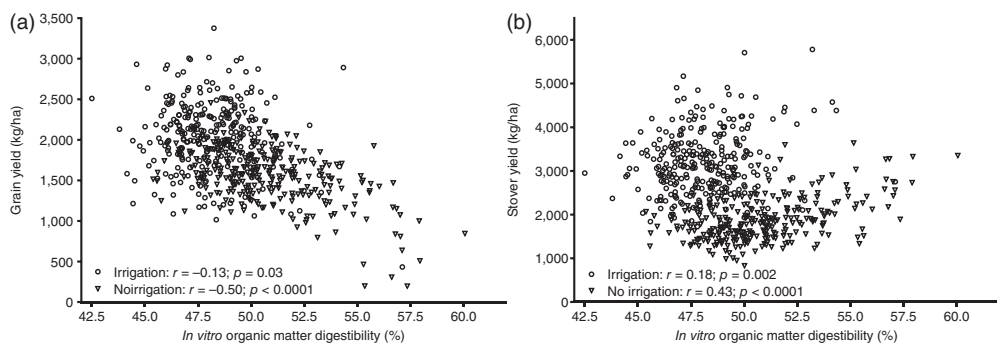
Fig. 14.9. (a) Relationship between haulm digestibility and grain yield in 280 chickpea cultivars and (b) Relationship between haulm digestibility and haulm yield in 280 chickpea cultivars. (Data from Blümmel *et al*., 2012b).

Evidence comes from the water production function for groundnut components. Water stress had a substantial negative effect on biomass yield in groundnut, while fodder quality traits such as N and IVOMD were much less affected (Table 14.5).

Outcomes and Aspects of Impacts of Multidimensional Crop Improvement

Outcomes are commonly defined by behavioural changes and changes in mindsets by secondary beneficiaries. The work presented in this chapter has contributed to such changes in both public and private crop improvement. The principal outcome of research on multi-trait crop improvement was the reconsideration of the single trait (i.e. grain) model in favour of the multi-trait and whole-plant (i.e. food and fodder) model. While there are as yet few formal decisions such as the decision of the NRCS (now IIMR) to include stover traits as new cultivar release criteria in sorghum (and now pearl millet, although under a different mandate), there are strong indications that public and private crop-improvement programmes have reoriented their efforts towards whole-plant improvement. In the design of the second phase of the CRPs, most crop commodity institutes targeted whole-plant improvement for which the expression 'full-purpose crop' established itself. Syngenta was joined by other private breeders such as Seed Co targeting dual-purpose maize in East and southern Africa, exploring branding and seed bag labelling for CR fodder traits in their hybrids.

Much of described work was conducted within the framework of CGIAR and its national partners. While drafting proposals for the second phase of the CRPs (2017–2022), several of the former crop commodity programmes, such as the CRPs on Grain Legumes and Dryland Cereals and on Maize, specifically devoted flagships to work simultaneously for grain and CR improvement, suggesting further mainstreaming of a paradigm shift in crop-improvement efforts. The CGIAR nomenclature chosen for food and fodder improved cultivars was 'full-purpose crops'. These CRPs have considerable reach as they work in global consortia comprising a wide range of national and international public and private research organizations, development practitioners and private-sector companies.

A milestone is reached when cultivar release agencies start to amend release criteria that include CR fodder traits, as has happened with the AICRPs on Sorghum and recently on Pearl Millet. Co-option and buy-in of the private sector will also be crucial. It is encouraging to see the increasing interest of the seed sector in exploring marketing of CR fodder traits. The discovery, proof-of-concept, pilot and, to a lesser degree, scale phases described above have helped to build a community of practice of experts and practitioners from animal nutrition, crop improvement, socio-economics and private-sector seed, feed and dairy companies, and from non-governmental organizations and NARES. This community of practice is the core around which further multi-trait crop-improvement efforts need to take place. CGIAR crop institutes have well-established relationships and collaborations with NARES mandated to work on specific crops.

Table 14.5. Means of grain yields, CR yields, and CR N content and *in vitro* digestibility in groundnut and sorghum cultivars grown under water and control condition at Patancheru, India, in 2009 and 2010. (Data from Blümmel *et al.*, 2012b, 2015a.)

Characteristic	Water management	Groundnut	Sorghum
Grain yield (kg/ha)	Stress	988	2542
	Control	1753	3526
CR yield (kg/ha)	Stress	2916	2970
	Control	3840	3788
CR nitrogen (%)	Stress	2.41	0.71
	Control	2.23	0.72
CR digestibility (%)	Stress	60.9	47.3
	Control	61.6	47.5

Economic impact of multidimensional crop improvement

Describing the adoption of new cultivars is a key variable for estimating the impacts of crop improvement. Assessing levels of adoption of new cultivars is usually done indirectly through the monitoring of seed production and sales and crop-specific seed rates to estimate the areas planted under new cultivars (Teufel *et al.*, 2011). An example of the problem of measuring and evaluating adoption is that of an early-maturing, high-yielding and drought-tolerant dual-purpose groundnut variety (ICGV 91114) introduced in the Anantapur district of semi-arid India. ICGV 91114 produced 15% higher pod yields, 17% more haulm and 11% better-quality fodder than the locally grown variety in on-farm trials in three villages in the Anantapur district of India. Farmers who fed their dairy cows and buffaloes the improved fodder saw daily milk production increase by about 10% per animal (Pande *et al.*, 2006, p. 23).

An impact study of 376 farmers estimated that adopters of ICGV 91114 earned 34% additional net revenue compared with traditional varieties, including a 29% gain in haulm value, while incurring unit costs that were 6% lower (Birthal *et al.*, 2011, p. 22). A non-governmental organization, the Rural Development Trust/Accion Fraterna, promoting the new cultivar estimated, based on seed production and sales, that by 2005 about 10,000–12,000 ha had been planted with ICGV 91114. However, when Teufel *et al.* (2011) tried to trace this adoption using randomly selected villages in the district, they reported only a 'handful' of adopters and concluded that the previous estimates of adoption were dramatic overestimates. ICRISAT staff have since maintained that: (i) ICGV 91114 is the third most popular cultivar in what is called 'Breeder Seed Indented', providing about 13% of all the groundnut seeds produced in this nationwide scheme in India; (ii) groundnut breeders estimated a lower figure of 4% of area coverage; and (iii) 4% of area coverage equals about 185,000 ha under ICGV 91114 (P. Janila, Hyderabad, personal communication, 2016). While the estimates based on seed production and area planted are in considerable disagreement, they are strongly suggestive of more than a 'handful' of adopters. Making direct assessments of areas under new cultivars has obvious logistical challenges; the approaches currently being explored are around genotypic fingerprinting of new cultivars (Kosmowski *et al.*, 2016).

The new cultivars benefit farms, fodder markets and livestock production. A general conclusion of our India work on dual-purpose crops is that adoption is faster and broader where the private sector is engaged. This conclusion usually applies to hybrids rather than to OPVs, where seed multiplication is public. Work on multi-trait crop improvement with OPVs identified promising new cultivars to scale (e.g. to more than 100,000 ha) or at least to pilot (more than 1000 ha), but this work was frustrated by a dearth of seed (for one recent trial, just 100 g of seed of a dual-purpose legume was provided). The reason for this lack of seeds in new public-sector OPVs might be related to misplaced incentives in public-sector crop improvement, where the release and registration of new cultivars is recognized rather than their adoption. Often, it would have been necessary, even before piloting, to multiply seed for several years – a challenging proposition. In contrast, where private-sector hybrids are concerned, as they are in maize, seed availability has rarely been a constraint.

The Future

The traditional large-scale seed sector can bring hybrid crop cultivars to scale and collaborate in their 'branding' and seed labelling processes. Small- and medium-sized seed enterprises can move new cultivars from proof-of-concept stage to pilot stage by multiplying basic/foundation seeds of OPVs/niche crops, often obtained from NARES. Once a threshold in supply of OPV seeds is passed, farmer-to-farmer seed exchange becomes significant. Small- and medium-sized feed enterprises can provide decentralized feed processing and value addition to improved CRs, can provide income and employment opportunities to disadvantaged rural people, and can act as a 'pull factor' for the adoption of new cultivars. Large dairy enterprises using smallholder milk suppliers can serve as mediators and conveyors of new cultivars, feed intervention packages and customers for existing small- and medium-sized enterprises, and as stimulators of new ones.

Acknowledgements

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Preface to Part III:
Research Spending and Publications on Tropical Livestock Systems

This preface first shows the estimated spending in the principal domains corresponding to four chapters in Part III – livestock systems, climate change and livestock in the tropics, economics and policy research and gender impact (www.ilri.org/ImpactBook/Finance).

The preface then presents 'scientific impact' as a function of publications and citations extracted from the Scopus database using search keywords relevant to the four domains.

Research spending

Data from the financial and annual reports of the International Livestock Centre for Africa (ILCA), International Laboratory for Research on Animal Diseases (ILRAD) and International Livestock Research Institute (ILRI) were used to compile a spending database for 1975–2018 (www.ilri.org/ImpactBook/Finance). Current spending for each year and institution was assigned to scientific domains using spending detail by project, by scientists' fields of expertise and, occasionally, from cost accounting by the institutions. Current annual spending in US$ was converted to constant annual spending in 2015 US$ using the global Manufacturers' Unit Value Index (Fig. PIII.1).

Total 1975–1994 spending by ILCA and ILRAD was US$636 million. Mean spending by domain at ILCA and ILRAD as a share of total spending was: (i) animal genetics, health and production, 50%; (ii) livestock systems, 11%; (iii) economics and policy, 7.6%; (iv) primary production, 4.1%; and (v) management, technical support and capacity development, 27%.

ILRAD investment in systems, economics and policy was limited to its role in the trypanotolerance network with ILCA before 1987, when ILRAD's veterinary epidemiology unit began. ILRAD spending on systems, economics and policy was less than 3% of its 1975–1994 total.

Total spending by ILRI was US$ 1.75 billion. Spending by domain over ILRI's lifetime was: (i) animal genetics, production and health, 39%; (ii) livestock systems, 10%; (iii) economics and policy, 11%; (iv) primary production, 6.4%; and (v) management, technical support and capacity development, 34%.

Altmetrics

An Altmetric search (www.altmetric.com/; accessed 13 March 2020) was carried out on the keywords 'livestock farming', 'farming system', 'mixed system', 'pastoralism' and 'grazing' as indicators of LSR content. ILRI work dominates the research (as measured by papers and citations) on sub-Saharan Africa but is typically small as a share of global research (Table PIII.1). An initial Altmetric analysis was done for the systems domain[1] on the expressions 'livestock farming', 'mixed farming', 'farming system' and 'crop–livestock' for papers relating to research in

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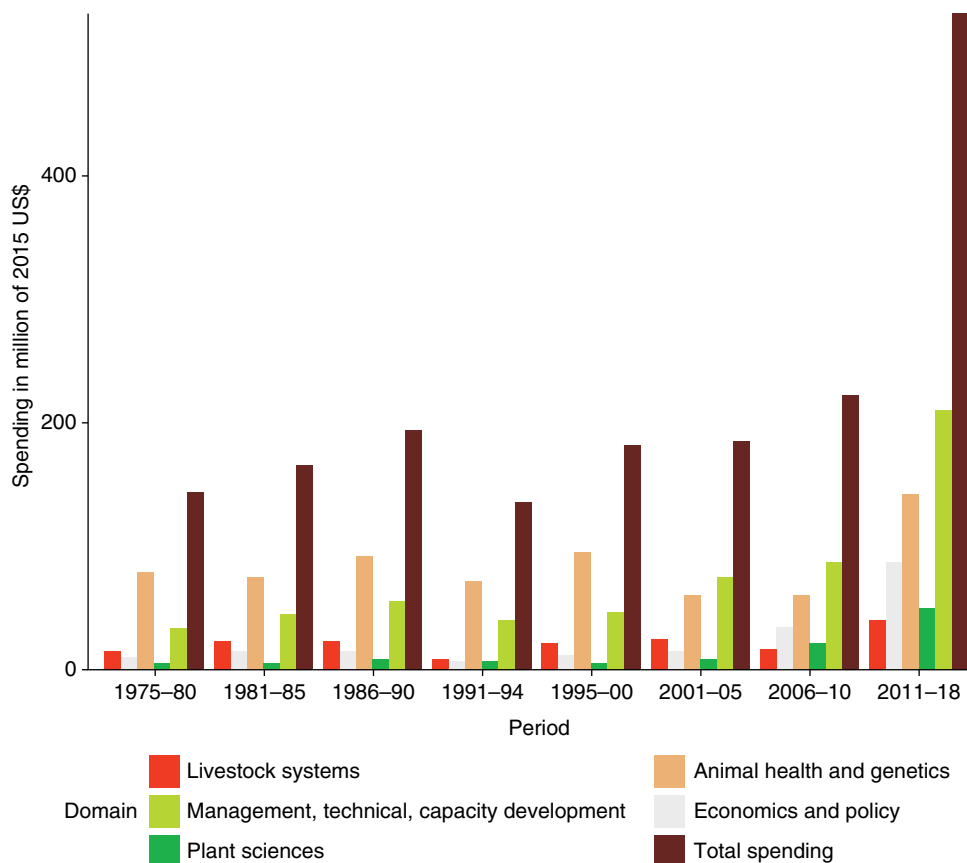
Fig. PIII.1. ILRI economics and policy research share of total ILRI spending, 1975–2018. (Data from ILCA/ILRAD/ILRI Annual and Financial Reports.)

Table PIII.1. Results of the Altmetric search for ILRI livestock systems and related studies. (Data from: www.altmetrics.com/explorer, accessed 13 March 2020.)

Keywords	Region	Share of papers (%)	Share of citations (%)
'Livestock farming'	Global (n=310)	8.7	3.4
	Sub-Saharan Africa (n=27)	55.2	67.3
'Farming system'	Global (n=1,453)	8.1	6.3
	Sub-Saharan Africa (n=118)	36.9	31.8
'Mixed farming'	Global (n=126)	15.1	18.9
	Sub-Saharan Africa (n=19)	64.0	64.7
'Pastoralism' + 'grazing'	Global (n=3,878)	2.5	2.3
	Sub-Saharan Africa (n=258)	20.5	15.5

sub-Saharan Africa. The Altmetric analysis does not generally allow analysis before the advent of the CGIAR research programmes (i.e. before 2011); Altmetric therefore excludes older ILCA and ILRAD papers and many ILRI papers before 2011. It does show substantial ILRI contributions at the global level, where papers having at least one ILRI author of any rank represented between 2.5% ('pastoralism' plus 'grazing') and 18.5% ('mixed farming'); citations from these

papers at the global level ranged from 2.3% ('pastoralism plus 'grazing') to 18.9% ('mixed farming'). Notable work with an ILRI author in these areas was Herrero *et al.* (2010) and Thornton and Herrero (2015) on adaptation to climate among mixed smallholders in Africa, Giller *et al.* (2011) on soil fertility management ('farming system') and Silvestri *et al.* (2012) on perception of climate change among Kenyan pastoralists ('pastoralism + grazing').

Spending on livestock systems research and the return in publications

ILCA spending on livestock systems was some US$71 million from 1975 to 1994, or 11% of the ILCA/ILRAD total of US$636 million (see Chapter 15,

this volume). The sum of livestock systems research, which often had a policy component, plus economics and policy research during the ILCA era was approximately US$120 million or 19% of the 1975–1994 ILCA/ILRAD total. The scientific return on this investment was 26 citations per paper; this return was skewed with a median of 11 and the top ten papers had 49% of all citations in a sample of 196 papers. Papers to which ILCA staff contributed generated about 46% of a global sample of livestock systems research papers before 1995 and about 53% of the citations, and clearly had a powerful influence in describing the rationale and operation of African livestock production (Fig. PIII.2).

ILRI lifetime spending on livestock systems has been about US$177 million since 1975, or 10% of the 1975–2018 total of US$1.75
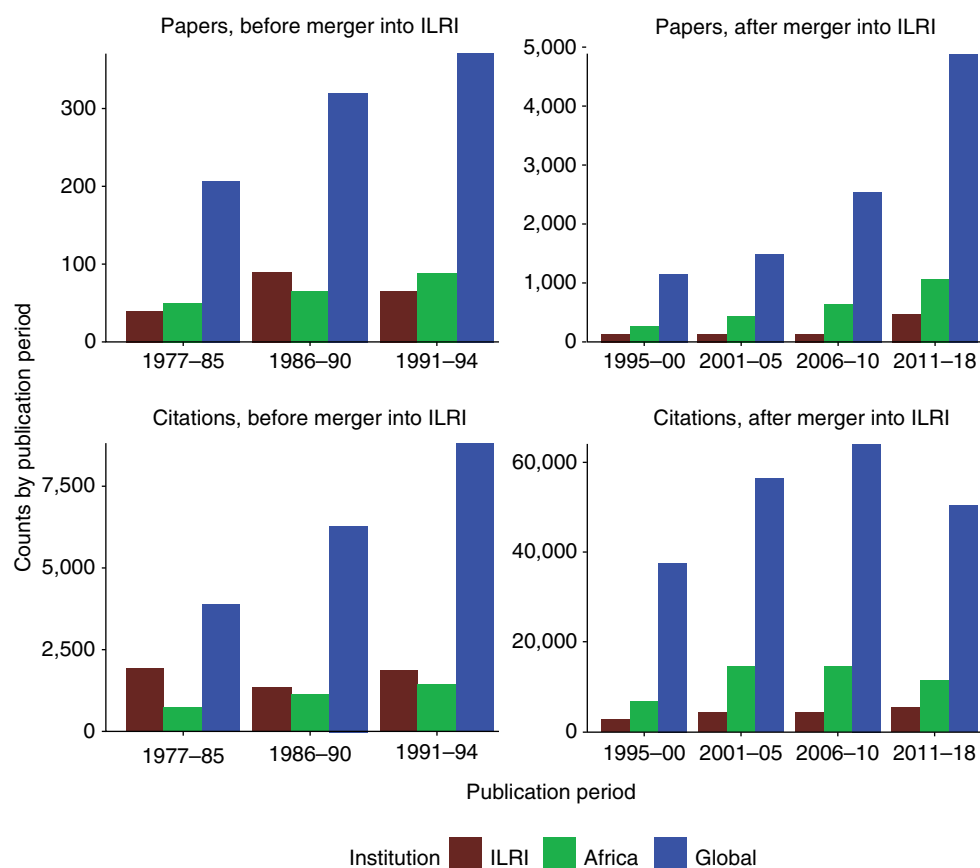
Fig. PIII.2. ILRI papers in systems research in Africa and globally, 1977–2018. ILRI papers before merger = 196 and after merger = 889. Africa papers = 207 and 2,475; global papers = 895 and 10,058. (Data from www.scopus.com/.)

billion. (The sum of economics and policy work plus livestock systems research, which nearly always made some policy recommendations, was about US$375 million, or 21% of the 1975–2018 total.) Mean citations per paper were 19, with a median of 8; the top ten papers had 17% of all citations in a sample of 1,085 papers. The major systems papers tended to be older, including the work of Sandford (1983) on pastoral development, Wilson (1986) on central Mali, Solomon Bekure *et al.* (1991) on Kenyan Maasailand, Coppock (1994) on Borana in Ethiopia, McIntire *et al.* (1992) on sub-Saharan Africa, and Hiernaux and Ayantunde (2004) on the Fakara subregion of Niger. Livestock systems work evolved after 1990 to include such landmark pieces as Norval *et al.* (1992) on the field epidemiology of *Theileria* spp., Reid *et al.* (2000) on land use in Ethiopia, Kruska *et al.* (2003) on mapping global livestock systems, Reid *et al.* (2008) on broader issues in pastoralism, including interactions with wildlife, and Robinson *et al.* (2011) who mapped poverty measures to global livestock systems. Papers produced by ILCA/ILRAD/ILRI staff, or in close collaboration with them, contributed about 29% of Africa-wide livestock systems research and about 31% of the citations and have clearly had a powerful influence on policy and development interventions since 1975.

Climate change

Climate change research has only become a major part of ILRI research since about 2000 (see Chapter 16, this volume). It was not possible to estimate spending on climate research, given that it is a transversal field, typically matched against several fields in the citations databases and was not, until recently, accounted separately. In the ILCA/ILRAD era, a sample of 48 papers classed as having some element of 'climate and agriculture' research generated a mean of 44 citations per paper, a median of 15 and with the top ten papers producing 77% of all citations (Fig. PIII.4).

After 1999, there was a burst of work on climate, crop and livestock interactions led by Philip K. Thornton and Mario Herrero. All of the major ILRI-affiliated papers on climate change,

with the exception of King (1983) on water, have been published since 2003. Over the lifetime of ILRI (1975–2018), scientists produced a sample of 568 papers on some aspect of climate and agriculture, generating a mean of 36 citations per paper, a median of 11 (Fig. PIII.4) and with the top ten cited papers producing 24% of total ILRI citations in this domain. Climate change papers tend to involve new tools (such as the rainfall data generator MarkSim), or global mapping of vulnerability and impact. Adaptation to climate change appears as a theme more frequently than mitigation of climate change effects, and ILRI has made a major global contribution in areas related to livestock and adaptation to climate change.

Economics and policy

ILCA/ILRAD spending on economics and policy research was about US$48 million between 1975 and 1994, or 8% of the total (see Chapter 17, this volume). From a sample of 86 papers in this domain, the mean of citations per paper in economics and policy research was 40, the median was 13 and the top ten papers contributed 70% of ILCA/ILRAD citations (Fig. PIII.3).

ILRI lifetime spending on economics and policy research has been about US$198 million since 1975, or 11.3% of the 1975–2018 total of US$ 1.75 billion. From a sample of 947 ILRI papers in this domain, the mean of citations per paper was 34, the median was 10 and the top ten papers contributed 24% of ILRI citations in this domain (Fig. PIII.3). The scientific return on spending was 5 papers per US$ million and 161 citations per US$ million over the long period of 1975–2018.

The older papers on economics and policy were typically microeconomic, notably in making benefit–cost estimates of technologies, evaluating public spending on agriculture, or testing efficiency in factor and product markets (McCarthy *et al.*, 1999, as discussed in Chapter 17, this volume). Major economics and policy papers in this century took a more macro view, and are usually of the characterization type, including the work of Delgado *et al.* (1999) on the 'Livestock Revolution', Thornton *et al.* (2002) on poverty
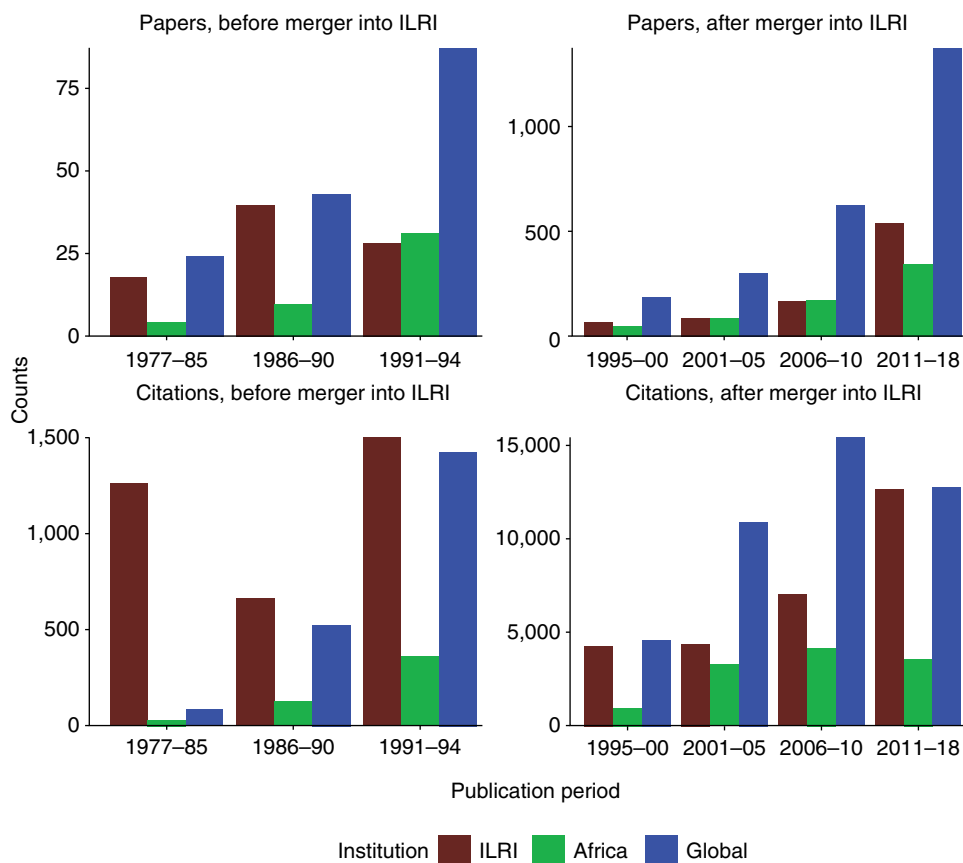
Fig. PIII.3. ILRI papers cited in economics and policy research on Africa and global problems related to livestock systems, 1977–2018. ILRI papers before merger = 86; after merger = 861. Africa papers = 45 and 644; global papers = 154 and 2,484. (Data from www.scopus.com/.)

and livestock development, Perry *et al.* (2002) on animal health research and poverty alleviation, and Herrero *et al.* (2010) on sustainable livestock investments. Two ILRI projects – one leading to beneficial reforms in Kenyan dairy policy (Kaitibie *et al.*, 2010) and another that created a new insurance instrument (Chantarat *et al.*, 2013) and Jensen *et al.* (2019) – had important development impacts.

High citation papers

ILRI research in livestock systems, economics and policy, and in climate change related to agriculture has been quite productive relative to global (Fig. PIII.5a) and African efforts (Fig. PIII.5b). (This subsample was limited to papers having at least ten citations.) One measure of major ILRI scientific contributions is the share of ILRI papers in the top 5% of citations in a given field, compared with the share of all papers – ILRI plus global – in the top 5%. This productivity is notable in the best cited papers for economics and policy, where ILRI-associated work was 32% of all global citations and 27% of citations in the top 5%. For livestock systems, the corresponding shares were 10% and 9%; for climate, they were 18% and 15%.
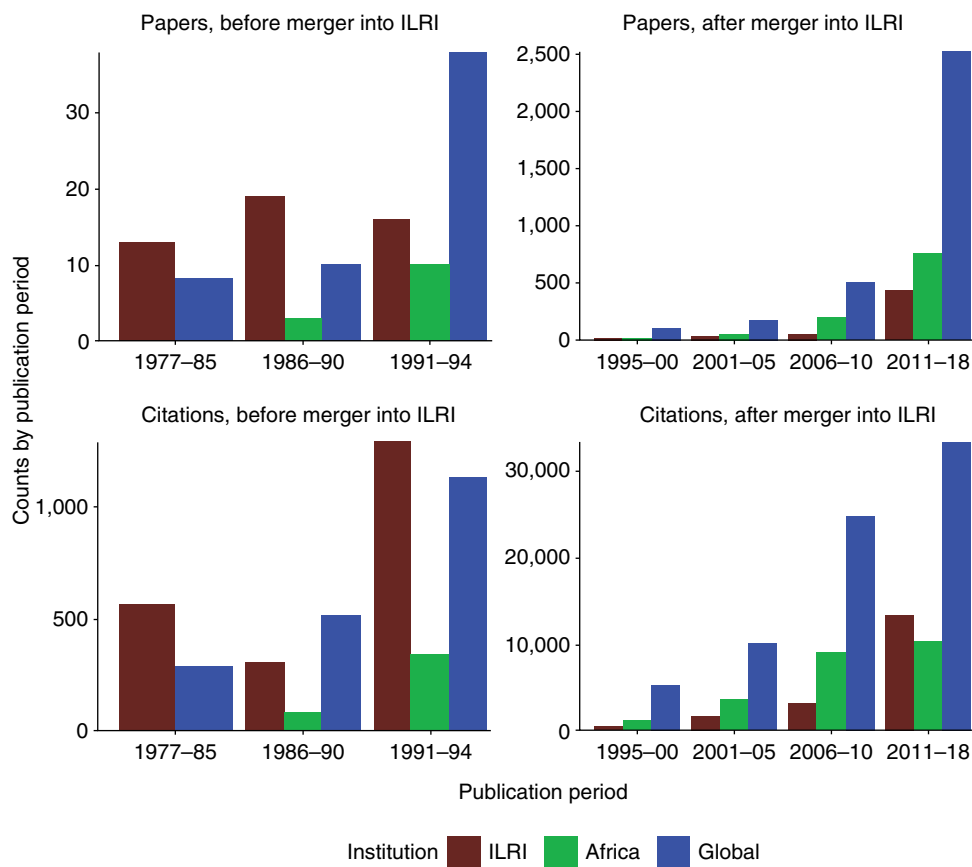
Fig. PIII.4. ILRI and other publications in climate change research related to livestock systems have become widely cited since 2000, 1977–2018. ILRI papers before merger = 48; and after merger = 520. Africa papers = 13 and 1,010; global papers = 56 and 3,276. (Data from www.scopus.com/.)
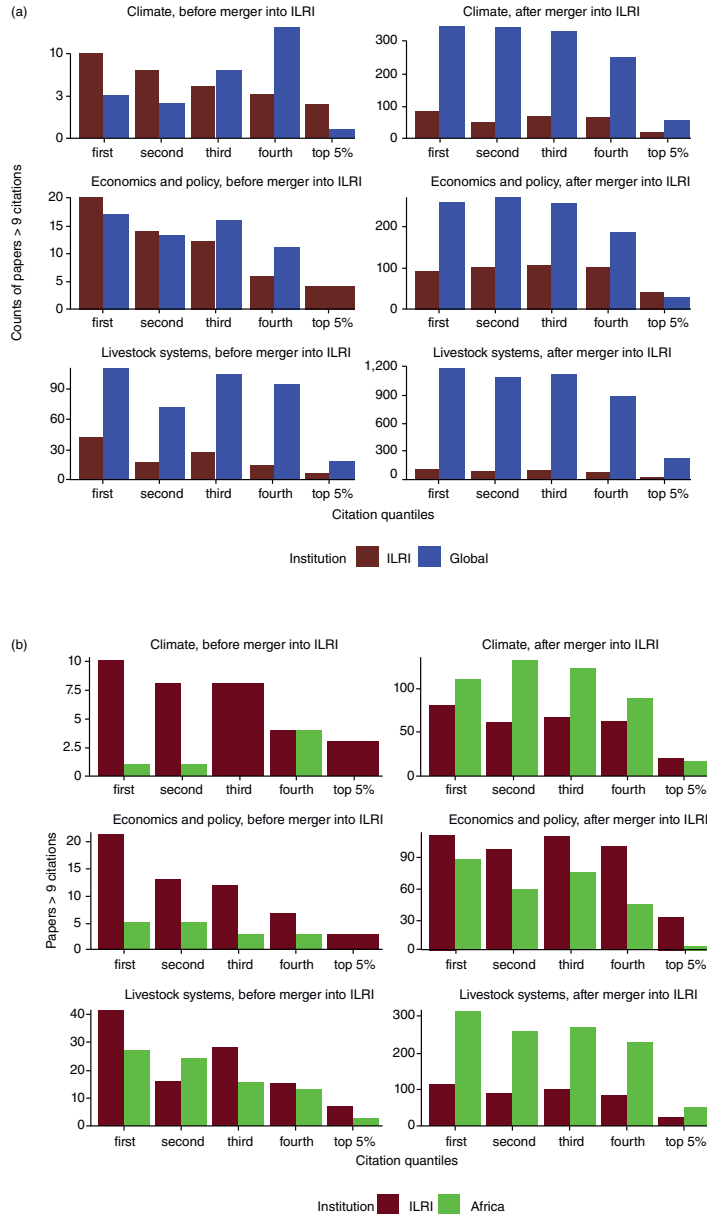
Fig. PIII.5 (a) Frequency of papers of ILRI and other institutions in global systems research, 1977–2018. ILRI climate papers before merger = 33; after merger = 289. Global climate papers, 31; 1,311. ILRI livestock systems papers = 107 and 407; global livestock systems papers = 398 and 4,478; ILRI economics and policy papers = 56 and 447; global economics and policy papers = 57 and 1,001. (b) Frequency of papers of ILRI and other institutions in African systems research, 1,977–2018. ILRI climate papers before merger = 33; after merger = 289. Global climate papers, 31, 1,311. ILRI livestock systems papers = 107 and 407; Africa livestock systems papers = 83 and 1,119; ILRI economics and policy papers = 56 and 447; Africa economics and policy papers = 16 and 269. (Data from www.scopus.com/.)

Note

[1] The Altmetric analysis returned very few matches for 'climate change' and related terms, compared with the Scopus database, and is therefore not reported.

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15 African Livestock Systems Research, 1975–2018

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Executive Summary

The problem

Livestock systems research (LSR) at the International Livestock Research Institute (ILRI) sought to answer two questions:

- What are the major livestock systems in the sub-Saharan Africa tropics and subtropics (Ruthenberg, 1980)?
- What technical and organizational changes can be introduced into these systems to make them productive?

This chapter reports the answers of decades of research at ILRI, its predecessors and its principal partners to these questions. The chapter continues to ask:

- What have been the scientific impacts of LSR since the 1970s?

- What have been the development impacts of LSR since the 1970s?
- Can the development impacts of LSR be distinguished from long-term trends in African livestock systems?

Research spending

ILRI[1] and one of its predecessors, the International Livestock Centre for Africa (ILCA), spent about US$212 million (in 2015 US$) on LSR from 1975 to 2018. This was roughly 22% of ILCA spending before 1995 and about 11% of ILRI spending from 1995 to 2018. The majority of this spending was on ruminants in sub-Saharan Africa, mainly in systems where cattle were the dominant stock. A crude estimate of expenditure by system was 80% on mixed systems and 20% on grazing/rangelands during the 1975–1994

era of ILCA and the International Laboratory for Research on Animal Diseases (ILRAD). No such estimate by system is possible for the ILRI era (1995–2018).

Scientific impact

The scientific impact of LSR was substantial:

- Mapping systems. The greatest scientific impact of LSR was in mapping systems and identifying their technical possibilities, potential for growth and poverty reduction, and research priorities.
- Understanding transversal and system studies. The second most important scientific impact was in understanding the evolution of animal production systems, grazing and mixed alike, to prepare appropriate technical interventions, to avoid repeating past failures in technology generation and transfer, and to identify promising sites for technical transfer from other regions.
- Estimating production parameters. Estimating input and output relationships from field data in the systems studies was feasible for the first time, using the work started in the 1970s by ILCA and continuing to the present by ILRI.
- Creating and defending a new view of African grazing systems.
- Understanding the value of mobility in grazing systems. The various field studies in sub-Saharan Africa showed the importance of mobility in grazing and revealed the costs of new policies and organizations that would compromise mobility. This includes understanding of seasonal and annual variability and the opportunistic character of pastoralism.
- Understanding complementarities in mixed wildlife and domestic livestock systems. This was most important in East Africa.
- Understanding the roles of crop residues and manure in soil nutrient cycling. These included quantifying the benefits and trade-offs among uses of crop residues and manure in mixed systems as functions of crop and livestock potential in given environments.
- Correcting the neglect of the feed value of crop breeding programmes in Africa by the crop research centres. ILRI work in India

and Ethiopia, led by Michael Blümmel, has done much to correct this neglect (see Chapter 14, this volume) and has shown the value of complementary field and station research.
- Quantitative modelling of livestock systems. Models of pastoralism often generated scientifically reliable projections of the outputs of policy experiments. They have succeeded in establishing new research lines, notably 'livestock as a pathway out of poverty' and the study of livestock and climate change.
- Defining how mechanization with animals evolved. This work had an immense scientific impact but little positive development impact in the sense of inducing new investments in mechanization. There was some additional scientific impact in elucidating why some apparently promising technical changes had failed.
- Ley farming in the Mediterranean and in the highlands of East Africa.
- Other efforts to introduce planted forages in smallholder systems, such as pasture improvement in arid areas, or into beef production in the humid and subhumid tropics.
- Smallholder dairying models borrowed from temperate areas[2] and introduced into the tropics.
- Station and farm studies of nutrition and other factors affecting output from working animals.

Development impact

The development impact of LSR was limited. It consisted of: (i) defining the economic weight and rationality of pastoralism[3] as a means of defending pastoralists' livelihoods against the incursion of crops and wildlife, corruption and bad policy; (ii) valuing land rights of pastoralists; (iii) defining the conditions in which external technologies could be introduced into mixed systems; and (iv) testing and validating improved dairying models for smallholders.

Defence of pastoralists' interests

The systems studies of ILCA, ILRI and their many collaborators demonstrated the economic

rationality of extensive grazing systems in sub-Saharan Africa. Homewood's contemporary book (Homewood, 2008) followed by that of Catley *et al.* (2013) are thorough analyses of how the new view has contributed to the defence of pastoralists' interests and avoided economic losses to the vulnerable groups. At the same time, such work called into question the 'inevitable overgrazing' critique of pastoralism. In so doing, this research thoroughly discredited, even if it did not eliminate, the 'mainstream view' of pastoralism. The new view of pastoralism, supported by research throughout sub-Saharan Africa, reduced some of the policy threats to those systems, including forced settlement, confinement into inviable grazing schemes and dispossession by elites.

Valuing land rights

Related to the 'defence of pastoralists' interests' was the impact of work on valuing land rights and thereby permitting better land policies. All of the systems studied – Maasailand, Borana, Kaduna, Niono, the Niger Delta and Fakara, plus the extensive work of independent researchers in East and West Africa – showed the economic and environmental rationality of pastoralism; these demonstrations strengthened the case of the pastoralists against forced sedentarization and other policies that threatened their livelihoods. The review of land rights research in Chapter 17 (this volume) on policy shows how a better understanding of land markets and land rights in Niger and Ethiopia supported policies that could lead to greater efficiency and equity.

Identifying conditions for successful technical change

The systems studies of ILRI and partners, complemented with findings from the transversal studies, made it possible to identify conditions for success or failure of proposed technical change. For pastoral systems, conditions of success included: (i) components that used local knowledge of production; and (ii) components that did not restrict animal mobility in search of water or pasture. For mixed systems with dominant cropping, conditions of success included:

(i) a degree of intensification that was compatible with local population density; (ii) a recognition that the introduction of animal power was not sufficient and was in many instances not necessary; and (iii) a recognition that flexibility in managing crops and livestock in the same farm should not be sacrificed to rigid external ideas of an optimal enterprise mix.

The single most important development impact was the design and extension of the broad bed maker (BBM) tool for cultivation on Vertisols in highland Ethiopia. This is one of three ILRI research programmes that has documented the costs and benefits of research and extension in relation to a specific product; the other two are ILRI's contribution to Kenya dairy policy (see Chapter 17, this volume) and the vaccine against East Coast fever (ECF) (see Chapter 6, this volume).

The problem of translating scientific impact into development impact

It was difficult or impossible to translate scientific impact into development impact for a number of reasons:

- Improving primary productivity in mobile grazing areas was generally unprofitable because of: (i) competition from natural pastures with introduced pastures; and (ii) the high costs of water, fertilizer, rotational grazing, fencing and other investments in relation to the weak productivity effects of introduced pastures.
- Introducing planted forages into grazing or mixed systems generally failed because of low incremental yields and low adoption rates outside dairy production areas.
- Introducing mixed farming only took place over many years and its utility as an integrated model for smallholders was limited where the conditions – population density, market access and seasonality – were not favourable.
- Introducing mechanization with animals as a project component. International agricultural research centre (IARC) research had no evident impact on technical change in animal production or on efficiency and

equity related to the ownership and use of livestock as draught animals. The exceptions to this generalization were found only where profitable cash crops, such as cotton and groundnut, received significant extension support.

- Application of randomized control trial methods for technology evaluation and for making policy recommendations to governments is generally too costly because of sample size problems in livestock research.

- Many models were inapplicable for policy advice. Using models, quantitative or not, failed to raise productivity. Many models were developed and later not used at all, even for scientific purposes, or were never used for investment analysis or policy simulations; some of the models were poorly documented and their results could not be replicated.

Introduction

This chapter covers the scientific and development impact of international LSR in animal health and management, grazing management and plant production, economics and policy, soil fertility management, farm mechanization and crop–livestock interactions. It reviews both extensive systems, in which mobile herding is the principal activity with little or no arable agriculture, and mixed systems, in which arable farming is the dominant enterprise, animals and crops are managed jointly, and where animals are much less mobile.

The chapter answers the following questions:

- What are the livestock systems in the tropics of sub-Saharan Africa?
- How have these systems evolved since around 1970 just before the founding of ILCA and ILRAD?
- What are the major findings of LSR in sub-Saharan Africa beginning around 1970 and continuing to the present?
- What are the scientific and development impacts of LSR since the 1970s?

The focus of the chapter is on ILRI, with reference to partners (e.g. Centro Internacional de Agricultura Tropical (CIAT), International Center for Agricultural Research in the Dry Areas (ICARDA), regional and national programmes, and others), given their important contributions in many areas. The chapter first defines the objectives, stages and potential impacts of LSR. It then summarizes tropical systems with animals as treated by Robinson *et al.* (2011) and earlier by Seré and Steinfeld (1996), Thornton *et al.* (2002), Steinfeld *et al.* (2006)[4], Kruska *et al.* (2003), Reid *et al.* (2008a) and Robinson *et al.* (2011). Subsequent sections review the scientific and development impacts of ILRI research on pastoral and mixed systems in sub-Saharan Africa, with some reference to South Asia and Latin America, and explains why the scientific impact has often been strong while the development impact has been weak[5]. The concluding part of the chapter summarizes the scientific and development impacts and the problems in translating scientific impacts into development impacts and indicates some future priorities.

The chapter does not cover mapping methods as discussed in Robinson *et al.* (2011) and in the agricultural land cover literature, such as Global Land Cover (GLC) 2000 (Mayaux *et al.*, 2004; Bartholomé and Belward, 2005), GlobCover (Bontemps *et al.*, 2011) and MODIS products (Morisette *et al.*, 2002), nor does it treat more recent efforts on composite products (Fritz *et al.*, 2015; See *et al.*, 2015).

Objectives of LSR

The broadest objective of system characterization is that of Robinson *et al.* (2011, p. 17): '…to predict how the production systems may change in the future…and to assess the potential impact of changes in crop–livestock systems on agro-ecosystem services'. While Robinson's is a recent statement, it is representative of the purposes of system characterization[6], as they were expressed when international centre livestock research began in the 1970s. The objectives were as follows:

- To define land and climate units by temperature, rainfall, altitude and soils to express

output potential in systems with a major livestock component.

- To describe and map crop and livestock patterns from field observations of land use and production within land and climate units.
- To describe animal health risks by system '…to develop a good understanding of the *differences among production systems* to…*minimize the risk of disease emergence* and spread (Robinson *et al.*, 2011, p. ix).'
- To apply maps of livestock densities and output (Robinson *et al.*, 2014) to illustrate disease risks and to project global and local environmental impacts of livestock (Gerber *et al.*, 2013).
- To estimate factor and input productivities by system and then to define constraints to development interventions that could be released by research and extension in the 'diagnostic stage' of the farming systems research sequence.
- To apply systems maps – comprising climate, soils, altitude, water, animal diseases and vectors, and productivity – to plan development interventions and to better target public investment in support of sectoral goals.
- To propose technical and managerial changes to relieve productivity constraints in the 'design and testing' stages of the farming systems research sequence.
- To provide information for process and agent models of technologies and policies.
- To improve risk management and assist recovery from shocks[7].

Stages of systems research

Norman and Collinson (1985) defined four stages in farming systems research: (i) a 'descriptive and diagnostic stage' to analysis of constraints to productivity; (ii) the 'design or planning stage' in which strategies are identified for resolving constraints; (iii) a stage in which strategies (e.g. new varieties) are tested on-farm, with varying degrees of researcher management; and (iv) an extension stage in which recommendations are applied. The comparative advantage of the IARCs, such as ILCA, CIAT and the International

Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in the 1970s to 1990s was chiefly in the first three stages, with national programmes leading in the fourth stage.

A major part of the descriptive and diagnostic stage in international livestock research was agroecological zoning, which classified agricultural systems by 'climate, soil and terrain' (Collinson, 2000, p. 51; Seré and Steinfeld, 1996) and later work in this century such as that of Kruska *et al.* (2003) and Robinson *et al.* (2011), which used data and tools that had not existed when the IARCs were expanding quickly in the 1970s and 1980s. Its purpose was to project carrying capacities, to identify domains for genetic and management improvement, to describe field conditions for experiments[8] and to show the scope for technology transfer among zones.

The basis of the design and planning stage was to create average farm typologies within agro-ecologies. These typologies would be used to make recommendations applicable to dairy farms using cut forages, to smallholders practising rainfed cropping without animal traction, or to systems such as watering practices for transhumant herders. The ILCA systems studies in grazing and mixed systems are a mix of the descriptive/diagnostic and design/planning stages[9]. The most similar CIAT study (Rivas Rios, 1974) is the second stage, in which beef ranches in the same agroecology of Colombia were grouped by farm size. The ICRISAT village-level studies in the semi-arid tropics of India drew samples of farms based, *inter alia*, on agroecological zoning and ultimately constructed Stage 2 farm typologies using irrigation, mechanization and the principal crop as variables (Walker and Ryan, 1990). The construction of farm typologies was a principal goal of the French tradition of agronomy in West Africa and this had some influence on the work of ILCA and ICRISAT in that region from the 1970s.

The third stage was to estimate productivity determinants and to test technologies using experiments in environments and farm types as defined in the first two stages. This stage is to calculate the levels, rates of change and determinants of enterprise and whole-farm productivity to be used in identifying constraints and in targeting extension. This estimation was done using farm data gathered in surveys, sometimes combined with farmer- or researcher-managed

experiments (an early summary of mainly crop work from sub-Saharan Africa and Latin America is given by Matlon *et al.*, 1984). The third stage was prominent in the early systems research portfolios; crop research tended to be more prominent, with the early ILCA work in Ethiopia, Mali and Nigeria and some CIAT work in Latin America being the main livestock exceptions.

The fourth stage was 'recommendation and diffusion' of new technologies. This was to be achieved by models of 'entry points' (as described much later by van Wijk *et al.*, 2009) at which technical changes could be introduced based on an understanding of the complex interactions among system components. This stage was broader in LSR than in cropping, which focused on crop cultivars and associated input packages, because of the need to integrate more components – animal species and breed, animal health, animal management (fencing, housing and grazing rotations) and feed production. Livestock-related examples include mechanization: animal traction, the use of cows for draught power and the BBM in Ethiopia; the introduction of trypanotolerant animals in combination with drug treatments and vector control (see Chapters 2 and 3, this volume); a vaccine against ECF, using the infection-and-treatment method (see Chapter 6, this volume); the use of trypanocidal drugs (see Chapter 3, this volume); feed improvements with grasses and legumes (see Chapters 11 and 12, this volume); various forms of land management, such as fodder banks with *Stylosanthes* spp. in central Nigeria; and alley farming in Nigeria and other humid countries in West Africa.

Potential impacts of systems research

We set the potential scientific and development impacts of LSR into the three classes of policy studies as defined by Zilberman and Heiman (2004, pp. 278–279).

Class I is scientific understanding, advanced by estimating system scale, productivity and sectoral accounts. Class I includes advances in research methods, such as using remote sensing to map production systems and carrying out long-term field studies on production and environmental relations.

Class II is contributing to technical change, which lifts productivity. This can involve estimating optimal levels of water, veterinary drug and feed use under controlled situations and testing these levels on farms or among herds. Other examples would be testing innovations, such as vaccines, tropical pastures and multidimensional crops, or improved processing.

A subset of Class II is to estimate the negative externalities (costs) of farming, such as greenhouse gas emissions, land degradation and water pollution from livestock effluents. Examples are the book *Livestock's Long Shadow* (Steinfeld *et al.*, 2006), which calculated the local and global environmental effects of animal production, and research on antimicrobial resistance.

Class III is advising on policies to raise productivity or to improve income distribution. This can involve adjusting terms of trade, devising better institutions, eliminating distortions in incentives, identifying costs of bad policies and proposing measures to achieve higher growth.

The potential scientific and development impacts of LSR would occur through the following:

- Defining and measuring land and climate units with similar production potential (Class 1).
- Characterizing and mapping production systems – combinations of resources by season – across the land and climate units (Class 1).
- Estimating productivity relationships to identify priority technologies in animal health, breed, feed and management, or to propose changes in organization or policy (Classes 1 and 2).
- Targeting these technologies (new methods of production or organization, or policy shifts) for controlled testing in relevant systems (Class 2).
- Simulating potential growth as functions of hypothesized changes in technologies, policy, organization or species/breed between domesticated animals and wildlife (Class 2).
- Providing information to guide extension of proposed technologies to farmers (Class 3).
- Writing *ex post* evaluations of the development and environmental impact of changes in technologies, policies and organizations (Classes 2 and 3).

- Proposing new research hypotheses after the *ex post* evaluations of new methods (Classes 2 and 3).
- Revising methods of experimentation and modelling to test the new hypotheses (Classes 2 and 3).

Classifying Livestock Systems

Classifying livestock systems has three steps: (i) describing the biophysical conditions of production in terms of climate and length of growing period, as determined by rainfall, temperature and altitude; (ii) describing the modes of livestock and crop production with respect to animal mobility, principal product and enterprise scale; and (iii) mapping the modes of crop and livestock production by biophysical conditions to define systems (see Maps 1–3. p. xvii-xix).

Climate and growing period

The typologies of the Food and Agriculture Organization of the United Nations (FAO, 1975) classified the physical conditions of animal production by climate and length of growing period (LGP)[10] as the following:

- Arid climates, of the Köppen types *BWh* (arid, desert, hot arid) and *BSh* (arid, savannah, hot arid), with an LGP of less than 75 days[11].
- Semi-arid to subhumid climates, of the Köppen types *Am* (equatorial monsoon), *Aw* (equatorial winter dry), *BSh* and *BWh*, and having an LGP of 75–150 days.
- Subhumid to humid climates, of the Köppen types *Aw* and *Am*, with an LGP of 181–270 days.
- Humid climates, of the Köppen types *Aw* and *Am*, with rare areas in *Af* ('fully humid'), with an LGP of more than 270 days.

Modes of production

Ruthenberg (1980) proposed four modes of tropical livestock production – ranching, commercial dairying, nomadic and semi-nomadic subsistence dairying, and mixed crop–livestock farming with irrigation or under rain-fed conditions. Ruthenberg used two variables – animal mobility (1980, p. 18) and rainfall (1980, pp. 322–323) – in his classification. He grouped animal mobility into permanent nomadism, seasonal (proximate or distant transhumance) or none, as with village grazing or stabulation.

Ranching

Ranching is a commercial system on large, private, fenced holdings, usually for beef production using grade animals, with no seasonal or annual mobility outside the ranch. The amount and seasonality of rainfall would vary from arid Botswana (Köppen climates *BWh* and *BSh*), Australia (Köppen climates *BSk, BWh*, plus the humid subtropical classes *Cfa* and *Cwa*) to subhumid and humid (Colombia and Brazil; Köppen climates *Af*, *Am* and *Cwb*). There is no reliable estimate of ranched cattle in the African tropics, but that number would be small as a share of all cattle in sub-Saharan Africa and certainly much less than the corresponding shares in the humid tropics of Latin America or in the arid tropics of Australia.

Commercial dairying

Commercial dairying is milk production for the market, with some form of sown pastures, little seasonal mobility, no annual mobility, and both large and small holdings. Commercial dairying in the tropics is typically in the cool subhumid highlands (East Africa and parts of Latin America) or in the hotter subhumid lowlands, both of which have high rainfall and year-round pasture production. In sub-Saharan Africa, commercial dairying is restricted to highland countries in East Africa with less risk of trypanosomiasis and ECF, or to parts of southern Africa with cooler climates and where insect-borne diseases can be better managed. No reliable estimate of animals or land in commercial dairying is available for sub-Saharan Africa in the 1970s, but both would have been small shares of their respective continental totals and with respect to the numbers of commercial dairy animals in Latin America and the Caribbean.

Nomadic and semi-nomadic grazing

Nomadic and semi-nomadic grazing is milk production for subsistence, in which extensive

seasonal and annual mobility are the defining features. The climate is arid[12] of the Köppen types *Bw* and *Bs* with rainfall usually below 300 mm in a single wet season. Grazing systems in sub-Saharan Africa cross a wide band from Senegal to Eritrea, into the northern parts of the West Africa coast (seasonally), into Sudan, Cameroon and the Central African Republic, and then south from Eritrea and Ethiopia around the Rift Valley into Mozambique. Practically all of the African nomadic and semi-nomadic modes are at altitudes below 1500 m above sea level (masl). These systems, although sparsely populated and understocked relative to their potential, were the most important in grazing areas and in ruminant numbers in sub-Saharan Africa at ILCA's founding.

GRAZING SYSTEMS. We use 'grazing systems', 'pastoral systems' and 'pastoralism' interchangeably to refer to African farming systems in which ruminants are the main stock. These are livestock/grazing/arid (LGA), livestock/grazing/humid (LGH) and livestock/grazing/tropical highlands (LGT) in the terminology of Sere and Stenfeld (1996) and Robinson *et al.* (2011).

The LGT system is livestock found only in humid and subhumid zones. These are found in Köppen climate *Aw* (tropical savannah), which is generally hot and wet with the driest month having less than 60 mm rainfall.

The LGH system is livestock only in (temperate and) tropical highland zones. The LGT and LGH systems constitute perhaps 26% of the sub-Saharan Africa grazing area, a similar share of the ruminant populations and perhaps one-sixth of the sub-Saharan African population.

African rangelands fall into two groups. The west and central group extends from Senegal to eastern Chad, nearly all of which is in the LGA and LGH systems[13]. All West African grazing systems have a single rainy season at elevations below 1000 masl. The shorter rainy seasons in West Africa (60–90 days), uniformly lower elevations, generally hotter temperatures and strictly monomodal rainfall imply lower average primary productivity, more variable grazing and therefore stronger reasons for extended transhumance (Pratt and Gwynne, 1977; Thornton *et al.*, 2002). The West African group would tend to have lower average pasture quality, as indicated by crude protein (CP) content per unit of dry matter.

The east and central group extends from central Sudan south and east into Eritrea, Ethiopia, Kenya, Somalia and parts of Uganda, Tanzania, Rwanda and Burundi. East African systems are more diverse, ranging from arid to semi-arid (LGA) to subhumid (LGT), with some bimodal rainfall, and some LGH systems at altitudes above 1000 masl. The east and central groups further differ from the western group in having: (i) longer growing periods (60–90 days and sometimes 90–120 days); (ii) colder minimum temperatures; (iii) higher CP content in native pastures; (iv) more competition with wildlife; and (v) because of (i), more diverse mobility patterns and more diverse human ecology (Homewood, 2008; Blench, 1999).

Systematic area data exist for 1991–1993 (Fig. 15.1; Seré and Steinfeld, 1996), for 1990–2000 (Kruska *et al.*, 2003) and for 2000–2010 (Robinson *et al.*, 2011). The data in Fig. 15.1 for 1991–1993 are adapted from Seré and Steinfeld (1996) as the nearest global benchmark for the ILCA studies that began in the late 1970s. Ruminant systems on grasslands (LGA, LGH and LGT) covered about 1463 million ha, of which 25% was in Latin America and the Caribbean, 40% in sub-Saharan Africa, 27% in Asia, and 8% in West Asia and North Africa. The largest single grassland was LGA in sub-Saharan Africa, covering some 392 million ha, which comprised 27% of the world's grasslands and 67% of sub-Saharan African grasslands. The grassland systems in Latin America and the Caribbean are in the humid and subhumid climates, while those in Central Asia, China, Mongolia and Russia are in the cold and arid climates. Shares of the global totals of ruminant livestock in agroecologies classified as 'grasslands' are (Table 15.1): Latin America and the Caribbean, 55%; sub-Saharan Africa, 33%; Asia, 12%; and West Asia and North Africa, less than 1%. The respective population shares are Latin America and the Caribbean, 22%; sub-Saharan Africa, 28%; Asia, 24%; and West Asia and North Africa, 6%. Animal density – animals per hectare or animals per human population – is highest for the three grassland systems in Latin America and the Caribbean and next highest in sub-Saharan Africa. Reid *et al.* (2005) reviewed 40 years of research on extensive systems in East African grasslands.

LGA is defined as livestock only. The grazing areas and animal numbers of the most arid
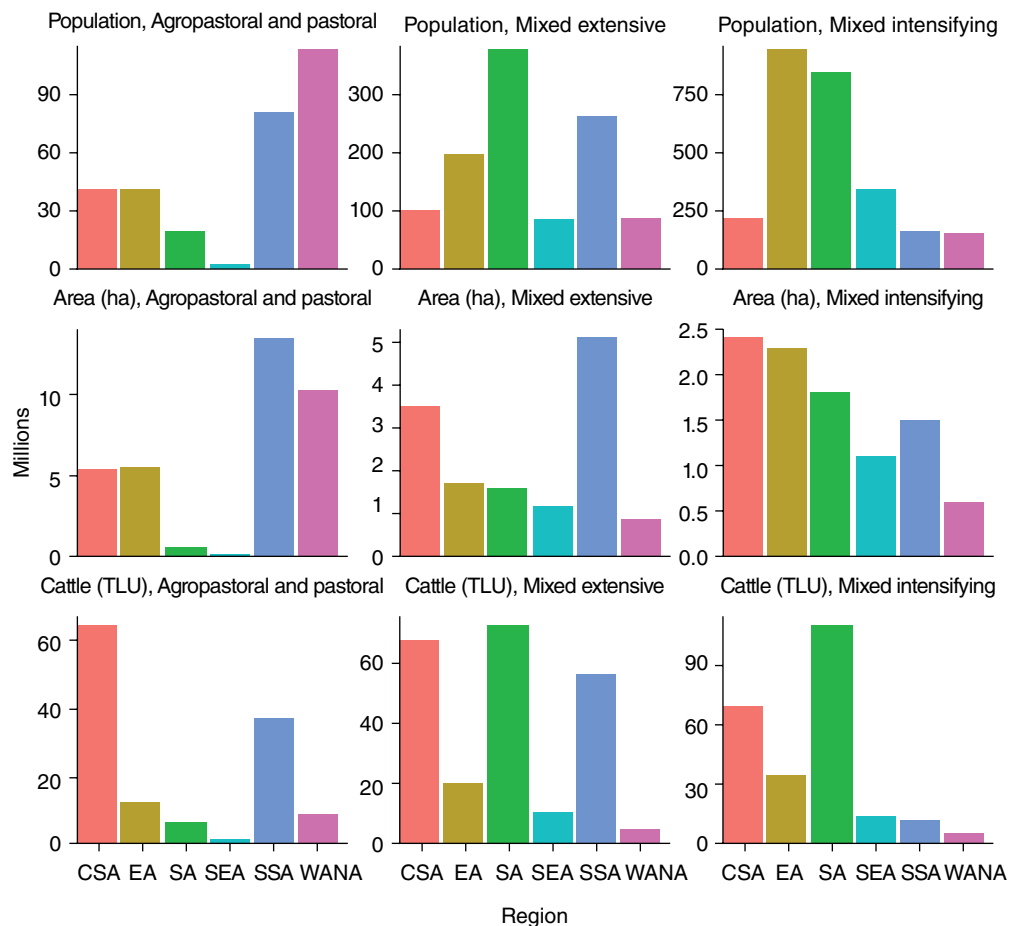
Fig. 15.1. Characteristics of global livestock systems by region, 1991–1993. CSA, central and southern Africa; EA, East Africa; SA, South Africa; SEA, South-east Asia; SSA, sub-Saharan Africa; WANA, West Asia and North Africa. (Data from Robinson *et al.*, 2011, p. 48.)

system are by far the highest in sub-Saharan Africa. These facts indicate that sub-Saharan Africa's most important growth potential in terms of animal numbers is also its highest cost area in terms of grazing land used per animal unit. LGA types are typically in the arid and semi-arid (Köppen climate *BSh*). They are generally hot with a single rainy season and with no month having a minimum temperature below 0°C. The LGA system (390 million ha in sub-Saharan Africa) covered some 27% of global grazing and some 53% of sub-Saharan Africa grazing. The great majority of African production in LGA systems is nomadic herding with milk as the subsistence good. Population density is low, typically

less than 25 persons/km²; ruminant stocking rates were generally from 5 to 20 ha per animal.

Mixed farming by smallholders

Ruthenberg's fourth mode of tropical livestock production – mixed farming by smallholders – has always been the focus of international agricultural research in sub-Saharan Africa. Such modes blend crop and livestock activities. Animals eat crop residues and provide draught power, dairy products, meat and manure. Animal mobility is restricted to seasonal grazing with some transhumance as part of animal tenure relationships between crop farmers and pastoralists.

MIXED SYSTEMS. We use 'mixed systems' from the classification of Seré and Steinfeld, 1996)[14]. This classification defines mixed systems as those in which '…livestock contribute more than 10 per cent to total farm output in value terms or where intermediate contributions such as animal traction or manure represent more than 10 per cent of the total value of purchased inputs'. 'Mixed systems' comprise the rain-fed types – mixed/ rain-fed/arid and semi-arid (MRA), mixed/rain-fed/ humid and subhumid (MRH) or mixed/rain-fed/ temperate and tropical (MRT) – and the irrigated types – mixed/irrigated/arid and semi-arid (MIA), mixed/irrigated/humid and subhumid (MIH) and mixed/irrigated/temperate and tropical (MIT).

The mixed-farming types[15] – MRA, MRT, MRH and some MIA– formed the majority of rain-fed cropped area and income in sub-Saharan Africa in the mid-1970s. These shares grew after the mid-1970s with the expansion of animal traction in much of West Africa and in parts of East Africa. MRA and MRH systems represented some 121.9 million poor rural livestock keepers in sub-Saharan Africa in 2000 or three-quarters of the total of all poor rural livestock keepers (Robinson *et al.*, 2011, pp. 145–152)[16].

The mixed systems are characteristically more diverse in enterprise and spatial patterns than the pastoral types[17].

African mixed-farming systems[18] differed from pastoralism in the following aspects:

- Most land use, income and employment were from cropping.
- Crop residues displaced pastures as the main feed.
- The shares of animal products in food consumption were less than among pastoralists.
- Animal mobility was limited to seasonal transhumance or to daily movements near permanent villages. In the Latin American systems, with private and fenced grazing, there would be no seasonal or annual mobility.
- The functions of livestock were more diverse. They included recycling soil nutrients and using draught animals for cultivation. These functions of animals were less important or even absent in Latin America where mineral fertilizers replaced manure and tractor mechanization replaced animal power.
- There were important shares in income and employment of annual and semi-perennial

cash crop – cotton, groundnut, rice and other cereals, roots and tubers – that did not exist in rangelands. In the Latin American and Middle Eastern mixed systems, animals were the cash commodity.
- Important shares in income and employment of perennial cash crops – coffee, tea, cocoa, rubber and oil palm – were found in mixed systems with poultry, swine and small ruminants, although much less often with cattle.
- There was smallholder commercial dairying with zero grazing, planted forages, purchased feeds, and cultivation of annual and perennial crops on the same farm.
- There was a more unequal distribution of cattle among households, although this was compensated to some degree by more equal distribution of small ruminants.
- There was commercial on-farm fattening of ruminants, swine or poultry, in zero-grazing or transhumant systems, using purchased feeds and crop residues from annual and perennial crops.

Trends in African Agricultural Systems

In this section, we discuss the trends in African agricultural production systems in a sample of countries where livestock production is prominent and where ILRI has had a significant research presence.

Human populations

Data on the distribution of African populations across agricultural systems have long been patchy. The information compiled by Jahnke (1982), as presented in the Introduction to this volume, show that perhaps 238 million rural people lived in sub-Saharan Africa in the mid-1970s in all five agroecological zones. Of that mid-1970s total, nearly 40% lived in the arid and semi-arid zones that were the initial focus of ILCA. The focus of ILRAD's work can be mapped largely to the humid and sub-humid agroecological zones given that trypanosomiasis and *Theileria* are more present there.

The more detailed estimates of Seré and Steinfeld (1996) for nine livestock production systems gave a 1991–1993 average of some

519 million people who depended on those systems. The latter estimated human populations as: (i) a total of 173 million people in the grassland systems, constituting about one-third of the sub-Saharan African population and implying a population density of approximately 30 persons/km² on grazing plus arable lands; and (ii) a total of 346 million in the mixed rain-fed and irrigated systems, implying a population density of approximately 140 persons/km² on grazing plus arable lands. Of this 1991–1993 total, about one-third lived in the LGA/LGT/LGH production systems, which is not greatly different from Jahnke's estimated share of the rural population living in the arid and semi-arid agro-ecological zones.

Robinson *et al.* (2011, p. 48) described four broad classes of livestock systems from vintage 2000 data: (i) agro-pastoral and pastoral, corresponding to the grassland systems LGA, LGH, LGT; (ii) 'mixed extensive' systems, corresponding to MRA, MRH, MRT, MIA, MIH and MIT; (iii) 'mixed intensifying' systems as those parts of MRA, MRH, MRT, MIA, MIH and MIT with higher production potential and better market access; and (iv) 'others', which were mainly urban and areas having less than '10 percent of the total land area covered by crops' (Robinson *et al.*, 2011, p. 46), as shown globally in Fig. 15.1. Sub-Saharan Africa is dominated by agro-pastoral and pastoral systems, and most of the original work of ILCA and ILRAD focused there (Fig. 15.2).
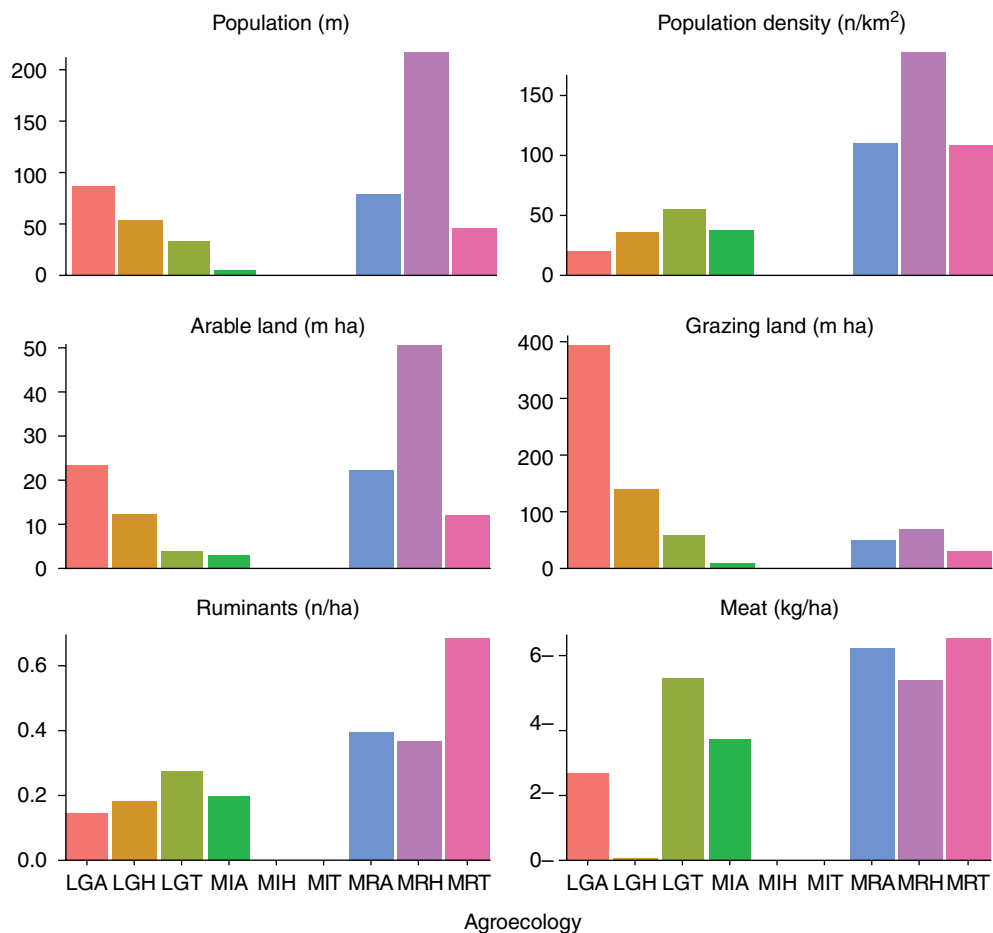
Fig. 15.2. Characteristics of sub-Saharan Africa livestock systems by agroecology, 1991–1993. (Data from Seré and Steinfeld, 1996.)

Livestock production

We know generally that the evolution of Africa livestock systems after the colonial era has been determined by: (i) rainfall and its effects on pasture and crop growth, as the latter is a partial determinant of fodder availability for ruminants; (ii) control of human and animal diseases; (iii) the growth of human populations and income and the resulting demand for agricultural products; and (iv) the expansion of cropland. These factors have been compounded by exogenous changes in farming methods, the introduction of arable and permanent cash crops, and the development of irrigated farming (e.g. Inner Delta of the Niger River in Mali, the Awash Valley in Ethiopia, the Niger–Benue confluence in Nigeria, the Senegal River Valley and along the other major river basins of sub-Saharan Africa).

Evidence about stock holdings – numbers, species, breeds, productivity and locations – is important for understanding the development impact of livestock research. Data on African livestock numbers and productivity vary erratically over time, agroecological zone, country, season and mode of production. Estimates of animal numbers are particularly unreliable because of systematic undercounting. It is generally impossible to relate stock numbers or their productivity to inputs of research, infrastructure or policy. With these warnings, the following summarizes information over the period 1970–2016 for aggregate information from sub-Saharan Africa on livestock production, stocks of ruminants and the species composition of ruminant numbers.

We defined a productivity measure as growth of the FAO livestock production index, in rural per capita terms, for the East and southern Africa (Fig. 15.3a) for the period 1970–2016. The total index grew at an annual rate of about 1.9% from 1970 to 2016; a related index, normalized by rural population, grew at an annual rate of 2% in those countries. The corresponding values for ten countries in West and Central Africa (Fig.15.3b) were 2.8% and 0.7% for the same period. In sum, the great majority of livestock production growth in sub-Saharan Africa for nearly 50 years is closely associated with population growth in 23 countries. The principal direct research/development influence would have been through the eradication of rinderpest, which was achieved early in the 21st century.

A measure of ruminant stock numbers is the tropical livestock unit (TLU)[19]. Figure 15.4 expresses 'TLU density' as the ratio of ruminant TLU to arable land. Growth in TLU numbers accelerated sharply in East and southern Africa and in West and Central Africa around the mid-1990s. This 'area-weighted TLU density' grew at an annual rate of 0.6% in East and southern Africa[20] during the period 1970–1994, at a rate of 2.0% for 1995–2016 and at 1% for the entire period of 1970–2016 (Fig.15.2a).

The estimated TLU density grew at an annual rate of 1.2% in West and Central Africa during the period 1970–1994 and at 3.6% for 1995–2016. Over the period of 1970–2016, TLU density in West and Central Africa rose at an annual rate of 2.3%.

Changes in species mix

One factor affecting the relevance and impact of research is long-term changes in ruminant species mix. This mix appeared to have shifted slightly to cattle from sheep and goats from 1970 to 2016 (Fig. 15.5). This continues the trend from 1950 to 1980 as noted earlier by Le Houérou (1989, p. 125). The ratio of cattle TLUs to sheep/goats TLUs was about 6.7 in 1960, about 4.1 in the mid-1980s and about 3.7 in 2009 (FAO/CIRAD, 2013, p. 6). De Haan (2016, p. 25) found similar patterns for stock numbers and species composition in East Africa, excluding Ethiopia, over the period 1960–2011. There was little change in the ratio of sheep and goat numbers to cattle numbers in East and southern Africa (Fig. 15.5a) over the period 1970–2016; this ratio rose modestly in West and Central Africa (Fig. 15.5b), which is possibly related to the rising scarcity of grazing in that subregion. The shift in species from cattle to small ruminants indicates that some opportunity has been lost by not focusing more on diseases specific to small ruminants, such as peste des petits ruminants (see Chapter 7, this volume).

The ILCA systems studies (Ethiopia, Kenya, Mali, Nigeria and Niger) were not conducted over a long enough period to say anything reliable about species mix over time. One exception was an analysis of a mixed sheep and goat flock at Elangata Wuas Group Ranch in Kenya where goats had become more numerous relative to
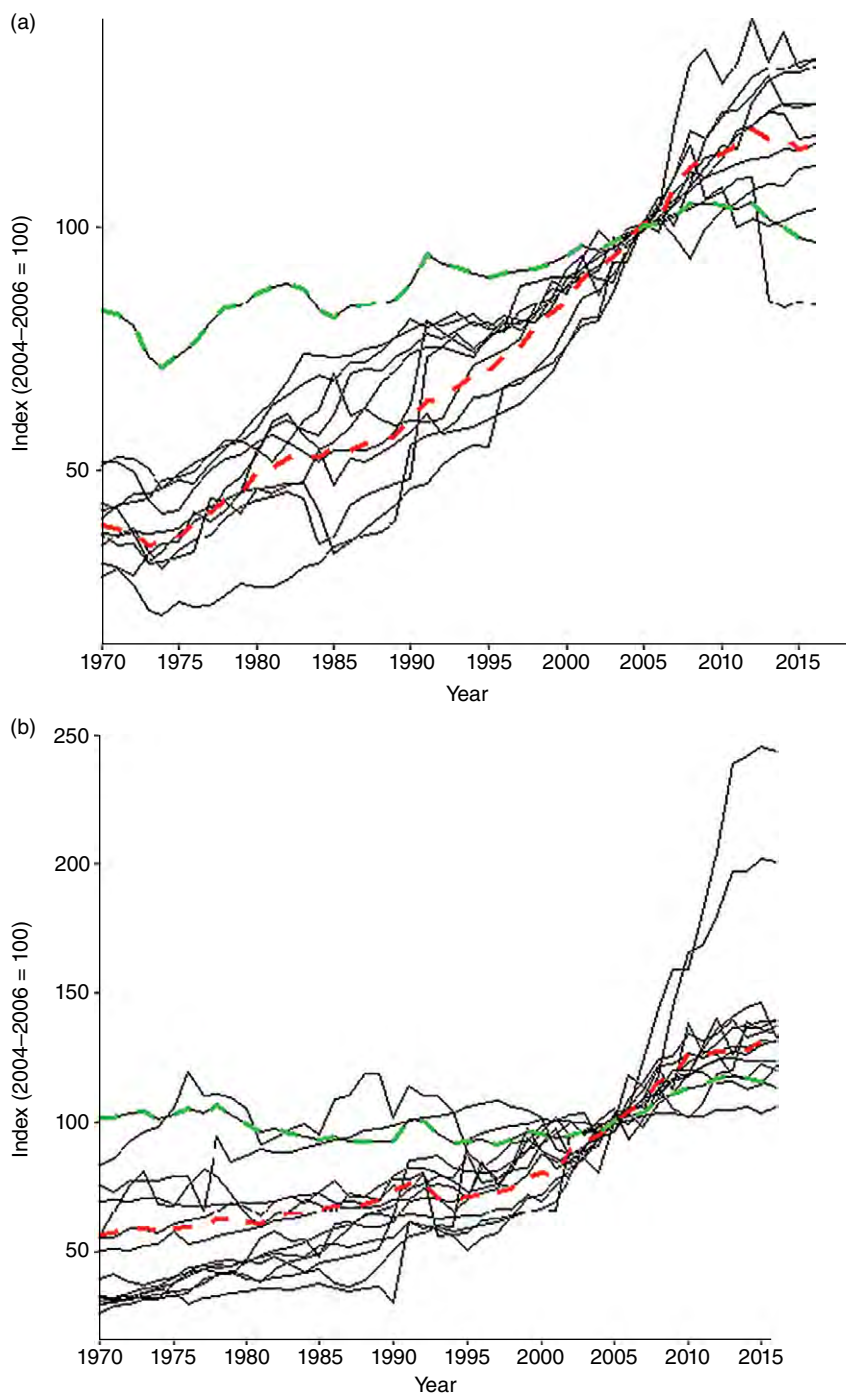
Fig. 15.3. Livestock production index for East and southern Africa (a) and West and Central Africa (b), 1970–2016. Black lines, selected countries; red dashed line, regional trend; green dashed line, regional trend per capita terms estimated by $\ln(Y) = 0.3599 + 0.0021 \times$ year (a) or by $\ln(Y) = -9.1269 + 0.0068$ (b). (Data from www.faostat.org; accessed 30 April 2020.)
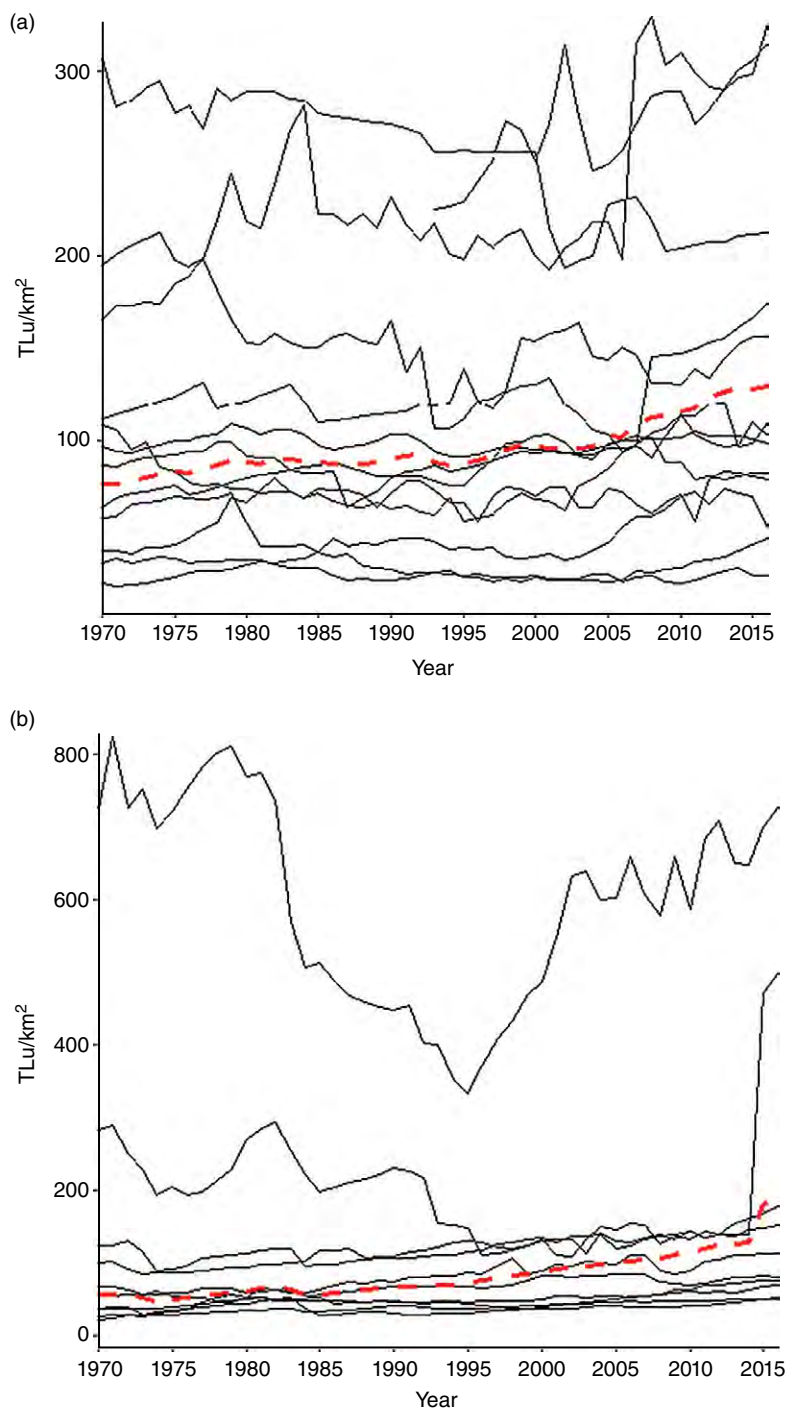
Fig. 15.4. TLU density for East and southern Africa (a) and West and Central Africa (b), 1970–2016. Black lines, selected countries; red dashed line, regional trend estimated by $\ln(Y) = -14.7 + 0.0097 \times$ year (a) or by $\ln(Y) = -42.1 + 0.0233 \times$ year (b). (Data from www.faostat.org; accessed 30 April 2020).
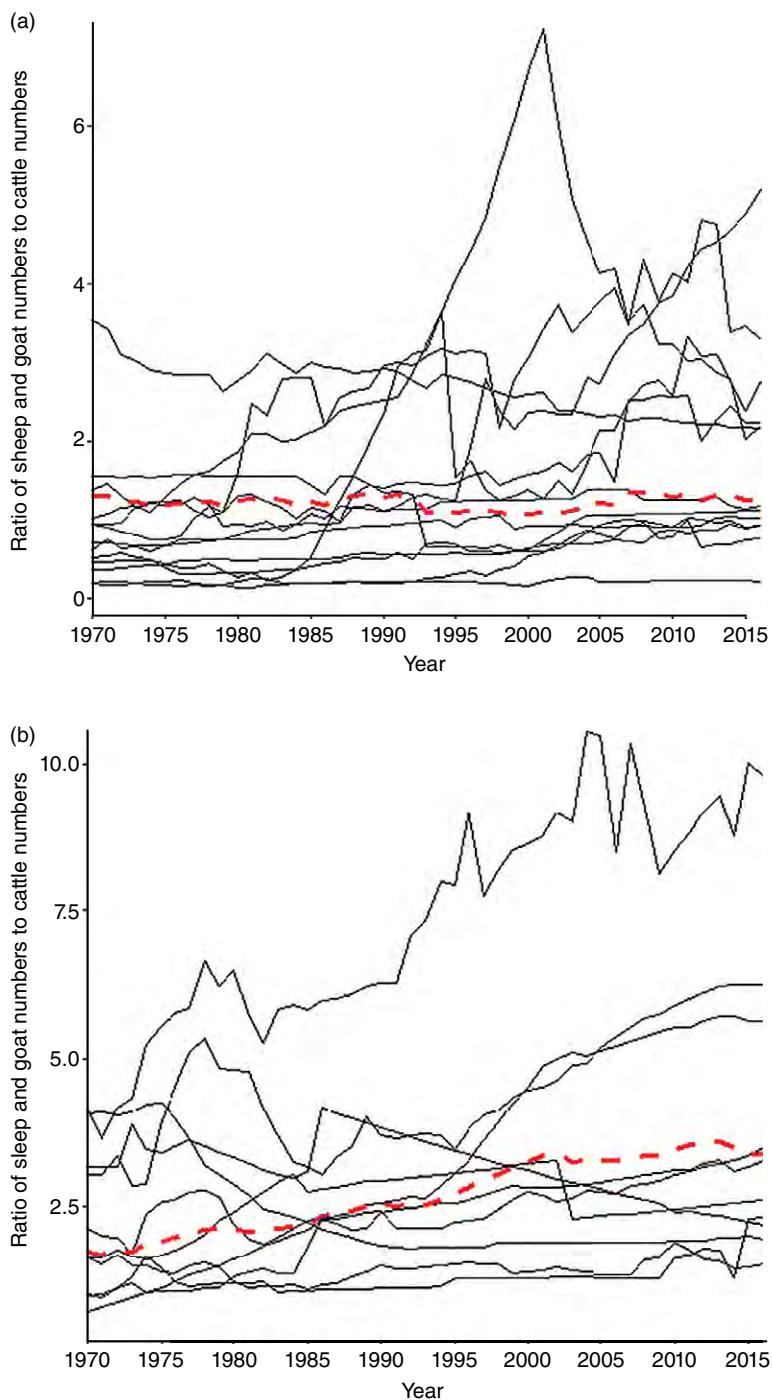
Fig. 15.5. Sheep and goat numbers relative to cattle numbers for East and southern Africa (a) and West and Central Africa (b), 1970–2016. Black lines, selected countries; red dashed line, regional trend estimated by $\ln(Y) = 0.1 + 0.0001 \times year$ (a) or $\ln(Y) = -33.2 + 0.0171 \times year$ (b). (Data from www.faostat.org; accessed 30 April 2020.)

sheep between 1978 and 1986 (Wilson and Maki, 1989). Coppock (1994, pp. 169–170) found that short-term droughts in Borana affected cattle numbers more adversely than small-ruminant numbers.

One aspect of species composition is the use of animals, mainly oxen, for power. Indeed, animal traction research was an important part of ILCA research until the 1990s. Systematic and comprehensive information on draught animals is unavailable in sub-Saharan Africa. We do know that animal traction has expanded widely in this area from a very low base of use, while tractor mechanization has displaced animal and human power in the other dryland and subhumid regions of the world, although lack of data make it impossible to estimate changes in stocks of TLUs according to the use of animals for power.

Land use, fertilizer use and cereal yields

Evidence about land holdings and rural population shows rising land pressure throughout sub-Saharan Africa. The stock of arable land per rural population fell continuously over the long period of 1970–2016. In East and southern Africa, there was about 0.3 ha of arable land per capita in 1970 and this had fallen to about 0.2 by 2016 (Fig. 15.6a); the annual rate of decline is estimated to have been –1.1%. In West and Central Africa, there was about 0.7 ha of arable land per capita in 1970 and this had fallen to about 0.3 by 2016 (Fig. 15.6b); the annual rate of decline is estimated to have been about –1.4%. The amount of arable land per rural population began to fall less sharply after the mid-1990s, reflecting the broad deceleration of population growth across Africa.

Evidence about fertilizer use and cereal yields suggests a modest intensification of farming systems in response to land pressure. National data on fertilizer use (Fig. 15.7) are not available before 2002. In both subregions, there had been a modest increase in fertilizer use per hectare to 2016, although levels in Africa remain much lower than in southern Asia or in Latin America. National data on fertilizer use for West and Central Africa are no more comprehensive than for East and southern Africa. The average rate in West and Central Africa was

12 kg/ha in 2001–2005 and had risen to about 17 kg/ha in 2011–2016 (Fig.15.7b).

The regional mean cereal yield in East and southern Africa was about 1.1 t/ha in 1970–1975 and had risen to 1.9 t/ha in 2011–2016 (Fig. 15.8a); the estimated average rate of growth for East and southern Africa was 0.9% from 1970 to 2016. The West and Central Africa mean was 0.6 t/ha in 1970 and had risen to roughly 1.4 t/ha by 2016 (Fig. 15.8b); the estimated average rate of growth for the ten West and Central Africa nations was 1.3% from 1970 to 2016, so this subregion's levels and growth rates lag behind those of southern Asia and of Latin America. The mean cereal yield in West and Central Africa was about 0.7 t/ha in 1970 and had risen to 1.4 t/ha by 2016 (Fig. 15.8b). The index of labour productivity in cereals therefore fell systematically over the long period of 1970–2016; it had been roughly 0.45 t per capita in the 1970s and fell to an average of 0.38 in the period 2010–2016.

There was some small improvement in an index of food production in East and southern Africa and in West and Central Africa over the period of 1970–2016. Food production per rural inhabitant among the 13 East and southern African nations (Fig. 15.9a) rose at an average annual rate of 1.4% from 1970 to 1994; it rose at a rate of 3.1% from 1995 to 2016. The corresponding values for West and Central Africa (Fig. 15.9b) were 0.5% and 1.7%.

The aggregate evidence, with all the qualifications about potential internal errors, shows the following: (i) 23 countries in sub-Saharan Africa have much less land per capita than they had 40–50 years ago; (ii) these countries have increased cereal yields at a rate close to that of rural population growth, indicating that rural labour productivity in the major crop group has barely grown; (iii) livestock productivity has similarly increased at an annual rate roughly equal to that of population growth; (iv) most of the gains in livestock productivity are due to more animals per unit of land, not to more productivity per animal; (v) there have been modest gains in fertilizer use per unit of land and sub-Saharan Africa still lags regions of the world where agriculture has grown more quickly; and (vi) there have been modest gains in food production per capita in the two principal sub-regions.
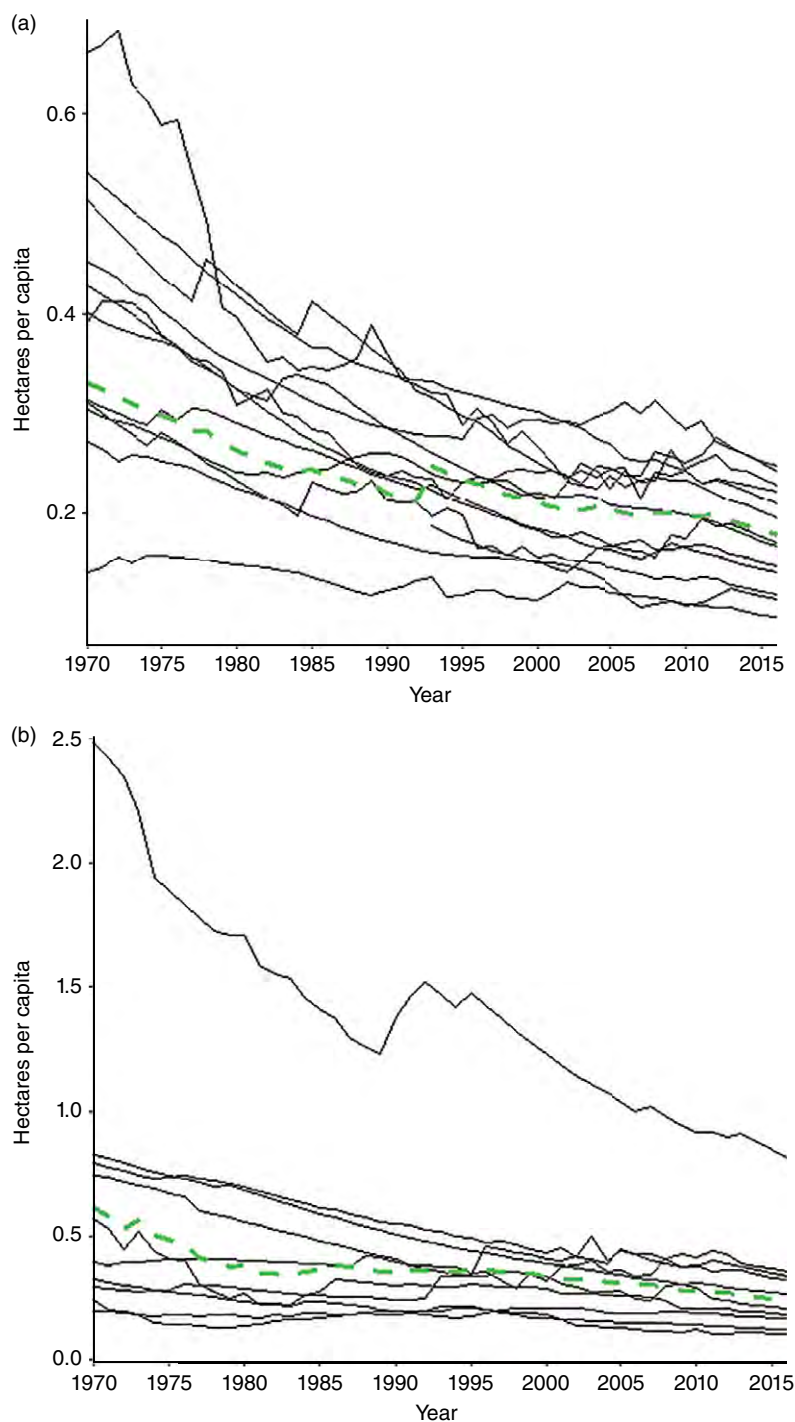
Fig. 15.6. Arable land per capita for East and southern Africa (a) and West and Central Africa (b), 1970–2016. Black lines, selected countries; green dashed line in per capita terms, regional trend estimated by ln(Y) = 21.4 − 0.0115 × year (a) or ln(Y) = 27.5 − 0.0143 × year. (Data from www.faostat. org; accessed 30 April 2020.)
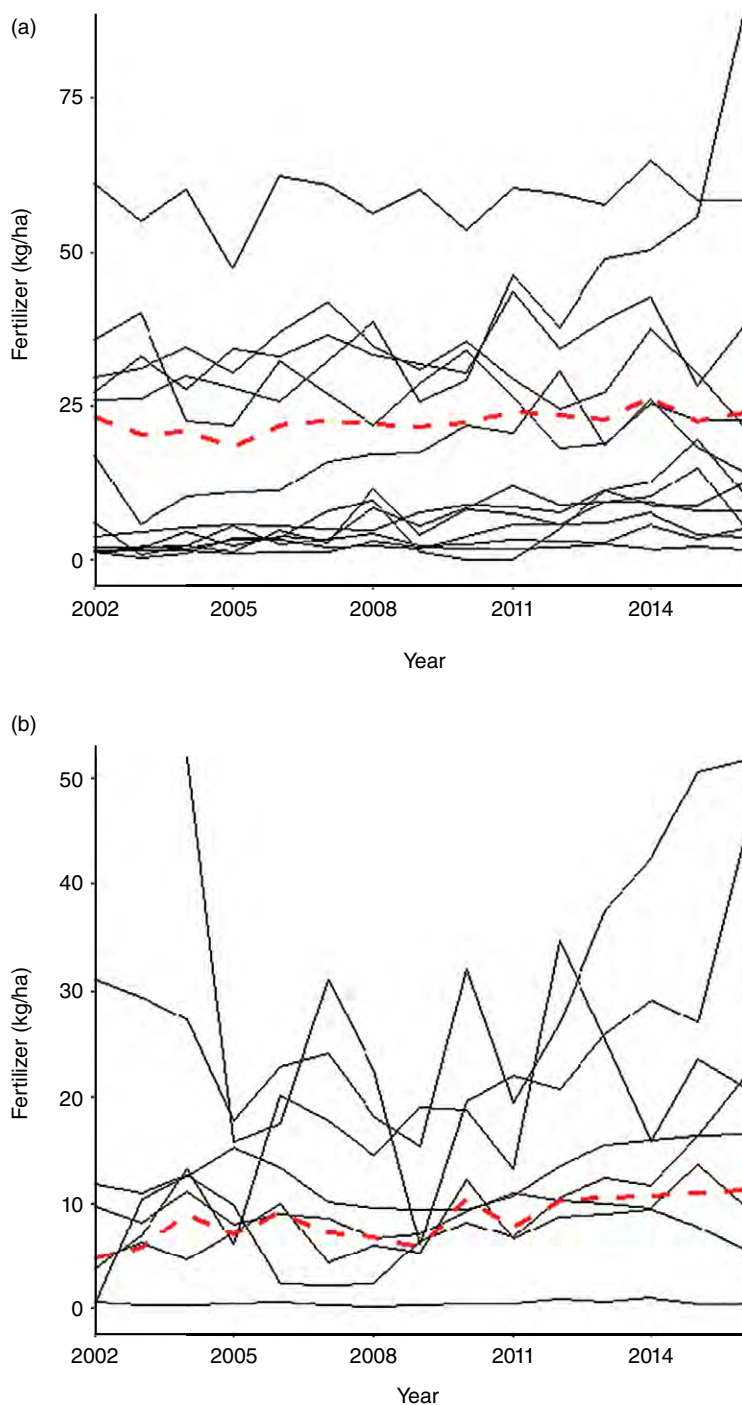
Fig. 15.7. Fertilizer use per hectare for East and southern Africa (a) and West and Central Africa (b), 2002–2016. Black lines, selected countries; red dashed line, regional trend estimated by $\ln(Y) = -19.4 + 0.0112 \times \text{year}$ (a) or $\ln(Y) = -93.8 + 0.0478 \times \text{year}$ (b). (Data from www.faostat.org; accessed 30 April 2020.)
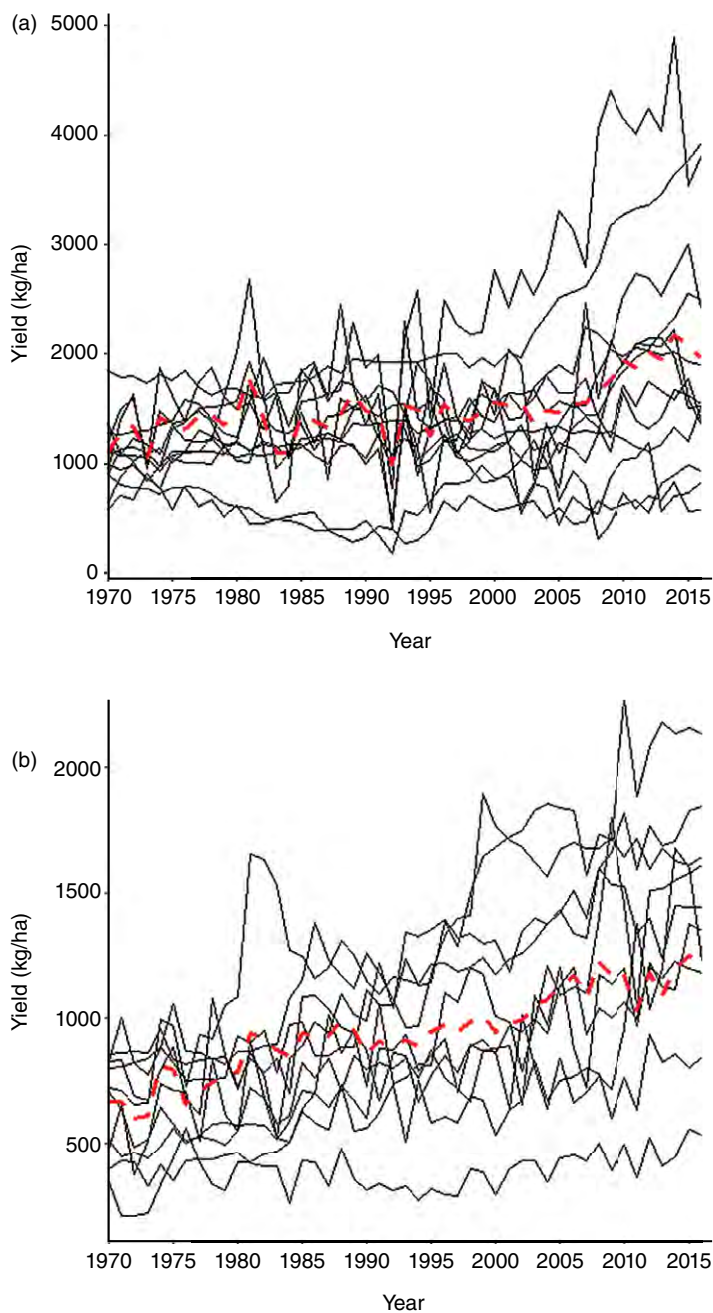
Fig. 15.8. Cereal yields per hectare for East and southern Africa (a) and West and Central Africa (b), 1970–2016. Black lines, selected countries; red dashed line, regional trend estimated by ln(Y) = −10.9 + 0.0091 × year (a) or ln(Y) = −18.6 + 0.0127 × year (b). (Data from www.faostat.org; accessed 30 April 2020.)

(a)

(b)
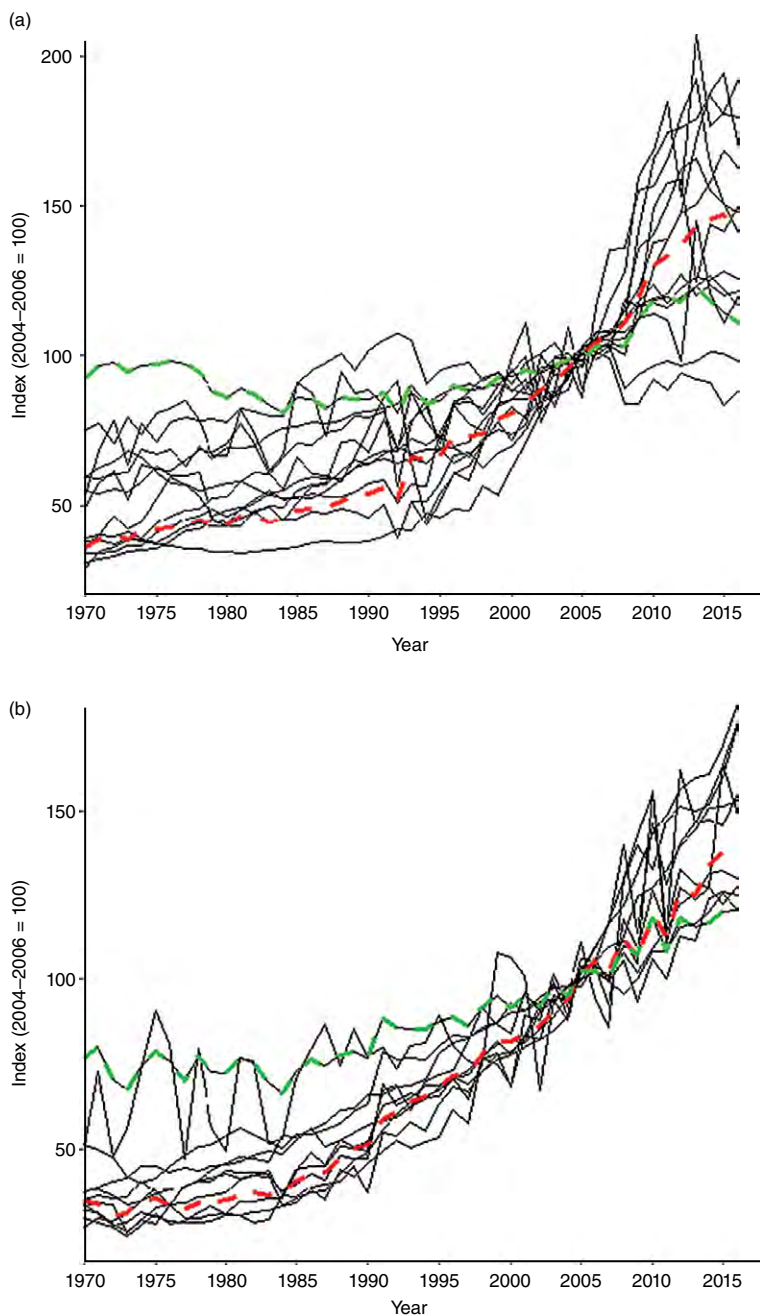
Fig. 15.9. Food production index for East and southern Africa (a) and West and Central Africa (b), 1970–2016. Black lines, selected countries; red dashed line, regional trend estimated by $\ln(Y) = -59.3 + 0.0319 \times$ year (a) or $\ln(Y) = -68.6 + 0.0365 \times$ year (b); green dashed line, regional trend in per capita terms estimated by $\ln(Y) = -5.6 + 0.0051 \times$ year (a) or $\ln(Y) = -19.2 + 0.0119 \times$ year (b). (Data from www.faostat.org; accessed 30 April 2020.)

Inequality of livestock holdings

Inequality of livestock holdings would determine to some extent the distribution of benefits from research across households within given agro-ecologies. The African field studies carried out by ILCA and later ILRI all showed substantial inequality among farm units in livestock holdings, indicating that research would benefit fewer households than in a more even distribution of animals across production units. Inequalities in ownership of cattle were high within and between Malian survey villages, as were those in ownership of small ruminants (Wilson, 1986, p. 23). High degrees of inequality in stock holdings were found in the Borana study led by Coppock (1994, Table D1). In the Maasailand study of Solomon Bekure *et al.* (1991, p. 84), 29% of households in three group ranches owned 57% of cattle in the sample while 24% of sample households owned only 4% of the cattle. Hiernaux and Ayantunde (2004, pp. 35–27) found significant differences in land and animal holdings per adult household member in a sample of 492 households in western Niger studied in the 1990s and in the early part of this century.

A comparison of global data from 12 countries[21] confirmed the general finding of livestock holding inequality across households. With household samples divided into expenditure quintiles, measured by the presence or absence of animals and by TLUs per household, the comparison showed that about 65% of rural households in all expenditure groups had livestock (1.9 TLUs on average across countries and expenditure quintiles); about 68% in the lowest expenditure quintile had livestock (1.4 TLUs on average), while 58% in the highest expenditure quintile had livestock (3.3 TLUs on average). Surveys of pastoralists from 2003 to 2011 in 11 sub-Saharan African nations showed a median Gini coefficient of 0.673 on TLU holdings (de Haan, 2016, p. 238). The older evidence is not directly comparable to the more recent data from the 11 countries and hence we cannot say if concentration of ownership has changed in recent years[22].

Climate to 2000

The ILCA systems studies in West Africa, beginning in the 1970s, took place at a time of rising temperatures and drier growing conditions. Global atmospheric studies (Hulme *et al.*, 2001) showed African temperatures to have risen from the mid-1970s to 2000. The most regular increases occurred in the northern hemisphere rainy (June–August) and post-rainy (September–November) months. There was less pronounced annual warming in East Africa and even a cooler period in the Borana and Turkana ranges. The mid-1970s to 2000 tended to be drier than the previous 75 years in the Sahel (about 25%); there was a mix of wetter and drier trends in East Africa, with more extremely wet years.

Vegetation trends in the Sahel, despite the apparent warming and drying, tended to show recovery from earlier drought cycles. Herrmann *et al.* (2005) contended that land degradation in the Sahel, caused by drought, had been partly reversed by conservation efforts. The effects of climate on sub-Saharan agricultural production, on the whole, were mixed in the final 30 years of the previous century and no continental generalization can be made about climate as a determinant of research success/failure in that context.

Poverty

Poverty was not a theme of ILCA/ILRAD/ILRI research before the mid-1990s and the words 'poor' or 'poverty' as keywords in published work rarely appear before 2000. There was some analysis of wealth disparities in Maasailand in the 1980s by King *et al.* (1984) and Grandin (1988) but no systematic or even sporadic effort to relate ILRI's work to poverty in Africa, or anywhere else, before the work of Thornton *et al.* (2002) and that of Perry *et al.* (2002).

There were no reliable estimates of rural poverty in sub-Saharan Africa before those of Thornton *et al.* (2002). Robinson *et al.* (2011) estimated that LGA, LGH and LGT represented some 29.8 million poor livestock keepers in sub-Saharan Africa, or about 18% of poor rural people. The dry (LGA, MRA and MIA) areas were about 45% of poor livestock keepers in sub-Saharan Africa. The most recent compilation (de Haan, 2016) confirms the historical pattern of higher poverty among animal keepers in the drier climates of sub-Saharan Africa, suggesting that little relative progress has been made in

those areas. While there was no poverty focus, as such, of ILCA/ILRAD work until this century, the choice of agroecologies for the original systems studies imposed such a focus on research at those sites.

Livestock Systems Research

Research impacts on livestock

Evaluations of the impact of LSR in sub-Saharan Africa confront difficult empirical problems of context, measurement and attribution. The availability of baseline estimates for other regions and production systems is limited. Published estimates of the impact of research on long-term productivity changes in livestock are uncommon globally and rare in Africa. A global review of returns to agricultural research in crops, livestock, fisheries and forestry found a livestock focus in 14.4% of a sample of 292 papers, which included a total of 1886 estimates. The great majority of papers were from the USA, Latin America and the Caribbean (Alston *et al.*, 2000), not from sub-Saharan Africa. The authors found livestock research – including 'beef, swine, poultry, sheep or goats, all livestock, dairy, other livestock, pasture, and "dairy and beef"' – to have a positive but highly variable, rate of return. A sample of 233 estimates gave a mean internal rate of return (IRR) of 120.7%, with a coefficient of variation of 4.0, a mode of 14.0 and a median of 53.0 (Alston *et al.*, 2000, p. 58). A meta-regression across research programmes (crops, animals and natural resources) with rate of return as the dependent variable had a livestock research coefficient of 12.1% ($p < 0.90$); field crops had a marginal return of 25.1% ($p > 0.99$) and natural resources research (fisheries and forestry) had a negative return of 94.5% ($p > 0.99$).

Other international comparisons of research effects on livestock productivity do not allow firm generalizations. Evenson and Rosegrant (2003) reviewed published studies of research productivity from US, Brazilian and Indian agriculture. They estimated that annual total factor productivity (TFP) growth in US livestock production was 0.55 from 1950 to 1982, of which 9% was due to public research, 17% to extension and 54% to private research and development.

They estimated that annual TFP growth in Brazilian livestock (1970–1985) was only 0.09, of which 55% was due to public research and 40% to other, unidentified, factors. They made no estimates for livestock in India, although their estimates of TFP growth in crops were from 1.27 (1956–1965) to 1.14 (1977–1989) and had public research shares of 22% and 45%, respectively. Hazell (2008) found no post-Green Revolution research impact on livestock productivity in South Asia. He mentioned the substantial expenditures of the Indian national programme (Hazell, 2008, pp. 5 and 16) but did not analyse their productivity effects.

Alene (2010) calculated an annual rate of growth in TFP, for crops and livestock, of 1.8%[23] across sub-Saharan Africa for 1970–2004 and a slightly faster rate of 2.1% from 1991–2004, possibly reflecting better weather or economic reforms. He estimated an elasticity of TFP with respect to research and development expenditures of 0.10–0.22, depending on the statistical model used. One specific estimate of research impact on African livestock productivity is that of Thirtle *et al.* (1998) for South Africa, which found rates of return ranging from 11% to 16% for livestock, pasture and range improvements, and returns to animal health research exceeding 36%. The estimates from South Africa were made for that country's national programme and hence include research failures as well as successes.

We will discuss mainly African systems with some reference to other regions whose studies are relevant to sub-Saharan Africa, given that most international livestock research has been in sub-Saharan Africa (Table 15.1). We focus first on grazing systems (LGA, LGT and LGH), of both nomadic and seasonally transhumant types[24], and later on mixed farming, both dryland (MRA, MRT and MRH) and dryland/irrigated (MIA, MIT and MIH), where crops and livestock interact[25].

The development problem of pastoralism

The initial studies of pastoral and agro-pastoral systems confronted a 'mainstream view'[26] which informed official and scientific opinions about

Table 15.1. Selected pastoral systems studies, various years.

Study	Region/period	Country/ sub-region/area	Climate	Population density at outset (n/km²)	Farming systems	Scales of research	Species	Livestock density	Cultivation intensity	Proposed technologies
Dyson-Hudson (1966)	East Africa, 1966	Uganda/ Karamoja	*Aw*, *BSh*	<20	Subhumid pastoral	Regional territory	Cattle	Variable, typically low	Very low	Not mentioned
Monod (1975)	1950s–1970s	North Africa and rangelands of sub-Saharan Africa	Arid	Variable	Arid grazing	Saharan, Sahel	Camels, cattle, goats	Variable	Very low	Not highlighted in book
ILCA (1975)	1960s–1975	Sub-Saharan Africa	Arid, semi-arid, *BWh*, *BSh*	Variable across continent	Arid grazing, arid cropping	Arid and semi-arid sub-Saharan Africa	Cattle, goats, sheep, camels	Varied across continent	Not studied	Grazing management
Dahl and Hjort (1976)	East Africa, 1976	East Africa, Somalia	Arid, semi-arid, *BWh*, *BSh*	<20	Arid grazing, limited cropping	Semi-arid and subhumid East Africa	Cattle, goats, sheep, camels	Very low	Not studied	Herd management, milk offtake
Fricke (1979)	Nigeria, 1960s and 1970s	Nigeria	Semi-arid, subhumid	Variable from 20 to 250	LGA, LGT, MRA, MRT		Cattle			Herd management, animal health, pasture production
Jahnke (1982)	Sub-Saharan Africa, 1970s	Sub-Saharan Africa	Arid to humid	Variable	LGA, LGH, LGT, MRA, MRH MRT	Nation, territory, farm	Ruminants	Variable	Variable	
Sandford (1983a)	1960s–1970s	Global tropics	Many, mainly arid and semi-arid	Variable; not highlighted in book	LGA, LGH, LGT	Territory	Cattle, camels, goats	Variable, typically low	Zero to low	Herd management, water development, secure land rights

de Leeuw and Milligan (1984)	Sub-Saharan Africa, 1984	Ethiopia, Mali, Niger, Nigeria	Arid, semi-arid	>100 in Ethiopia; <25 in Mali and Niger; variable in Nigeria	LGA, LGH, MRA, MRH	Territory, aerial survey	Ruminants	13–31 ha/TLU in Niger	Low to medium	Integration of remote sensing and field verification methods for animal and land-use surveys
Wilson (1986)	West Africa, 1980s	Mali	*B*		LGA, LGH, MRA, MRH, MIA, MIH	5000 km² (Niono only)	Ruminants			Grazing management, health, forage production, water
von Kaufmann *et al.* (1986)	West Africa, 1979–1986	Central Nigeria; Abet, Ganawuri, Kurmin Biri; study area of 11,225 km²	Subhumid (*Aw*); area of 455,000 km²	Kurmin Biri: 4–12; Abet: 70; Ganawuri: 85; surveys 1979–1984	Pastoral (grazing reserve); mixed farming with cattle; largely sedentary; some nomadism	2500 km²; no. of animals studied as % of *n* animals in the study zone; 2475 km²	Cattle, goats, sheep, camels	Abet: wet season, ~25; dry, ~40; Kurmin Biri: wet, 5; dry, ~10–18; Ganawuri: wet, NA; dry, ~20–25	Abet: ~25; Kurmin Biri: 5–15; Ganawuri: ~30–40	Grazing reserves, sown forages, manure management, crop residue management
Ellis and Swift (1988)	East Africa, late 1970s–early1980s	Northern Kenya/Turkana	Arid, semi-arid; 200–600 mm annual rainfall; LGP 60–90 days	Not stated	LGA	9000 km² territory	Cattle, camels, goats, sheep	Low, highly variable	Zero to very low	Grazing dynamics, grazing management
Le Houérou (1989)	Grazing lands of the Sahel		Arid, semi-arid	Variable	LGA, LGH	West African Sahel	Cattle, sheep, goats, camels	~5–20 TLUs/km²	Low	Grazing management, pasture production, water development
Solomon Bekure *et al.* (1991)	East Africa, 1980–1991	Kajiado County, Kenya ('Maasailand')	Semi-arid to subhumid		LGA, LGH		Cattle, goats			Grazing management; group ranches

Continued

Table 15.1. Continued.

Study	Region/period	Country/sub-region/area	Climate	Population density at outset (n/km²)	Farming systems	Scales of research	Species	Livestock density	Cultivation intensity	Proposed technologies
Fratkin *et al.* (1994)	African pastoralist systems				Various sub-Saharan Africa					
(Homewood and Rodgers 2004)	East Africa	Kenya/Maasailand, Tanzania/Serengeti	Mix of *Af*, *Am*, *Aw*, *BWh*, *BSh*, *Cwa*, *Cwb*, Cfib		LGA, LHG	Kenya/Maasailand, Tanzania/Serengeti	Ruminants and wildlife	~5–40 TLUs/km²	Very low	Water management
Behnke *et al.* (1993)	East Africa, 1970s–1980s			Variable, typically <30						
Coppock (1994)	East Africa, 1980–1991	Ethiopia/Borana	Arid to subhumid	<10	LGA, LGT, MRA	16,000 km²; 90,000 people	Cattle, camels, goats, sheep	~20–30 TLUs/km²		Fodder banks, water development, grazing management, social organization
Williams *et al.* (1999)	West Africa, 1990s and 1980s	Niger	Arid, semi-arid	10–100	LGA, MRA		Mainly cattle			Grazing management, social organization, manure, fertilizer, plant varieties
Barbier and Hazell (1999)	Niger, 1990s	Niger	Arid, semi-arid	Variable	LGA, MRA		Mainly cattle	~5–20 TLUs/km²		Livestock transhumance, seasonal labour migration, feed purchases as alternatives to transhumance
Kruska *et al.* (2003)	2003	Global	All agroecologies	Global range	All	Region	Ruminants	Global range		Production models and forecasts; poverty analytics; policy modelling

Reference	Time period	Region	Climate	Number	Production system	Scale	Livestock		Crops	Notes
Devereux (2006)	Early 2000s	Somali region, Ethiopia	*BWh*, *BSh*	Roughly 10–15	Pastoral and agro-pastoral	Region, household	Camels, ruminants	Unknown	Limited, maize, barley, wheat, sorghum	Build processing and marketing facilities, impose international phytosanitary standards, conflict resolution, education, financial services, social safety nets, mixed urbanization, rather than sedentarization
Reid *et al.* (2008a)	Various regions	Many								
Lesororgol (2008)	East Africa, 2000–2005	Northern Kenya, Turkana	Semi-arid		Pastoral and agro-pastoral	Region, household	Camels, ruminants	Unknown	Limited crops	
Homewood (2008)	Sub-Saharan Africa	Kenya, Tanzania	Mix of *Af*, *Am*, *Aw*, *BWh*, *BSh*, *Cwa*, *Cwb*, *Cfb*		Pastoral	Region, household	Ruminants and wildlife	Unknown	Limited crops	Brief review of modelling literature
Hiernaux *et al.* (2009)	West Africa, 1990s	Niger								Grazing management, health, forage production, water
Bollig *et al.* (2013)		Mainly East Africa			Various sub-Saharan Africa					
Catley *et al.* (2013)										
Konczacki (2014)										

the rangelands (Sandford, 1983a, pp. 11–19). This 'mainstream view' held that tropical pastoralism was unproductive, for two reasons. The first reason was the biophysical determinants of animal productivity[27] and the lack of adapted technology and management to raise productivity. This technical pessimism about potential output was attributed to the arid and variable climates[28] in the tropics, which made crop production infeasible without irrigation and which restricted agriculture to extensive stock raising and oasis farming.

Most of the papers in Monod (1975) expressed the 'mainstream view'. Gourou (1966, p. 192), a leading post-war geographer of the tropics, had earlier argued that tropical cattle productivity could converge to that of the temperate zones only under strict technical conditions involving: '...the importation, full application and adaptation of all the technical progress made in the temperate lands, namely selection of fodder plants, the use of irrigation, abundant and precise application of manures, careful breeding of animals, controlled feeding, and, above all, complete and lasting victory over microbial and parasitic diseases.'

The biological reasons for pessimism were well founded, as recognized early by the United Nations Educational, Scientific and Cultural Organization (UNESCO 1963, pp. 168–169), ILCA (1975), Pratt and Gwynne (1977), Le Houérou (1989) and in the Dutch–Malian study of Sahelian rangelands (Penning de Vries and Djiteye, 1991). The economic reasons for pessimism were given by Pratt and Gwynne (1977, pp. 100–128). They showed that the economics of range improvement – water development, fencing, overseeding of the range, managed grazing and seeding with new species of grasses – were unfavourable in drier conditions and risky in wetter ones. These biological and financial findings were generally confirmed by Le Houérou (1980) for browse and in the global review by Sandford (1983a) of pastoral development. A review nearly 40 years later of rigorous impact studies of CGIAR research in grazing systems found few productivity effects of that research (Jutzi and Rich, 2016).

Le Houérou (1989, pp. 149–155) synthesized Sahelian investigations over many years and concluded the following:

- Irregular rainfall, a long dry season, and competition from native grasses and forbs

made the introduction of higher-yielding plant species unsuccessful.
- There had been no commercial success in reseeding pastures at rainfall around the 550 mm isohyet, with local or introduced grasses or with legumes[29].
- There had been only one success[30] in establishing browse species at rainfall less than the 400 mm isohyet in West Africa.
- The high cost of fencing, firebreaks and water made it nearly impossible to achieve higher plant yields even if browse and pasture production could be improved under experimental conditions (Le Houérou, 1989, p. 150; see also Montgolfier-Kouèvi and Le Houérou, 1980).

The second reason for 'livestock pessimism' of the 'mainstream view' was the persistent belief among external observers that African pastoralists were inefficient managers for 'cultural' reasons. The cultural reason, common around the time of the founding of the African livestock centres, was that herders kept too many animals relative to range capacity because they derived utility from keeping stock rather than selling them. This interpretation impelled the view that rangelands management practices, especially open-access land tenure, would lead to overgrazing[31] and should therefore be modified to avoid the destruction of the range.

That overgrazing would eventually destroy the range was a common argument in East and West Africa alike. The work of colonial scientists in Niger is representative of francophone scientific and administrative opinion (Peyre de Fabrègues, 1984). The same perceived risk of overgrazing was the basis of the colonists' agricultural policy in Kenya[32]. Pratt and Gwynne (1977, p. 38), working mainly in East Africa, argued that: 'Overgrazing may often be the direct result of human biological needs... It is, however, also a common situation that the pastoralist maintains a herd far larger than needed for his own subsistence. This is usually attributed to sheer greed, prestige, or the concept of livestock as movable wealth.' Dahl and Hjort (1976, p. 17) were unusually prescient in rejecting the prestige argument about overgrazing.

A leading observer of tropical agriculture, Ruthenberg (1980, p. 332) concluded, at the beginning of the modern livestock research in Africa, that it was '...usually advisable to leave totally nomadic systems undisturbed' because

they were unsuited for ranching for both biological and managerial/cultural reasons.

Ruthenberg (1980, p. 343) was pessimistic about semi-nomadic systems, contending that regulation of stock numbers in semi-nomadic systems occurred through 'disaster' and not through rational management. Ruthenberg, whose books are deeply insightful nearly 40 years after their final editions, was dissatisfied enough with semi-nomadic herding to refer to its 'malpractices' (Ruthenberg, 1980, p. 342): 'uncontrolled animal densities, over-grazing'; 'inadequate fodder distribution over the year'; inefficient placement of camps to water, resulting in long daily treks; low calf productivity owing to competition with people for milk; and inefficient grazing practices (Ruthenberg, 1980, p. 342). He concluded that neither greater efficiency nor better environmental stability could be achieved without human population control through emigration. He continued to say that replacement of collective land tenure was necessary by allocation to groups or individuals 'whereby grazing rights were both allotted to the herdsmen and enforced' (Ruthenberg, 1980, p. 343).

Ruthenberg's view of the difficulty of realizing the potential of tropical pastoralism was part of a general pessimism about technical and policy measures. Grigg (1974) had earlier concluded that 'the conversion of pastoralism to ranching has proved difficult'[33]. Jahnke's (1982, p. 149) review of African livestock systems argued that extensive herding in areas under trypanosomiasis challenge should sometimes 'be left to the fly' given that ranching is not economic and that the recurrent costs of long-term tsetse control are unsustainable on small farms and ranches. Coppock's (1994, p. 273) multidisciplinary study of southern Ethiopia found that previous rangelands development projects had not produced a 'documented increase in cattle offtake or a widespread and sustained improvement in human welfare from veterinary campaigns or ponds, roads, and markets'. Coppock further noted that the 'ranch experiment' in southern Ethiopia had 'failed to transform traditional pastoralism' (Coppock, 1994, p. 35). Mortimore's (2000, pp. 104–105) review of northern Nigeria found that efforts to establish ranches and grazing reserves in the 1960s had failed because of high fixed costs per reserve, competition from cropping and the incompatibility

of (enforced) limited mobility in the reserves with erratic rainfall.

Productivity of subsistence and commercial grazing systems

The 'mainstream view' (as described and criticized by Sandford, 1983a, pp. 11–19) was that African rangelands, like commercial ranches in Latin America, the USA and Australia, should be open-air factories to produce meat. Following this view was the contention that traditional grazing, in Asia and sub-Saharan Africa, was less productive in live weight per hectare or per worker than ranching. This contention encouraged measures to raise stocking rates and offtake from grazing systems and to shift herd composition from females to males to make them more productive in terms of meat supply (Sandford, 1983a: pp. 123–126; Wagenaar *et al.*, 1986, pp. 50–51) and hence more efficient in terms of land use.

A few early studies tested the proposition that grazing was less productive than ranching in live weight per hectare (Cossins, 1985 for Ethiopia; Sandford, 1983b, for sub-Saharan Africa; Sandford, 1983a, pp. 123–126; Wilson, 1986, for Mali; Behnke, 1985, for sub-Saharan Africa; Wagenaar *et al.* 1986, p. 47, for five systems in three countries; Table 15.2). These studies tended to show that grazing productivity per unit of land exceeded that of ranches. Extending the comparison, Breman and de Wit (1983) found that the protein production per hectare in Mali was higher than on large ranches in Texas and Australia. Ocaido *et al.* (2009) found much higher annual returns per hectare for pastoralism than for ranching when the two were compared in the same area of Uganda.

Behnke (1985) concluded that the gap between grazing and ranch productivity *in the same environment* was usually small, based on observations from Botswana, Kenya, Uganda and Zimbabwe. Behnke further argued that the putative gap between ranch and grazing output had been exaggerated in favour of commercial ranches by cultural bias among external observers, including scientists, who were too eager to find overgrazing and low productivity among traditional herders. Homewood (2008, pp. 63–65), using a larger sample of studies, later restated the critiques of the 'mainstream view', notably the lack of evidence for range degradation. A se-

Table 15.2. Productivity comparisons of ranching and pastoralism, various years.

Study	Region/period	Subregion/country	Climate/system	Species	Pastoral productivity estimates (TLUs/ha)	Ranching (TLUs/ha)
Dyson-Hudson (1966)	East Africa, 1966	Karamoja, Uganda	Warm semi-arid (*Bsh*), tropical savannah (*Aw*), LGH, LGT	Cattle	Not specific	Unknown
Dyson-Hudson and Dyson-Hudson (1980)	Global	Global	Tropical, temperate, highland	Ruminants, camels	Not specific	Not specific
ILCA (1975)	1960s and 1970s	Drylands, sub-Saharan Africa	Semi-arid (*Bsh*), tropical savannah (*Aw*), LGA, LGH, LGT, MRA, MRH	Cattle, goats, sheep, camels	Variable; 0.05–0.2 in Sahelian conditions	Verify in Breman
Dahl and Hjort (1976)	East Africa, 1976	Western Sudan, Kenya	Arid, semi-arid, LGA, LGH	Cattle, camels, sheep, goats	Not stated	Not stated
Fricke (1979)	1970s	North-central Nigeria	Semi-arid, subhumid, LGH, MRH	Mainly cattle		
Pratt and Gwynne (1977)	1960s and 1970s	East Africa	Arid, semi-arid, subhumid, LGA, LGH	Mainly cattle		
Jahnke (1982)	Sub-Saharan Africa, 1970s	Sub-Saharan Africa	Very arid to humid, LGA to MIT	Ruminants	0.1–0.5 by climate, ~0.35 considered max subhumid	
Wilson (1986)	West Africa, 1980s	Niono, Mali	Arid to semi-arid, LGA, LGH, MRA, MRH	Ruminants	0.02–0.25 in arid and semi-arid conditions	
Breman and de Wit (1983)	1970s and early 1980s	East Africa and some temperate countries	Arid, semi-arid, temperate, LGA, LGH	Ruminants	In protein kg/ha, 0.4 for nomads, 0.6–3.2 for seasonal transhumants, 0.3 for sedentary	In protein kg/ha, 0.3–0.5 for USA, 0.4 for Australia
Sandford (1983a)	1960s–1970s	Developing countries	Mainly arid to semi-arid	Cattle, camels, goats		

Ellis and Swift (1988)	East Africa, 1980s	Northern Kenya	Arid, semi-arid, subhumid, LGA, LGH	Cattle, camels, goats, sheep	Low, highly variable	Greater than pastoral, but highly variable
de Leeuw and Milligan (1984)	Sub-Saharan Africa, 1984	Ethiopia, Mali, Niger, Nigeria	Arid, semi-arid, LGA, LGH, MRH	Ruminants	Niger: 0.07–0.03; Mali (Niger Delta): 0.05–0.78	
Cossins (1985)	East Africa, 1980s	Borana, Ethiopia,	Semi-arid to subhumid	Cattle	~2 kg animal protein/ ha/year	~2 (Kenya)
		Semi-arid Mali	Arid, semi-arid	Cattle	~0.6–3.2 kg animal protein protein/ha/year	~0.5 Australia
Homewood and Rodgers (2004)	East Africa	Maasailand, Kenya; Serengeti, Tanzania	Semi-arid to subhumid	Ruminants and wildlife		
Solomon Bekure et al. (1991)	East Africa, 1980–1991	Kajiado County, Kenya ('Maasailand')	Semi-arid to subhumid	Cattle, goats	0.25–1, function of wealth index	Not shown
Coppock (1994)	East Africa, 1980–1991	Borana, Ethiopia	Semi-arid to subhumid	Cattle, camels, goats, sheep	Cattle 10–13, goats 1–2, sheep 1–2	2–4 traditional cattle,10–15 introduced
Behnke et al. (1993)	East Africa, 1970s–1980s		Arid to semi-arid to subhumid	Cattle, camels, goats, sheep	Many, various rangeland sites	Not presented
Hiernaux and Ayantunde (2004)	West Africa, 1990s	Fakara, Niger	Arid to semi-arid	Cattle, sheep, goats		Not presented
Barbier and Hazell (1999)	Niger, 1990s	Niger	LGA, LGH	Cattle, sheep, goats		Not presented
Kruska et al. (2003)	2003	Global	Tropical and temperate	Ruminants and monogastrics		Not presented
Lesorogol (2008)	Kenya, 2000 and 2005	Turkana, Kenya	LGA, MRA	Cattle 0.05–0.1		
Homewood (2008)	Sub-Saharan Africa	Many		Ruminants and wildlife	Sahel, East Africa	Not presented specifically
Reid et al. (2008b)	1990s and 2000s	Athi-Kaputiei plains, Kenya	Arid, semi-arid	Ruminants and wildlife	Highly variable	Unknown
Konczacki (2014)	2014	Sub-Saharan Africa	Tropical	Mainly cattle	Not specified	Unknown

cond counterattack against the 'low productivity of subsistence grazing' argument was that the objective of African rangelands systems was not to produce meat for sale but to produce milk for consumption by the herders and to provide security against drought and disease. This alternative view of the objectives of grazing systems – confirmed notably in the Borana, Maasailand, Kaduna and both Mali studies and in the reviews by Dyson-Hudson and Dyson-Hudson (1969), Nicholson (1984) and Behnke (1985) – is consistent with common features of grazing modes. These are: (i) low weaning weight of calves because of competition for milk with people; (ii) more females than males in the herd to sustain milk production with limited feed; and (iii) seasonal grazing rotations between milk and dry herds to provide milk for subsistence.

The problem of animal mobility

The ILCA systems studies (Ethiopia, Kenya, Mali, Nigeria and Niger) were not designed to estimate long-term changes in the mobility of grazing ruminants, although they are definitive on the role of traditional mobility patterns in exploiting seasonal changes in feed, water and markets. Older studies (ILCA 1975; Pratt and Gwynne, 1977; Le Houérou, 1989) have the same shortcoming as does the most recent major compendium on African pastoralism (Catley et al., 2013). The FAO/CIRAD (2013) review of Sahel grazing systems, covering 1970–2010, is the only long-term study of the issue. It found that 'movements have become longer and more dispersed, especially southward' in response to climate, markets and cropping density (FAO/CIRAD, 2013, p. 14).

Bourn and Wint (1994) reviewed 20 aerial and ground surveys of livestock and land use between 1980 and 1991 in Mali, Niger, Sudan, Chad and Nigeria. The surveys confirmed the greater importance of stock mobility in the West African subhumid climates, related to the stronger seasonal variability of rainfall and hence of plant biomass in the '750–1250 mm rainfall band' (Bourn and Wint, 1994, p. 9). They noted that seasonal mobility was weaker in arid and humid climates than in the subhumid climates, presumably because the latter is a transition zone in West Africa north of the equator. The single-point sampling frame in Bourn and Wint

(1994) does not permit conclusions about long-term changes in mobility.

Turner et al. (2014) completed an unusually detailed study of livestock mobility in 32 mixed-farming villages in Mali and Niger. They found that mobility was a dominant strategy among all groups (farmers, herders, artisans and fishers) and that mobility became more dominant as stock density rose. Mobility, and the type of mobility (within village, proximate or distant seasonal transhumance), were not strongly affected by species in the rainy season, although it was reduced for all species in the dry season. Apparent longer-term trends affecting mobility in this study were: (i) insecurity in grazing areas outside the survey villages, whether these areas were proximate or distant, reduced mobility; (ii) higher cultivation densities in the survey villages increased the risk of livestock damage to crops and hence the risk of conflicts among farmers and herders; and (iii) changes in livestock corridors related to planning of water points also hampered mobility and changed its paths.

There is a long chain of research confirming the importance of mobility to pastoralists and highlighting the potential costs to their livelihoods if mobility were to be restricted. This chain includes the ILCA systems studies for Mali, Kenya and Ethiopia (Behnke and Scoones, 1993), the studies on Niger (Hiernaux and Ayantunde, 2004; Turner et al., 2014), the FAO/CIRAD compendium on the Sahel (FAO/CIRAD, 2013) and later de Haan (2016). They confirmed the potential damage to productivity from policy restrictions on mobility, and the long-term adverse trends related to insecurity, cultivation density, and the competition for water among herders and between herders and farmers.

ILCA's programme

ILCA began from the general idea that not enough was known about African grazing systems, or about mixed systems in which the actual productivity of livestock appeared to be less than its potential, to permit the introduction of technical, managerial or policy changes. The specific origin of grazing systems research was to test the founding hypothesis of ILCA: that there had been '...a failure to integrate the

biological, economic and sociological components of research and development programmes' (Tribe *et al.*, 1973, p. 1). Multidisciplinary research was therefore proposed to provide the scientific basis for programmes to expand livestock production and to improve herders' welfare.

ILCA accordingly launched a series of livestock systems studies, which continued for 25–30 years in various parts of sub-Saharan Africa, to investigate the economic, biotic, abiotic and organizational constraints to improving livestock systems. ILRAD's involvement with systems analysis was almost nil for its first decade and began only in the 1980s with its role in the African Trypanotolerant Livestock network (ATLN) and its leadership of epidemiology and economics work of ECF. These studies ultimately filled some of the gap between the development importance of livestock in sub-Saharan Africa and the research effort on livestock problems.

ILCA's studies had two generations. The first generation followed extensive communal rangelands in Ethiopia, Kenya and Mali from the early 1970s until the early 1990s. These studies featured little collaboration with the crop centres. The first generation of ILRI research took place mainly in the LGA/LGH and MRH/MRT types. The second followed smallholder mixed systems in Nigeria, Ethiopia and Mali (with enhanced collaboration among ILCA, the International Institute of Tropical Agriculture (IITA) and ICRISAT), in the Middle East (with ICARDA) and in Central America (with CIAT). The second generation concentrated more on mixed systems.

The broad purposes were to describe how the systems functioned, to define types of production units and to estimate productivity parameters and thereby to understand constraints to productivity. A specific goal of the first studies was to collect primary field data on crop and animal performance, which in the late 1970s were unavailable in most of sub-Saharan Africa. A second goal was to estimate input–output relationships and later to test new technologies.

Paul Neate's history of ILCA (ILCA, 1994) maps several milestones:

- ILCA's pastoral work began with a compendium on mapping sub-Saharan Africa rangelands (ILCA, 1975), with some reference to Tunisia, India, Iran and Australia.

- The ILCA (1975) rangelands book was followed by studies of browse in Africa (Le Houérou, 1980), the rangelands of Kenya (de Leeuw *et al.*, 1984; Solomon Bekure *et al.*, 1991), Ethiopia (Coppock, 1994) and tropical Africa (Sandford, 1983a).

- ILCA published extensive literature reviews on trypanotolerance (Trail, 1979a,1979b), on livestock in the subhumid zone (ILCA, 1979a) and on small ruminants in Africa (ILCA, 1979b; Gatenby and Trail, 1982), which outlined the state of knowledge and suggested priorities for new research in these areas.

- Research on management and productivity of extensive mixed systems in semi-arid central Mali (Wilson *et al.*, 1983; Wilson, 1986; Wagenaar *et al.*, 1986), with data collection from 1978 to 1984.

- Research on management and productivity of mixed systems in subhumid central Nigeria (von Kaufmann *et al.*, 1986), with data collection from 1978 to 1986.

- Mixed systems in highland Ethiopia (Gryseels and Anderson, 1983), with data collection from 1978 through 1985.

- Mixed systems in semi-arid, subhumid and highland areas of sub-Saharan Africa, plus the related work of McCown *et al.* (1979), McIntire *et al.* (1992), the collaboration of ILCA with Pingali *et al.* (1987) and Winrock International (1992).

- The productivity of pastures, crop residues and other feeds, with a new focus on browse, which had not been well studied in sub-Saharan Africa before the mid-1970s (Le Houérou, 1980; Walker, 1980).

- Soils, water and vegetation (complemented by the Dutch–Malian work of Penning de Vries and Djiteye, 1991; and Breman and de Wit, 1983) in semi-arid Mali and by the compendia of ILCA (ILCA, 1975) and of Pratt and Gwynne (1977).

- The volume of Powell *et al.* (1995) on livestock and nutrient cycling.

The following section sketches the main characteristics of the research sites and the specific experimental and survey treatments done at each site.

Borana, Ethiopia

ILCA and national partners studied an area of 15,475 km² in the Borana Plateau of southern Ethiopia (Coppock, 1994, p. 39)[34] from 1980 to 1991. The site was chosen within the much larger area of a regional livestock development project that provided background information on the environment, social organization and technology of crop and livestock production (Coppock 1994, pp. 38–60). Previous research on the Borana areas of northern Kenya and southern Ethiopia had concentrated on social organization and not on biological constraints to productivity.

Scientists identified four ecologies in the study area:

- Subhumid, with varying patterns of livestock, forest, cropping and urban, with annual rainfall as high as 750–1000 mm, and some areas of bimodal rainfall (March–May and September–November).
- 'Upper semi-arid', with about 600 mm of rainfall, with a mixed landscape of savannahs and woodlands, varying in elevation.
- 'Lower semi-arid', with about 400–600 mm of rainfall in a single season, varying soil types and landscapes of wooded areas and grasslands.
- 'Arid', with varying soil types and landforms, and less than 400 mm rainfall in a single season.

Measures of LGP at five sites were between 114 and 151 days, summed between the 'long' and 'short' rains. The systems would be classified as LGA and MRAc. The longer growing seasons, compared with West African areas of similar rainfall, were related to higher elevation and bimodal rainfall not found in West Africa. The extended growing periods typically produce pastures with a higher CP content and with longer periods of CP availability than in West Africa. The longer growing seasons and greater variation in altitude of East Africa produce a much greater diversity of plant species than in the West African Sahel (Le Houérou, 2009, p. 133).

Household survey and aerial surveys were used to estimate aggregate resource use in the 15,475 km² area studied. A combination of the two methods was used in the 1982–1985 period to arrive at estimates of 66,000 people (4.3/km²), 325,000 cattle (21/km²) and TLUs of nearly 350,000. The latter gives an average stocking of about 4.5 ha/TLU.

A rough estimate of land use in the early 1980s was that perhaps 4% was cropped (Coppock, 1994, p. 85). Measurements of cropped area per household were not reported in the grazing territories (*madda*) studied. The main crops noted were maize, beans, teff (*eragrostis tef*) and wheat. No strict division of land use between grasslands and wooded areas was possible at the time but the majority would have had 10–40% woody cover (Coppock, 1994, pp. 84–85). Perhaps half of the grazing territories would have been 'unsuitable for cultivation'.

Livestock provided the largest proportion of income for survey households. The average number of livestock stock units per person in a sample of 49 households from 1981 to 1983 (Coppock, 1994, Table D1) was 13.8 (range 4.6–39.8) averaged across grazing territories. There were major wealth differences across Borana households, reported as livestock holdings per adult equivalent household member (Coppock, 1994, pp. 174–175).

Experimental and survey treatments in the Borana programme were:

- Fodder resources (introduction, conservation, feed gardens and rehabilitation of degraded areas).
- Herd management (offtake, calf feeding and breed improvement).
- Water surveys and experiments (Nicholson, 1987a,b, 1989).
- Novel work on the intergroup inequality of herd holdings.

The Borana volume did not clearly present feed composition although it is evident that pasture was the principal feed. The unusual features of the Borana Plateau compared with West African pastoralism – two rainy seasons, hence less intra-annual variability of grazing and better forage quality throughout the year; a scarcity of cropping, hence less crop residue production; and the constant battle against bush encroachment, hence greater incentive to feed browse – impelled feed research into characterization of pasture and browse and away from work on crop residue quality, which was significant in the Kaduna study.

The Borana study outlined a development path for the region. The first step was to raise

stocking rates on undergrazed areas through water development. The argument was that higher well density, and lower labour costs of lifting water, would divert energy spent by animals on trekking and watering into weight gain.

The second step proposed for Borana was to manage stocking rates – numbers per unit of land, species, seasonality and stock preferences among forages – to prevent overgrazing, to adapt stocking rates to rangeland potential and to exploit unused feeds, notably browse[36]. This step has failed as it was originally conceived, because it depended on the assumption that cattle would remain the dominant species and hence excluded species shift as an alternative to the management of cattle stocking rates on common land. The explanation for the failure to manage stocking rates was that it was uneconomic. In long wet cycles with good pasture growth, there was no good reason to destock. When good pasture cycles ended, destocking would occur naturally through sales and mortality.

The third step was to augment external inputs, such as fertilizers and new plant species, to raise primary production and therefore carrying capacity. Using external inputs to raise range productivity has typically failed, as one sees little trace of mineral or organic fertilizer use in African rangelands and/or of introduced herbaceous species. There appears to have been progress in leguminous tree hay making and fodder banks (see Chapter 13, this volume, on planted forages including trees), but the benefit and costs of such methods are poorly known and cannot be attributed to research or extension. A variant was to use external inputs (fencing, mineral fertilizers and new forage crops) to rehabilitate degraded sites.

Maasailand, Kenya

The ILCA studies of Maasailand in Kajiado County of south-eastern Kenya – of water, soils, climate, animal health, herd management, vegetation, pastures, economics and labour use – began in 1978 and continued into the mid-1980s[37]. The outstanding study is that of Solomon Bekure et al. (1991), covering 1979–1991, followed by the later contributions of Homewood and Rodgers (2004), among others. The general area of Maasailand covering much of southern Kenya and north-central Tanzania

has since been studied by scientists of many disciplines over the past 40 years.

The Maasailand studies differed from the others in two respects. One was that they could use historical data on system structure and productivity that was unavailable in Mali, sub-humid Nigeria and later Niger[38]. Another was that the Maasailand had been the site of dramatic changes in pastoralism. Land availability and therefore herd mobility had diminished with the appropriation of Maasai lands by the colonists at the beginning of the 20th century (as summarized for an area north of Kajiado by Reid et al., 2008b). The later introduction of group ranches by the independent Kenyan government in the 1960s further limited the land and mobility of Maasai.

The Maasailand system, classed as LGA by Robinson et al. (2011) at an altitude around 1500 masl, was semi-nomadic with a low human population density, poor market access, low stocking rates, milk as the staple and very little cropping. The population density was about eight persons per km^2 in 1979 (Solomon Bekure et al., 1991, p. 16). Stocking rates ranged from 1 TLU/ha to 0.25 TLU/ha across the study sites with significant wet- and dry-season variation. Cropping density was almost nil.

Species and breed composition of herds and flocks changed little in the years before and after the group ranches. Herd structure did not change notably over time from a two-thirds share of females; offtake changed little as a share of herd size. There was limited infrastructure development and new road, water and dipping infrastructure fell into disuse from lack of maintenance. The use of variable inputs was uncommon except for acaricides and veterinary drugs.

Inequality in stock ownership was high. The Gini coefficient of cattle and small stock ownership in three Kenya group ranches (1980–1981) was about 0.50 (Solomon Bekure et al., 1991, p. 3) but there are no corresponding earlier data. The effect of group ranches on the inequality of stock ownership was unknown. A later summary of the effects of subdividing group ranches found that population pressure in Maasailand in the final quarter of the 20th century would have reduced livestock/person numbers enough to make ranch subdivisions inviable without outside income from wage labour or remittances (Thornton et al., 2006).

Experimental and quasi-experimental treatments were: (i) higher-yielding fodder resources; (ii) policies to encourage greater offtake from the herd; (iii) grazing and water management; and (iv) management and health of sheep and goats.

Niono, Mali and the Malian Delta

The Mali livestock systems (LGA) research was led by ILCA and the Malian Institut d'Economie Rurale (IER) around the town of Niono in central Mali near the Niger River. There were two studies, one of the agro-pastoral systems in areas farther from the Niger and the second in and around the Inner Delta of the Niger. The principal themes of both were animal health and productivity, herd management, vegetation and grazing patterns, and crop agronomy. The areas were LGA, with generally low human population density, highly variable seasonal livestock density, monomodal rainfall, good market access in regional towns, and a diverse mix of rain-fed and irrigated crops near the animal production zones. The altitude was between 200 and 300 masl in the Niono and Interior Delta areas. The hot dry conditions (Köppen climate *BSh*) made trypanosomiasis rare and *Theileria* unknown.

The main reports were those of Wilson (1986) and Wagenaar *et al.* (1986). Wilson (1986) was a research project on cattle and small-ruminant productivity among agro-pastoralists[39] near Niono in north-central Mali with field work over the period 1976–1983. The study by Wagenaar *et al.* (1986) from 1979 to 1983 covered cattle productivity among agro-pastoralists in the Inner Delta of the Niger River in central Mali. Both Mali studies were in areas without major trypanosomiasis challenge and where internal parasites were the principal animal health risk. The Inner Delta study area differed from the Niono one chiefly in that water was available year-round and that the divide between wet- and dry-season pastures was much less pronounced.

There were associated studies of vegetation and biomass carried out by Breman and Cissé, (1977), Hiernaux (1980, 1984) and Hiernaux *et al.* (1983), and on primary productivity and soil–water relationships led by the University of Wageningen (Penning de Vries and Djiteye, 1991). A later comprehensive review of Sahel grazing systems (Le Houérou, 1989) relied heavily on the ILCA/Malian IER work at Niono and in the Niger Delta of Mali and on earlier research by the L'Institut d'Elevage et de Médecine Vétérinaire des pays Tropicaux (IEMVT) on Sahelian livestock and agrostology in Niger and Senegal.

The Mali studies differed from the others in not having formal experiments with productivity treatments. They relied on statistical analysis of implicit 'treatments' arising from surveys of herd and flock effects on reproductive performance, nutritional status, young stock mortality and seasonal respiratory diseases. The Niono study (Wilson, 1986, p. 108) used the statistical results to make general recommendations about feed, management, and prophylactic and curative health measures without benefit–cost analysis. The Inner Delta study did a more thorough analysis of calf weaning policies leading to recommendations that could be applied by herders (Wagenaar *et al.*, 1986, pp. 45–51) and leading to other proposals for pasture management involving existing forage species rather than the introduction of new forage species.

Kaduna, Nigeria

The Kaduna sites (von Kaufmann *et al.*, 1986)[40] were chosen to contrast livestock systems under different land-use patterns imposed in part by the natural environment and in part by policy. The Kaduna area is in Köppen climate *Aw* (tropical savannah). The livestock systems are LGT and MRT. Two of the three sites – Kurmin Biri, between a grazing reserve and a national forest, Abet – were around 2500 km². Annual rainfall in Kurmin Biri and Abet was 1200–1300 mm in one season. Ganawuri is a higher-cultivation-density site, with slightly higher rainfall, of which 800 km² was subject to aerial survey and 40 km² was subject to ground truthing (von Kaufmann *et al.*, 1986, p. 45). Kurmin Biri and Abet were at about 600 masl and Ganawuri above 1250 masl.

Waters-Bayer and Taylor-Powell (1986a) summarized population and land use in the three sites. They distinguished three groups: (i) pure pastoralists, who do not practise cropping and are nomadic; (ii) agro-pastoralists, whose main activity is livestock but who do have crops and are less nomadic than 'pure pastoralists'; and (iii) mixed farmers, whose main activity is crops but who do keep some ruminants; animal

traction for power was rare in this production type, which was the largest.

Cultivation intensity varied from 5–15% of all land in Kurmin Biri to 25% in Abet to as much as 40% in Ganawuri. Wet-season livestock density ranged from five heads/km^2 in Kurmin Biri to 25 in Abet. Dry-season stock density ranged from 10–20 head/km^2 in Kurmin Biri to 40 in Abet to 20–25 in Ganawuri. Kurmin Biri had at one time been declared tsetse free, although the vector was apparently still found at Abet during the study period. Ganawuri, at some 1000 masl, had a cooler climate and lower vector incidence.

The Kaduna studies carried out careful experiments of practices to improve productivity. These tests focused on supplementary feeding of cattle, planted forages (mainly *Stylosanthes* spp.) and on manure for crop production (Powell, 1986a,b; Mohamed-Saleem, 1986a,b; Bayer, 1986).

Fakara, Niger

The ILRI studies in the Fakara subregion of western Niger – of soils, vegetation, grazing practices, soil nutrient recycling, herd management, vegetation, household economics and labour use – followed earlier work in the same zone by ICRISAT, ILCA and the International Fertilizer Development Center (IFDC), beginning in the early 1980s. The Fakara studies (Williams *et al.*, 1999, and Hiernaux and Ayantunde, 2004, reporting on work from 1994 to 2005) were in Köppen climate *BWh* at altitudes of less than 300 masl. Annual rainfall in the Fakara is reported to have been 560 mm from 1905 to 1989. There is a monsoon seasonal pattern with rainfall from June to September, a transition period in October and November, a relatively cool season from December to February and a very hot dry season from March until the onset of the rains. Surveys in the 1990s showed the population density to be low, in the order of 10–50 rural persons per km^2 depending on the proximity to water.

The livestock system is a mix of seasonal and annual transhumance. Animal density per unit of land was low, ranging from 5 to 12 TLUs/km^2. Animal density in TLUs per person was comparatively high, ranging from 0.15–0.20 among poorer families to as high as 2.5 among richer ones. The principal feeds were natural grazing, mainly of browse and annual grasses, and crop residues. Animal disease prevalence is low enough that Hiernaux and Ayantunde (2004) did not mention it at all; the principal disease problem appears to be internal parasites. The hot, dry conditions made tsetse and therefore trypanosomiasis very rare. ECF is unknown in West Africa.

The Fakara field studies were complemented by station investigations of dry-season supplementation, sheep fattening, alternative grazing practices such as rotational grazing and seasonal grazing, and soil fertility management including manuring and mineral fertilization of arable crops. The field and station studies were subsequently used in bioeconomic models of soil fertility management and household behaviour (Barbier and Hazell, 1999).

What did the pastoral systems find?

Sedentarization

Three tenets of the 'mainstream view' of pastoralism were that it was unproductive; that it inevitably involved overstocking, which led to environmental damage and to conflicts with farmers; and that reducing nomadism was a path to higher productivity and less pasture damage due to lower grazing pressure. One result of these beliefs was that sedentarization of herders was sometimes advanced as an appropriate, even urgent, policy. In addition to raising productivity, sedentarization would, moreover, allow provision of housing, education and health services to herders. It followed from this view, which was widely held among administrators and scientists, that policy should seek to sedentarize completely, settle partially by season or otherwise restrict the mobility of pastoral groups.

A prediction from the agricultural evolution literature is that sedentarization of nomads responds to two forces. The first is a push effect – population pressure and the expansion of land for crops or wildlife cause herders to lose grazing access. This loss of grazing limits feasible herd numbers, restricts mobility and productivity of the remaining animals, and eventually obliges pastoralists to abandon nomadism for cropping in whole or in part. A related prediction was that disasters such as drought or animal disease would aggravate herd loss and therefore accelerate

sedentarization. The second force is a pull effect – by sedentarizing, herders can benefit from access to land, cereal production, crop residues, water and even political representation.

The strength of these predictions has varied greatly by agroclimate, population density and the emergence of markets for milk, commercial meat and cash crops. Both 'push' and 'pull' predictions have been confirmed in the densely populated areas of northern Nigeria by Waters-Bayer and Taylor-Powell (1986b), and also by Blench (1994) who gives many examples of successful spontaneous sedentarization of herders throughout Nigeria, and in at least three pastoral systems of southern Ethiopia and northern Kenya (Fratkin, 2001). In more recent research in semi-arid western Niger, Hiernaux *et al.* (2009) showed a progressive sedentarization of herding groups into rain-fed farming, caused by drought, with a concurrent integration of crop and animal activities on previously settled farms, caused by demand for land and access to fodder. Northern Nigeria, and parts of semi-arid India, illustrate the impact of population density and service availability on sedentarization, while East Africa illustrates the impact of recurrent droughtsc.

A related prediction was that pastoralism, because of herders' knowledge of animal production, would evolve more easily into mixed farming than arable farming without livestock. The latter would involve aspects of arable farming, ley farming, animal traction, use of manure for cropping, and commercial livestock, such as dairying or ranching for meat. This set of predictions seems to have succeeded only in some aspects of arable farming and to have generally failed with respect to ley farming, animal traction, planted forages and commercial livestock production. The successful predictions – use of manure in cropping, use of crop residues to feed animals, use of animals for transport and cultivation – were confirmed by McCown *et al.* (1979), in a study of agro-pastoralists in central Nigeria (Powell and Taylor-Powell, 1984), in the ILCA research on agro-pastoralists in north-central Mali (Wilson, 1986), more generally across semi-arid and subhumid Africa (McIntire *et al.*, 1992), particularly Chapters 5 and 6) and Hill's (1982, pp. 21–23) book on two dry farming villages in Hausaland and in the international comparisons by Baltenweck *et al.* (2003).

Enforced sedentarization policies generally failed. Grigg (1974, p. 122) that '...efforts to establish Maasai families on 'ranches'...foundered on the refusal of the Maasai to cull their herds to a level compatible with the grazing resources available, and their reluctance to sell their cattle'[42].

Sandford's (1983a) review of African and other work (ex-Soviet Union, the Middle East) found that efforts to settle nomadic herds, while integrating their owners into cropping or moving them into ranching, usually failed because of the cost of foregone mobility and the unwillingness of pastoralists to abandon their livelihoods. The sedentarization of herders in northern Nigeria was indeed found to create conflicts with farmers, as indicated by numbers of lawsuits for crop damages caused by animals (Waters-Bayer and Taylor-Powell, 1986b, pp. 213–214). Blench (2001, pp. iv and 61–64) found that policies of enforced sedentarization 'had a very unsatisfactory history', citing the instances of Tanzania, Iran, Kenya and Somalia. Homewood (2008) cites many examples from East and West Africa where explicit or implicit settlement policies have failed, sometimes with disastrous consequences for the rights and livelihoods of herders. Induced sedentarization may, moreover, have produced land degradation by concentrating people and animals in smaller areas of scarce resources, such as dry-season water and pastures, but it is not possible to quantify such adverse effects with existing information[43].

After enforced mobility restrictions during the collective era in Mongolia, herders 'very rapidly reverted to traditional mobile transhumance' when the collectives were dismantled (Suttie *et al.*, 2005, p. 294). Arable farming was indeed taken up by pastoralists (Blench, 1994, 2001), with marked differences among subregions in sub-Saharan Africa. The reasons for sedentarization were necessity – herders had to settle after losing most or part of their animals, in part because of long-term conversion of grazing and forest to cropland and in part because of opportunity to exploit interactions between crops and livestock in the same enterprise. Sedentarization could not be sustainably enforced by public policy. It was also reversible – as soon as assets would allow, settled pastoralists would revert, at least for part of their family, back to a mobile system.

The extensive systems most carefully studied – Borana, Maasailand, Kaduna, north-central

Mali, south-western Niger, the Kenyan–Tanzanian border – seem to have regressed in area under pressure from arable farming (Kaduna), bush encroachment (Borana) and wildlife reservations (Maasailand). One study of northern Nigeria[44] found that the principal land-use change was loss of woodland. Another factor, which has been more difficult to map, is the taking of land for cropping, whether by governments for sugar estates in the Awash Valley of Ethiopia or by small holders on what was formerly lowland seasonal grazing in central Nigeria (von Kaufmann *et al.*, 1986). The review by Reid *et al.* (2005, pp. 46–48) noted that the encroachment of crop farming had reduced wildlife (wildebeest) populations but not those of cattle on the Kenyan–Tanzanian border areas.

Grazing organization

A concomitant policy to sedentarization was to modify the traditional social organization of grazing. This traditional organization was typically labelled as 'collective', 'communal' or 'common property'. It was believed to provide weak incentives to sell animals by lowering the private costs of grazing while simultaneously encouraging overgrazing.

A common measure was to re-allocate pasture by giving selected groups exclusive access to grazing. Such policies were enforced in Maasailand (Solomon Bekure *et al.*, 1991) and in north-central Nigeria (von Kaufmann *et al.*, 1986; Blench, 1994). In Maasailand, this was the introduction of group ranches[45]. In northern Nigeria, it was the definition of grazing reserves with remapping of herding family access to the reserves. In several francophone nations of West Africa, it was the promulgation of a 'code pastoral' that delimited (very large) grazing areas and corridors through arable lands but without reorganization of pastoral groups (FAO/CIRAD, 2013). In Mongolia, it was the collectivization of pasture lands during the later Communist era (1950s–1980s; Mearns, 1996, p. 310) with reorganization of herding districts into brigades under the control of the local collective administration.

There were common problems in each attempt at reorganizing pastoral groups and their grazing rights. First, there was the cost of restricted mobility in terms of increased exposure

of herders to drought (or, in Mongolia, to extreme cold) and related pasture loss. Second, there was the devaluation of traditional herding authorities in allocating resources and in managing conflicts about pastures and water. Third, there may have been some productivity loss caused by greater exposure to epizootics as herds became denser in smaller areas. Last, there were conflicts between herding and farming groups, which may again have become more frequent as herds sought access to smaller areas for water and dry-season pasture.

Organizational changes in grazing have often been proposed and have nearly as often failed. An early example of a failure to manage mobility was the attempt to introduce grazing blocks among cattle and camel herding pastoralists in semi-arid north-eastern Kenya (Helland, 1980). Helland found that the complex management required for the grazing blocks was incompatible with the traditional institutions charged with managing the seasonality of water and forage in the area. Galaty (2013a) found that group ranches in Maasailand in both Kenya and Tanzania harmed the interests of the traditional herders through a process of institutionalized land grabs. Similarly, confiscation of grazing lands and associated settlement policies by the Imperial and *derg* regimes of Ethiopia from the 1950s to the 1980s had adverse effects on pastoralists' interests (Mulatu and Solomon Bekure, 2013).

One path by which subdivision of grazing would have affected the distribution of animals was through its effect on pasture productivity. Subdivision tended not to affect productivity in ranges of very low or very high productivity but tended to reduce it significantly on ranges of intermediate productivity. The effect of restructuring on the inherent seasonality of pastoralism, especially on dry-season grazing, is not clear at the different study sites. In Maasailand, Solomon Bekure *et al.* (1991, p. 35) found that 'the degree to which group ranches altered management strategies cannot be determined with available data'. The same study noted *impressions* of changes in watering frequency, use of salt licks and acaricides, and introduction of the improved Sahiwal breed, but could not quantify these changes or estimate their impact on productivity[46].

Ellis and Swift (1988) had earlier shown that the non-equilibrium rangelands model depended so much on mobility that demarcation

of ranches would damage system productivity. The effects of conversion, and related changes, were carefully studied by Angassa and Oba (2008) in Borana. They found that range enclosures led to grazing land fragmentation; associated with new arable farming, the overall effect was a degradation of range productivity. Earlier work related a 'decline in total biomass production and animal performance' to 'increases in human and animal populations' and to 'decreases in grazing land' (Angassa and Beyene, 2003). The adverse effects of restricting pastoral mobility were also observed in Inner Asia (Sneath, 1998).

A related example is from Borana. The land reform imposed by the *derg* government (1974–1991) in Ethiopia was associated with 'semiprivatization' of grazing lands, range enclosures and the suppression of fire as a bush management practice (Angassa and Oba, 2008). These policies had the aggregate effect of '...forage scarcity and greater vulnerability of stock during drought years'. These parallel findings from Maasailand and Borana are good examples of policy ignoring what research had predicted about the value of traditional management in maintaining rangeland productivity and in reducing the environmental costs of invasive species.

Water

Water was long understood to be an essential component of higher pastoral productivity, of resistance to drought and of recovery after drought. Basic questions about water development were:

- Could potential water supply support livestock production growth? What are the barriers to water development?
- Can water consumption by pastoral stock become more efficient?
- What has been the impact of water development on pastoralism?
- Have there been adverse effects of water development?

Research on pastoral water was of four types: (i) literature reviews; (ii) experiments on stations and in other controlled conditions; (iii) original field investigations, including the system studies; and (iv) recent surveys and modelling of the 'water footprint' of livestock, which became a way of estimating total water use by animals.

LITERATURE REVIEWS. ILCA commissioned three literature reviews of livestock water use in Africa. King (1983) studied water intake and metabolism by different species and their effects on productivity, Sandford (1983b) focused on water planning and Classen *et al.* (1983) characterized water use in tropical Africa[47].

Sandford (1983b) recommended the following:

- Collecting new data on livestock and water point density, which existed then only in arid zones.
- Gathering new data on watering practices in semi-arid areas, which were (then) scarcer than in arid areas.
- Studying actual water use and comparing it with optimal use to test the hypothesis that producers overwater.
- Studying site design to reduce production costs.
- Recovering water costs from users to pay for system maintenance.

Water for pastoralism has expanded greatly since the 1970s, pushed by voluminous public and private investments. Research has identified defects in the design and management of pastoral water supply (Sandford, 1983b, pp. 63–67; Homewood and Rodgers, 2004, pp. 249–253), but its contribution to better designs is unproven.

EXPERIMENTS. An important point in the studies by King (1983) and Sandford (1983b) is the effects of water availability on feed intake in arid zones and on the energy used in trekking to water. Restricted water availability by season and because of distance incurred costs of foregone milk and live-weight production; estimates of trekking energy and its productivity effects could therefore be used to optimize water investments. The evidence of Sandford (1983a, pp. 73–85) on water-productivity effects was generally positive from arid zones in India, Australia and the Middle East.

Experiments on water and productivity were sparse in Africa, despite the importance of the water-energy–productivity relationship stressed by King (1983). A rare and important contribution to understanding water-productivity functions was Nicholson (1987a; 1987b; 1989) in Borana. He established that traditional 2-day and 3-day watering of Zebu cattle would

not compromise productivity if the animals were adequately fed[48]. There are few other experiments that studied water-use efficiency among African pastoralists. The reviews of range productivity of ILCA (1975), Pratt and Gwynne (1977, for East Africa), Le Houérou (1989, for West Africa) and de Haan (2016) scarcely mention water except to apply standard consumption coefficients per animal. The limited research on water and livestock productivity in arid Africa can be partly explained by the fact that additional water is seen as unambiguously good. The demand for water among pastoralists is so high that public agencies and private water producers are often willing to invest beyond what is technically optimal.

SYSTEM STUDIES AND OTHER FIELD INVESTIGATIONS. The pastoral system studies (Niono, Mali Delta, Maasailand, Borana and Fakara) identified water as a constraint, yet their contributions to answering the water questions are surprisingly limited. The Maasailand and Borana studies are the only ones to answer two of the basic questions about water adequacy for production growth and the cost of new production, while the Borana study is the only one to conclude about efficiency. The Niono and Mali Interior Delta studies mention water only in passing and have nothing quantitative on consumption, production, cost or efficiency. The subhumid Nigeria study says little about water, except to report daily livestock watering times (von Kaufmann *et al.*, 1986, p. 431) and to make the evident point that seasonal water is less limiting than it would be in a semi-arid zone such as Borana or Niono. The Maasailand study did detailed research on pastoral water infrastructure (type, scale and location), production and consumption. The principal books on African pastoralism, all based at least in part on field investigations since the mid-1970s[49], say very little about technical water issues.

The pastoral studies usually made general qualitative recommendations to raise water production, to allocate water more equitably among users and to prevent damage around wells and ponds. Water research had little or no impact on productivity except in the sense of understanding system dynamics and explaining geographic patterns (e.g. Mesele *et al.* 2006 on the Yabelo district in Borana). One of two major recent pieces on African pastoralism analyses many policy/technical options but does not treat water development as one of them (de Haan, 2016); the other (Cervigni and Morris, 2016) makes the rather general recommendation to develop 'water resources to allow better access to underexploited rangelands' (p. 85).

ADVERSE EFFECTS OF WATER DEVELOPMENT. There are adverse effects of water development. The main negative effect is soil erosion caused by intensive cultivation, or by trampling stock, near water points (Sandford, 1983a, pp. 76–78; Wilson, 2007). A 4-year station study of grazing effects on soil properties in western Niger found variable impacts on soil compaction and water infiltration as functions of grazing pressure (Hiernaux *et al.*, 1999). Pratt *et al.* (1997) did not quantify the adverse effects of water development although they argued that such effects can be managed with simple technologies.

Another potential adverse effect is that mechanization of boreholes might reduce labour demand. If labour is an important mechanism of patron–client relationships among animal-rich and animal-poor herders, then mechanization can weaken such relationships (Coppock, 1994). Lower labour requirements owing to mechanization would reduce the bargaining power of poor pastoralists and deprive them of employment, income and, potentially, finance. The West African literature is silent on possible labour displacement effects of wells, although it says a great deal about water as a cause of conflict between herders and farmers (Wilson, 1986; Wagenaar *et al.*, 1986; Le Houérou, 1989).

WATER FOOTPRINT AND PRODUCTIVITY. The water footprint literature can provide information about changes in feed composition and water-use efficiency per animal (Hoekstra and Mekonnen, 2012; see also Chapter 11, this volume). One application of this literature is to partition change in total livestock water use per unit of output as the sum of direct consumption by animals and indirect consumption by forage plants. One long-term study in arid, semi-arid and humid zones of Kenya found that total water consumption by cattle, sheep and goats, and camels in each of the three zones was closely proportional to animal numbers (Bosire

et al., 2015, p. 36, covering 1977–1990 and 2001–2012). This implies that indirect water consumption has not changed relative to the total because feed composition has not changed, nor has water-use efficiency per animal. Additional inferences are that species and breed composition within zones have not shifted towards water-efficient animals.

Feed systems

Most African pastoral research focused on its geography, society and anthropology until the volumes of ILCA (1975) and Pratt and Gwynne (1977) and the initial ILCA literature reviews. While it was long evident that feed, after disease, was the principal limitation to livestock production in grazing systems, older research had done little on possible technical changes in feed, such as introducing fencing, legumes, exotic grasses, fertilization or mechanization[50]. The technical aspects of older work emphasized water and veterinary problems almost exclusively, with less attention to other biological issues, to economics or to introduced technical change through research and extension[51]. Feed research in Africa therefore began from a comparatively weak basis.

Feed systems research had four components: (i) field characterization of available and potential feeds and their use, with emphasis on rangelands characterization (many of the papers in ILCA, 1975); (ii) station characterization of the productivity and nutritive value of such feeds as planted forages, crop residues, and browse; (iii) field experiments of these feeds; and (iv) adoption studies of promising new materials.

FIELD CHARACTERIZATION. The early pastoral studies found that feed consisted of grass, forbs, crop residues and tree browse, as shown in ILCA (1975), Fricke (1979, for Nigeria) and in the references in Le Houérou (1989), McIntire *et al.* (1992) and Baltenweck *et al.* (2003). Purchased feeds and planted forages were practically non-existent, even in stall-feeding systems where crop residues and cut grasses dominate. Even in South Asia and highland Ethiopia where the use of animals for power is common and hence creates a constant source of demand for feed among immobile animals, the principal forage was residues from multidimensional cereals, such as teff, sorghum, pearl millet, maize or wheat. For nomadic herders without arable crops, pasture grazing and cereals residues, obtained by transactions with farmers[52], dominated.

Natural pastures, crop residues, browse and planted forages were the major themes of the initial ILCA systems studies[53]. Every pastoral study started from the understanding that average feed availability from all sources – grazing, cut grass, shrubs, forbs, browse and crop residues – limited animal productivity; and that interannual and interseasonal variability in feed supply was a constant threat to herd viability[54] and growth.

Every study of mobile grazing recommended improvements to feed quantity and qualities. Suggested improvements involved planting legumes and more productive grasses (both African and exotic species), control of bush encroachment, fertilization of pastures and grazing management. For example, the study by Penning de Vries and van Heemst (1975) argued that '…it is expected that appropriate legumes and *Rhizobium* strains can be found to increase the soil nitrogen supply in Sahelian natural grasslands and agricultural fields'.

EXPERIMENTS. Some experiments on feed productivity were done by the colonial and national programmes before the advent of international livestock research. The general conclusion of the many detailed empirical investigations of feed improvements in pastoral zones of sub-Saharan Africa is that it has been practically impossible to make economic improvements in range productivity under African conditions. This holds under such treatments as planted forages, whether legumes or grasses, and with soil fertility amendments, such as mineral fertilizers or manure. Pratt and Gwynne (1977, pp. 110–128) arrived at this conclusion for East Africa. In West Africa, Le Houérou (1989) found the same when referring to more than three decades of research, as did Fricke's (1979) review of field and experimental work on cattle in Nigeria in the 1960s and the 1970s.

A careful long-term experiment was the Projet Productivité Primaire au Sahel (PPPS) study of Mali, (Penning de Vries and Djiteye, 1991), which found that: (i) soils could support higher stocking rates where water is available; and (ii) grazing cover management reduced soil degradation and bush encroachment.

Studies of soil fertility management using mineral fertilizers in African grazing systems were rare because the null hypothesis of no treatment effect was strong, even from qualitative observations. Introduced treatments – fertilizers, recycling manures or residual vegetation, planted forage legumes or grasses – have not generally succeeded. The magisterial work of Penning de Vries and Djiteye (1991, p. xix, passage translated from the French by the editors) covering 5 years of experimentation in semi-arid central Mali noted that, 'The immediate introduction of new forage legume species is likely to fail for the same reasons – competition from cereals, low germination capacity, lack of soil P, and low rainfall'. The review by Thomas and Lascano (1995) found benefits in soil quality, pasture productivity and animal productivity from mixing legumes into acid-soil pastures in Latin America; however, they did not specify the ultimate adoption of the proposed legume innovations and hence it is not possible to estimate the development impact of their research. Macharia et al. (2011) showed that introduced legumes on semi-arid pastures in Kenya could improve soil quality (pH, organic carbon, nitrogen and potassium) on station, but the on-farm phase of the trial only lasted 1.5 years, did not conclusively show a soil-quality effect and apparently did not lead to field adoption of legume technologies[55].

Studies at one site in semi-arid central Mali (Penning de Vries and Djiteye, 1991) established the basic abiotic (soil and water) and biotic (competition from grasses) constraints to planting legumes in extensive grazing systems. These conclusions are replicable throughout the semi-arid tropics of Africa and South-east Asia; exceptions in Latin America are discussed in Chapter 12 (this volume). The Mali research concluded that, in arid situations of less than 750 mm annual rainfall, the introduction of legumes into natural pastures was unlikely to be economic (Penning de Vries and Djiteye, 1991, p. 435), in part because of higher temperatures that lowered legume yields and in part because of adverse meat:fertilizer price ratios (Penning de Vries and Djiteye, 1991, p. 470).

PASTURE IMPROVEMENT[56]. Pratt and Gwynne (1977, p. 122) analysed the technical and managerial aspects of sown pastures in East Africa. Despite not considering the costs of sown pastures,

Pratt and Gwynne (1977) concluded that research on range reseeding using exotic grasses showed 'little promise' and should be considered 'a last resort'. Ruthenberg (1980, pp. 110–125 and 322–355) was negative on ley farming for pasture improvement for the same reason – in the absence of dairying, expected benefits were negative. The PPPS study in Mali found little average effect of reintroducing perennial grasses (Penning de Vries and Djiteye, 1991, p. 469) but some effect on the 'stability' of soils and pastures. A hypothetical model of ley farming in a cotton-based system of southern Mali gave inconclusive results and does not seem to have stimulated adoption of pasture fertilization (Bosma et al., 1999). Doppler's (1980) book on beef cattle production in subhumid Togo found that mineral fertilizers and pasture improvements were generally too unprofitable for smallholders, although they would be suitable for ranches and larger farms.

ILCA studied the agro-pastoral areas near Niono in central Mali (Hiernaux et al., 1983; Wilson, 1986) over the period 1978–1984. Wilson et al. (1983, Chapter 6) elegantly describes vegetative composition, tree density and cover in the three principal land-use types near Niono. Its analysis of the species composition and yield of natural pastures compared treatments with manure, added phosphorus, grazing management and ploughing. It showed (Wilson et al., 1983, pp. 47–50), as had the PPPS work, that the Sahelian rangelands had a high production potential but that added mineral fertilizers at a rate of 22 kg ha^{-1} were 'probably not profitable' (Wilson et al., 1983, p. 50, authors' translation of the French original). Farm management research near Niono station, as reported by Toulmin and Fulton (1983, pp. 107–119), found overseeding of introduced forage species to be unsuccessful for both grasses and legumes in agronomic and economic terms over the years 1977–1980.

An example of the benefit:cost ratio of planting a tree legume (Leucaena leucocephala), simulated under commercial beef ranch conditions, came from the initial ILCA cattle model in Botswana (Cartwright et al., 1978, pp. 55–58). Depending on projected tree establishment costs and Leucaena yields, the model projected an IRR of between 2.7% and 22.4% at median establishment costs and tree yields (Cartwright et al., 1978, p. 78).

Recent experience is that the use of planted or protected forages, whether as arable crops or as browse trees and shrubs, has grown very slowly from the 1960s to the present. Such forages are still insignificant in East African and West African pastoralism, even where formerly highly mobile grazing systems have evolved to include more arable farming (e.g. Beyene, 2016, for eastern Ethiopia).

BUSH ENCROACHMENT. Bush encroachment was carefully studied many years ago. The basic East African text on rangeland management (Pratt and Gwynne, 1977, pp. 128–138) gave an overview of 'troublesome' bush species and their potential control, including by fire, machines and grazing (e.g. using goats to graze species unpalatable to cattle and sheep). The Borana study (Coppock, 1994) reviewed bush encroachment and control in the context of grazing dynamics, vegetation succession and soil. Its conclusion (updated in Angassa and Oba, 2008) is that there is no general prediction about the effects of bush encroachment, which might even be positive in some stages of land-use evolution. Prediction of crop encroachment reducing pasture area and pasture productivity was later confirmed by satellite image studies in Borana (Mesele *et al.*, 2006).

The economic analysis of bush control is not well established. Pratt and Gwynne (1997) apparently concluded that fire was the most cost-effective technique for controlling bush encroachment in East Africa but did not systematically compare fire with other methods. Sandford (1983a) concluded that chemical, mechanical and biological methods of bush control are unlikely to be effective in the African tropics, as did Homewood and Rodgers (2004, p. 252) for the rangelands of the Ngorongoro Conservation Area of Tanzania. Fricke (1979) did not really discuss the financial aspects of bush management but noted the importance of fire for the sustainability of grazing systems in Nigeria. The central Mali study at Niono ranch examined the effects of fire, species and cutting on vegetation, palatability and soil quality but did not review chemical or mechanical control (Penning de Vries and Djiteye, 1991, pp. 346–352).

Chief among the reasons for the failure of pasture improvement and related efforts to control bush encroachment through biological means (introduction of competing crops and use of mineral fertilizers) are low soil fertility and lack of water (Penning de Vries and Djiteye, 1991). There is some evidence of benefits from overgrazing in terms of preservation of perennials via the effect of lesser competition from heavily grazed annuals and protection against invasive species, again via lessened competition.

IMPACT. The impact of feed improvements in grazing systems has been very weak in sub-Saharan Africa (Table 15.3). Over the 40 years of research on grazing systems, novel plant materials remained a small fraction of feed intake, although total animal production grew substantially. There is little evidence of planted forages in sub-Saharan Africa in extensive grazing systems, even on limited areas such as feed gardens for segments of mobile herds or as calf supplements. There have been successes in humid areas of Latin America (see Chapter 13, this volume), but these have most often been on large ranches or on commercial dairies. From the Mediterranean mandate area of ICARDA, we know that long-term research on *Medicago sativa* was unsuccessful in achieving agronomic or development impact on a large scale[57] although there have been some benefits from feeding spineless cactus (Chapter 13, this volume; Jutzi and Rich, 2016) in Brazil and in North Africa.

The negligible impact of African agricultural research on forage productivity in grazing systems has some precedent. Two studies of China mention no significant impact from research on sown pastures or planted forages. Perkins' (2013) study of Chinese farming over six centuries makes no reference to pastures or planted forages in any subsystem – not in grazing or mixed systems, in temperate or tropical areas, or with reference to milk, meat or draught power. Even discussions of cereal crop residues and multidimensional crops, such as sugar beets and soybeans, do not mention their use by animals. A contemporary comparison of the lessons of Chinese agriculture for Africa does not mention livestock research – breeding, management, pastures, sown forages, genetics or nutrition – as a factor in the more rapid agricultural growth of China compared with sub-Saharan Africa (Li *et al.*, 2012). Some of the failure to intensify pasture production stems from the failure to understand that conversion of

Table 15.3. Feed recommendations in systems studies, various years.

Study	Region/period	Country/ subregion/area	Climate	Farming system	Species	Feed recommendations	Labour intensity of recommendations
Dahl and Hjort (1976)	East Africa	Western Sudan, northern Kenya	Arid to semi-arid	LGA	Cattle, camels, sheep, goats	Not specific	Unknown
Dyson-Hudson and Dyson-Hudson (1980)	Mainly East Africa	Several	Arid to subhumid	Extremely variable mobility types	Ruminants	None	Unknown
Jahnke (1982)	Sub-Saharan Africa, 1970s		Very arid to humid	LGA, LGH, LGT, MRA, MRH MRT	Ruminants	Grazing, deferred grazing plus fertilizer	Probably much higher
Sandford (1983a)	Sub-Saharan Africa, 1960s-1970s	More on East Africa	Mainly arid to semi-arid	LGA, LGH, LGT	Cattle, camels, goats	Variable across production subsystems	Unknown
de Leeuw and Milligan (1984)	Sub-Saharan Africa, 1984	Many	Arid, semi-arid	LGA, LGT, LGH	Ruminants and wildlife	Not specific	Unknown
von Kaufmann et al. (1986)	1978–1986	Kaduna, Nigeria	Semi-arid to subhumid	MRH	Cattle, sheep, goats	Crop residues, pasture with S. hamata	Mixed (highest for S. hamata)
Wilson (1986)	West Africa, 1980s	Mali	Arid, semi-arid	LGA, LGH, MRA, MRH, MIA, MIH	Ruminants	Non-specific fodder and forage crops, including browse	Unknown
Ellis and Swift (1988)	East Africa, 1980s	Northern Kenya	Arid, semi-arid, subhumid	LGA	Cattle, camels, goats, sheep	Not specific	Unknown
Solomon Bekure et al. (1991)	East Africa, 1980–1991	Kajiado County, Kenya (Maasailand)	Semi-arid to subhumid	LGA, LGH, limited MRA, MRH	Cattle	Feed gardens with *Panicum maximum* or *Pennisetum purpurem*, cowpea, pigeonpea or *Leucaena*	Mixed (highest for *Panicum*, less for browse)
Homewood and Rodgers (2004)	East Africa	Kenya/ Maasailand, Tanzania/ Serengeti	Semi-arid to subhumid	LGA, LGH, MRA	Ruminants and wildlife	Natural vegetation (pasture, browse)	Unknown
Behnke et al. (1993)	East Africa, 1970s–1980s	Ethiopia, Kenya, Tanzania	Several	LGA, LGH, MRA	Ruminants and wildlife	Natural vegetation (pasture, browse)	Unknown

Continued

Table 15.3. Continued.

Study	Region/period	Country/ subregion/area	Climate	Farming system	Species	Feed recommendations	Labour intensity of recommendations
Coppock (1994)	East Africa, 1980–1991	Ethiopia/Borana	Semi-arid to subhumid	LGA, LGT, MRA	Cattle, camels, goats, sheep	Hay making with grass, *Acacia* browse, pigeonpea	Highest with hay, lowest with browse
Barbier and Hazell (1999)	Niger, 1990s	Niger	LGA, LGH	LGA, LGH, MRA, MRH	Ruminants	Purchased feed of unspecified origin	Unknown
Kruska *et al.* (2003)	Early 2000s	global	Arid, semi-arid	LGA, LGH, MRH	Ruminants	Not specific	Unknown
Hiernaux and Ayantunde (2004)	West Africa, 1990s	Fakara, Niger	Arid to semi-arid	LGA, MRA	Ruminants	Crop residues (millet, cowpea), millet	Bran mentioned in passing, not included in economic analysis of traits
Homewood (2008)	Sub-Saharan Africa	Many		LGA, LGH	Ruminants and wildlife	Natural vegetation (pasture, browse)	Mentions division of labour, not linked to feed practices
Reid *et al.* (2008b)	1990s and 2000s	Athi-Kaputiei plains	Arid, semi-arid	LGA, LGH, MRH	Ruminants and wildlife	Not specific	Not studied
Hiernaux and Ayantunde (2004)	West Africa, 1990s	Niger	Arid, semi-arid	LGA, LGH, MRA, MRH	Ruminants	Crop residues	Careful analysis of labour use in crops
Konczacki (2014)	Literature review	Global	Arid, semi-arid	Several	Ruminants	Not specific	Unknown

grazing land to cropland is not necessarily a net loss of feed. The net change is positive at lower levels of cultivation intensity and may not become negative until quite high levels. This apparent paradox is due to the fact that crop residues from newly planted areas are valuable feeds and can be stored more easily into the dry season(s) than pastures. Cropping would be accompanied, to some degree, by destruction of invasive browse species during the fallow parts of the cropping cycle, thus improving the fodder value of the fallow. In addition, such pasture substitutes as processed feeds or cut fodder are sold near expanding towns (e.g. for the groundnut basin of central Senegal (Mortimore, 2000); the Kano close-settled zone and other parts of northern Nigeria; and the areas around Niamey, Ouagadougou, Bamako and Addis Ababa). Moreover, secondary feed effects occur, as noted by Mortimore and Turner (2005), including planting trees on cropland to replace woodlands lost to cropland expansion with variable effects on feed balances depending on climate, crop density and tree species.

ANIMAL HEALTH.   Animal health was not the main point of pastoral characterization research, except for field studies of epizootics, because so much was already known and because ILRAD's focus was on parasitology and immunology. The main diseases of grazing ruminants were: (i) trypanosomiasis, caused by protozoan parasites transmitted by the blood-feeding tsetse flies of the genus *Glossina*, which tend to be more abundant in the humid and subhumid zones; (ii) Theileriosis, most often known as ECF, another protozoan parasite transmitted by a tick of the genus *Rhipicephalus* (*Boophilus*), which is limited to 12 East African countries; and (iii) rinderpest. The principal contributions of animal health work, in terms of systems research, were those on trypanotolerance and ECF[58] as shown in Chapters 2–6 and 10 (this volume).

Animal health was the domain in which ILCA systems research had the weakest impact precisely because the principal animal health work was laboratory based or was already the object of international control campaigns. For Borana, Coppock (1994, p. 140) reported that 'animal health was never a significant focus of research'. The principal afflictions of cattle were pasteurellosis and external parasites, affecting mainly young stock and having a strong interaction with animal nutrition. There was a low incidence of trypanosomiasis in cattle (Coppock, 1994, Table E2) because herders made careful choices of grazing territories. Despite detailed animal health status measures taken in the Mali Inner Delta study on brucellosis, internal parasites, contagious bovine pleuropneumonia and trypanosomiasis (Wagenaar *et al.*, 1986), this work did not lead to animal health improvements or to associated productivity gains. The same lack of productivity effect of the field health research was seen in the Niono and Kaduna studies.

Modelling pastoralism

Numerical models, based on coefficients derived from experiments and surveys, are useful for simulating the impact of technology and policy on livestock and crop production. Many models were developed to simulate livestock demography and technology in the expectation that new methods could be adopted by herders or that such methods could be promoted by appropriately targeted policies. Despite the effort invested in models, they have generally failed, in African situations, to promote new technologies or policies. The reasons have been: (i) complex data requirements; (i) failure to measure important parameters in many studies; (iii) sampling variation in model parameters estimated from surveys and experiments; and (iv) inability to use natural parameters, especially rainfall, as control variables for policy experiments.

Significant research in rangeland modelling – soils, water, pastures, live-weight response to feed intake, management, species and breed effects – was made outside ILCA's mandate area before the mid-1970s, as presented at the 1975 rangelands symposium (ILCA, 1975)[59]. Much of this work was not directly applicable to sub-Saharan African conditions because model processes were derived from range situations – climate, breed and animal disease – in the USA, Australia or Latin America[60]. Hence, field modelling work began at ILCA in the 1970s from a narrow database and confronted difficult problems of using data and model structures from situations in the USA, Australia and Latin America that were rarely closely comparable.

PRIMARY PRODUCTIVITY. Animal production in extensive grazing systems depended more directly on grazing resources than it did on mixed-farming systems because the latter can more economically exploit cut fodder and purchased concentrates. Despite their importance, studies of primary productivity in grazing systems were rare until comparatively recently because of the long-term data requirements necessary for integrated soil–water–plant–animal models and the resulting high cost of such studies[61].

What did the models show about the potential primary productivity gains as functions of climate, soils and technology?[62] The literature review by Le Houérou and Hoste (1977) found close relationships between rainfall, as a good proxy for water availability, and pasture production in Mediterranean areas (sites ranging from 70 to 900 mm of rainfall) and in the Sudano–Sahelian zone of sub-Saharan Africa (200–600 mm). The most comprehensive early work on potential primary production around the time of the founding of ILCA and ILRAD was that at the Niono ranch (Penning de Vries and Djiteye, 1991, is a summary of many papers). A model of primary productivity, derived with annual rainfall levels below 600 mm in a hot Sahelian climate, was reported by Penning de Vries and Heemst (1975, pp. 323–328). They concluded that a basic plant production function of water availability was applicable to annual grasses on sandy soils under arid and semi-arid conditions in Mali. Later work (van Keulen *et al.*, 1981) on semi-arid pastures concluded that the model's predictions were not 'very sensitive' to most weather parameters, except rainfall, and could be 'applied with reasonable confidence' to sparse data situations in hot climates. It was noted that this primary model was only applicable to annual grasses and not to legumes or to woody species, even in the same climate and soil conditions (ILCA, 1975, pp. 336–337).

The principal findings of the Niono ranch study were that day length limits biomass production, and this can only be managed within narrow boundaries set by other constraints, such as water and soil nutrients. Water was identified as the second limiting factor for biomass production; the growth response to water is linear until it reaches a boundary set by soil fertility. Phosphorus was the next limiting factor, followed by

nitrogen once the ratio of phosphorus:nitrogen reached a given level as determined by soil type. Subsequent station and field research tested how two major constraints – water and soil fertility – could be managed biologically while producing adequate financial returns.

These soil–water–plant models established the determinants of plant production in the grazing areas. However, it has been impossible to apply their findings to technology and policy in sub-Saharan Africa given that rainfall is so variable and cannot be managed in arid climate without irrigation. The inability to control the main exogenous variable – water – becomes more binding in arid sites where most of the animals graze.

HERD DEMOGRAPHY AND STOCKING RATE. Models having stocking rate as a control variable were typically only possible under ranching conditions. For this reason, several early simulations (Cartwright *et al.*, 1978, 1982; Konandreas and Anderson, 1982; Konandreas *et al.*, 1983) adapted a US model for ranch and rangeland conditions in arid Botswana. These efforts specified a detailed model of cattle production in which pasture productivity was exogenous and in which the live-weight response to feed intake was the main function to be estimated.

This model's major result was the projected relationship between feed resources and a 'permissible' stocking rate for different classes of herders over a 30-year period, which included a sample range of very good to very bad years. It evaluated four production alternatives – calf weaning age under ranch conditions (Cartwright *et al.*, 1978, pp. 46–49) and three innovations on traditional rangeland cattle posts: a lower weaning age, a shorter breeding period and reserve pastures for calves (Cartwright *et al.*, 1978, pp. 49–55). None of the rangeland innovations appeared profitable in the simulations and, applied jointly, the three achieved only 'modest' productivity gains (Cartwright *et al.*, 1978, p. 55). Konandreas and Anderson (1982) defined policy experiments for supplementary feeding, calf offtake, weaning, sales/purchases and a drought response consisting of sales and supplementation for stock remaining in the herd. Konandreas and Anderson (1982) did not report policy simulations as functions of price, weather or exogenous technology.

CALF NUTRITION. Lambourne and Butterworth (1983; in IDRC/ILCA, 1983) stressed the importance of calf nutrition for herd growth and argued that the conflict between calves and people for milk incurred an opportunity cost in herd productivity. The initial comprehensive cattle model of ILCA (Cartwright et al., 1982, pp. 51, 58–65) examined this argument by simulating alternative milking strategies, with and without supplementary feeding, on traditional rangeland cattle production in Botswana. The economic return to milking, without supplementary feeding, was positive in the first 3 years and fell in the following two, final, model years. A mean IRR of −14.0% was estimated for the no-milking strategy without supplementation, indicating that traditional herders in Botswana had foregone significant cash income by not milking[63].

Wagenaar et al. (1986, p. 48, Table 38) subsequently measured calf live weight by milk offtake for traditional Fulani cattle in semi-arid central Mali. Their major result was an elasticity of calf live weight with respect to milk offtake between −0.27 and −0.38; a doubling of milk offtake would reduce calf live weight by about one-third. The Wagenaar et al. (1986) model was deterministic and did not generate a frequency distribution of productivity or economic benefits with respect to the milk offtake treatment; hence, it could not conclude anything about the riskiness of offtake strategies.

The Borana, Maasailand and both Mali studies all identified calf survival and weight as a major constraint to productivity; accordingly, they proposed supplementary feeding of calves as a solution. The Mali studies reported nutritional stress causing poor reproductive performance in both cattle and small ruminants as the chief cause of productivity below potential (Wilson, 1986; Wagenaar et al., 1986). Wagenaar et al. (1986, p. 51) recommended calf supplementation but only as 'a practice worth exploring', although they concluded, given the prices of meat and milk and expected live weight as a function of milk offtake, that the herders' observed average milking period of 6–13 months was roughly optimal given local conditions[64]. Solomon Bekure et al. (1991, p. 145) found calf supplementation with purchased feed to be profitable but only if cow and calf mortalities were reduced 'drastically' and only if workers were available to meet the additional labour demands resulting from supplementation.

The work of Coppock (1994) and Solomon Bekure et al. (1991) generated long-term predictions for the viability of the Borana and Maasailand systems. Coppock (1994) predicted that the Borana would be 'increasing dependent on grain purchases'[65], more cattle marketing and 'less sustainability in terms of per capita milk production and asset accumulation'; an additional implication of these trends would be greater cultivation of crops by the pastoralists and greater recourse to wage labour.

VECTOR CONTROL. Biting insects and ticks and other vectors of disease can be controlled by spraying and trapping, by killing wildlife that are reservoirs of the pathogens and by destroying vector habitats (Jahnke, 1982, pp. 142–149). Vector modelling to make control more effective has taken many forms. Estimates of the coverage of spraying campaigns are quite old[66]; recent detailed estimates are not available, but it is likely that vector control through spraying and trapping has been effective, although sporadic and on relatively small areas (Grace, 2003, p. 2, estimated that vector control was effective on 2% of the tsetse-infested area of sub-Saharan Africa). The killing of wildlife reservoirs has probably adversely affected the vector and hence limited the disease. Destruction of tsetse habitats caused by the expansion of human population and crop cultivation has been successful but is not a manageable control policy. A long-term study by Reid et al. (2000b) for 1960–2040 projected that many of the 23 African tsetse species would 'begin to disappear' but that 'for the foreseeable future' a large area in sub-Saharan Africa would remain 'infested by tsetse and under threat of trypanosomiasis'.

A NEW GRAZING MODEL. The major change in grazing systems theory, associated with the field observations derived from farming systems research, was the shift from equilibrium to non-equilibrium models (Ellis and Swift, 1988; Behnke et al., 1993; Vetter, 2004). In the former, systems are density dependent on such biotic factors as grazing intensity and population density; these factors determined the average system performance, its variability and its resilience. Non-equilibrium

systems are density independent, and abiotic factors, such as the frequency and duration of drought, are determinant. Non-equilibrium rangeland systems would not revert to a steady state, or to a long-term trend, as a function of grazing pressure or population density[67]. The shift in the basic grazing model from 'equilibrium' to 'non-equilibrium' affected the proposed technical and managerial changes in the domains of feed, species choice, the transition to settled cropping, water use and animal health.

Observations over long periods are too infrequent in semi-arid conditions to test equilibrium and non-equilibrium models. One comparison included a study over 27 years in semi-arid Senegal, which found that dry periods, with higher rainfall variability, tended to be 'non-equilibrium', while wetter periods, with lower rainfall variability, tended to be 'equilibrium' and to show density dependence (e.g. overgrazing) (Miehe *et al.*, 2010). A subsequent paper, using data from the same sites, concluded that vegetation dynamics are 'driven by precipitation not by grazing' and hence are explicable by the non-equilibrium model (Retzer, 2006). Coppock's (1994, p. 193) study of southern Ethiopia argued that density dependence is stronger in higher rainfall areas and weaker in drought-prone areas, and that long-term loss of grazing reserves has tended to increase density dependence, but these arguments have not been rigorously tested.

The policy implications of a non-equilibrium model would be that, because destocking occurs with variations in rainfall, especially in droughts longer than 1 year, efforts to impose generalized destocking independent of weather to preserve range quality fail because they impose the cost of underutilization of available grazing on herders. Blench (1994, 2001) reviewed global rangelands and argued that destocking has failed and, moreover, that restocking after drought or epizootics has been ineffective because it cannot mobilize the feed and water resources needed to revert to the previous stocking rates. Public restocking programmes have sometimes failed because of inequitable distribution of new stock because of corruption.

Homewood (2008 p. 70) asserts that an 'expanded view [one that incorporates both equilibrium and disequilibria reasoning into specific situations of rangeland ecology] has fundamental policy implications for sub-Saharan Africa'. True as this generalization may be, it has been very difficult to find examples of technology or policy research to which economic or environmental benefits may be attributed using either the equilibrium or non-equilibirum model. Attempts to apply non-equilibrium grazing practices – such as rotational grazing from more temperate climates (Vetter, 2004, p. 11) – have often failed in Africa and in the tropics more generally because rainfall is low and variable; low and variable rainfall makes rotational grazing riskier, because of its effects on the level, spatial and temporal distribution of pasture productivity, and enforces mobility across a much larger area than is possible for most pastoralists.

What did the mixed-systems studies find?

The second focus of international livestock research was on smallholder mixed farming where crops were the dominant source of income and employment and where livestock had a secondary role.

Characteristics of mixed systems in sub-Saharan Africa

Seré and Steinfeld (1996, p. 11) defined a mixed system as one 'in which more than 10% of the dry matter fed to animals comes from crop by-products or more than 10% of the total value of production comes from non-livestock farming activities. In these systems, more than 90% of the value of non-livestock farm produce comes from rainfed land use.' Ruthenberg's (1980, pp. 1–18) classification for cropping systems applied the keys of: (i) population density; (i) degree of cultivation in the system (arable land as a share of arable plus pasture); (iii) type and duration of fallow; (iv) share of irrigated cropping in total of irrigated plus rain-fed; and (v) agro-climate, typically measured by LGP and cross-tabulated against temperature, altitude and bimodal/monomodal rainfall regimes.

A more recent classification of mixed cropping systems describes them by matching details of

crops and livestock enterprises against the resource base (Dixon *et al.*, 2001). This classification[68] compared with Seré and Steinfeld (1996) has the following groups:

- Irrigated farming ('MIT' in the model of Seré and Steinfeld, 1996), included by Ruthenberg (1980, pp. 178–250) under 'arable irrigation'.
- Wetland rice ('MRT'), included by Ruthenberg (1980, pp. 178–250) under 'arable irrigation'.
- Rain-fed farming in high-potential areas, such as the West African savannahs and much of Brazil ('MRT').
- Mixed crop–livestock rain-fed farming in highland areas, such as central Ethiopia ('MRH').
- Mixed crop–livestock rain-fed farming in semi-arid areas, such as the West African Sahel north of the 500 mm annual rainfall isohyet ('MRA').
- Dualistic – a mix of large commercial and smallholder in the same general environment; these were restricted to former areas of European colonization in Africa but were common in much of Central America and Latin America.

Dixon *et al.* (2001, p. 13) defined three specific mixed smallholder systems:

- Mixed crop–livestock rain-fed farming in the highlands (corresponding to MRT), such as central Ethiopia and parts of Kenya. Such farms were typically less than 3 ha in operated area, with animal traction featuring in Ethiopia although not in Kenya, and feature mixes of annual crops, permanent crops and ruminants.
- Mixed crop–livestock rain-fed farming in low potential areas (corresponding to MRA), overlapping with grazing (LGA), such as the West African Sahel north of the 600 mm annual rainfall isohyet; farms would be much larger in such areas, with low cereal and grain legume yields per hectare.
- Rain-fed farming in high-potential areas (MRT for rain-fed and MIT for irrigated), such as the West African savannahs and in much of Brazil and Colombia. Farms in Latin America were typically much larger than those found in the Sahel or in the highlands of East Africa.

Mixed farming in these three systems differed from pastoralism by the presence of the following:

- Majority shares of cropping in total income and employment.
- Varying shares of livestock in income and employment, with lower shares in food consumption compared with pastoralism.
- More unequal distribution of cattle between households, although this was compensated to some degree by more equal distribution of small ruminants.
- Less animal mobility or none, which was limited to seasonal transhumance or to daily movements near permanent villages. In the Latin American systems, with private and fenced grazing lands, there would be no seasonal or annual mobility.
- New livestock functions, notably nutrient recycling and the use of draught animals for cultivation. These functions would be much less important or even absent in Latin America.
- Important shares in income and employment of annual and semi-perennial cash crops – cotton, groundnut, rice, roots and tubers – that did not exist in rangelands. In the Latin American and Middle Eastern production types, animals are the cash commodity.
- Important shares in income and employment of perennial cash crops – coffee, tea, cocoa, rubber and oil palm – that are found in mixed systems with poultry, swine and small ruminants, although much less often with cattle.
- Commercial dairying with zero grazing, planted forages, purchased feeds, and cultivation of annual and perennial crops on the same farm.
- Commercial on-farm fattening of ruminants, swine or poultry, in zero-grazing or transhumant systems, using purchased feeds and crop residues from annual and perennial crops.

Although it is evident that people and animals are more concentrated in the mixed systems, estimates of the distributions of tropical smallholders, and their livestock, are difficult because of a lack of accurate data linking production and input use to farm size and structure. It is even more difficult to derive productivity estimates for

individual farming systems, for example by the share of livestock in income or assets.

LEVELS AND RATES OF CHANGE IN FARM SIZES.   Levels and rates of change in farm sizes in the 1960s–1980s are impossible to estimate by agroclimate in sub-Saharan Africa because of a lack of comprehensive data. However, published meta-analyses make the trends clear for farm size, as measured in area per worker, and in type of farm. Masters *et al.* (2013) found that 'Africa and Asia experienced a gradual decline in total land available per rural worker' over the period 1960–1970 to 1999–2000. The same decline can be seen over the period 1990–2015 (Masters *et al.*, 2013, p. 2). Associated with this decline would have been some consolidation of subsistence farms into commercial farms in densely populated areas. An earlier paper of Hazell *et al.* (2010, p. 11) found a decline in median farm size in 16 countries (all regions) over periods ranging from 1970 to 1990 to 1998 to 2001.

Hazell (2013) compared farm size trends in Asia and Africa from 1970 to 2011 and further projected trends to 2030 and to 2050. He noted that rural population growth would fall (Hazell, 2013, p. 1) substantially from 2011 to 2030, compared with the earlier period, and would fall again from 2030 to 2050. While the expected fall in rural population growth reduces pressure on farm sizes, it is associated with other problems of farm consolidation, the transition from subsistence to commercial farming and the potential for extreme inequality among smallholders.

A global summary (Lowder *et al.*, 2016) found the usual problem with data coverage in tropical countries. It confirmed other findings about the fall in mean and median holdings in sub-Saharan Africa, while stressing the fact that land abundance in sub-Saharan Africa was limited to a few countries. The great majority of sub-Saharan African smallholdings would be less than 5 ha (Lowder *et al.*, 2016, Fig. 5) and such holdings would be 50–70% of agricultural area.

IMPROVED PLANT CULTIVARS.   Improved cultivars of cereals have become nearly universal on farms of all types in India, Indonesia, China and Brazil. Sub-Saharan Africa has lagged East and South Asia in adopting modern cultivars but has recently begun to converge. Walker and Alwang (2015, pp. 265–293) studied diffusion of modern plant varieties in sub-Saharan Africa from the 1960s to 2011. Technical progress in crop management, as indicated by uptake of modern varieties in sub-Saharan Africa, was significant during that period. At the beginning of CGIAR research on mixed livestock systems (1976–1980), the share of cropped areas in seven major cereals – sorghum, maize, pearl millet, rice, teff, wheat and barley – was low, ranging from roughly zero in teff and barley, to 6% in sorghum, to 37% in wheat, with an area-weighted average of 3.0%. The area sown to modern varieties grew at an average annual rate of 1.4% (Walker and Alwang 2015, p. 389) from 1998 to 2011. The average for the seven cereals had grown to 31% in 2006–2010, with values of 52% in maize, 62% in wheat and 36% in rice; most of the area growth was in maize (52% of the total growth from 1976–1980 to 2008–2010) and in sorghum (20% of the total growth from 1976–1980 to 2008–2010). There were important increases in the areas planted to improved cultivars of other crops such as cassava, yam, soybean, cowpea, common beans and groundnut (Walker and Alwang, 2015, p. 344).

There are no comprehensive data on modern variety adoption by agroclimate in sub-Saharan Africa from Walker and Alwang (2015). The national averages (Walker and Alwang, 2015, p. 346) show rapid growth of area under modern varieties in countries and crops – maize and sorghum in Nigeria; maize, sorghum and teff in Ethiopia; and pearl millet in Mali, Senegal and Niger – where mixed crop–livestock are the principal farm types in humid (Köppen climate *A*) and semi-arid (Köppen climate *B*). These patterns imply that important benefits accrued in mixed livestock systems from additional crop residue output produced by modern varieties, although we cannot quantify these benefits or attribute them to (crop) research fields other than plant breeding and pathology[69].

Data on the yields of modern cultivars in sub-Saharan Africa are less comprehensive than data on area planted. Walker and Alwang (2015, p. 354) estimated that a 1% increase in the share of area under improved cultivars was associated with an increase in TFP of about 0.47 in a sample of 30 countries covering most of sub-Saharan Africa. Older data reported by Walker and Alwang (2015, p. 355) gave average

yield increases of 41% for nine crops and 38% for 21 crops at varying periods from 1970 to 2000.

FERTILIZER USE. Fertilizer use in the initial ILCA studies of mixed farming – Debre Zeit and Debre Berhan in highland Ethiopia, Kaduna in subhumid central Nigeria, Ibadan in southwest Nigeria, and Niono and the Inner Delta of the Niger in semi-arid Mali – probably did not exceed 10 kg/ha at any site before 1990. Input use grew as average cultivated land per person fell. While fertilizer-use data are unreliable before 2000, it was clearly very low across sub-Saharan Africa before this century. Current estimates are less than 15 kg/ha in West Africa and less than 20 kg/ha in East and southern Africa.

The delay in developing and extending productive seed/fertilizer packages for crop farming in sub-Saharan Africa, compared with South Asia and East Asia, had a negative indirect effect on livestock production. Seed and fertilizer packages were not always highly profitable under experimental conditions, especially in more arid sites, indirectly reducing potential feed production for ruminants. New seeds and fertilizer were less profitable under farmers' conditions in sub-Saharan Africa; strong evidence for this fact is the 20–40-year lag between the rapid growth of high-yielding variety/fertilizer packages in South Asia and the slower growth of these packages in sub-Saharan Africa.

Crop–livestock interactions in mixed systems

Most of the work on mixed systems was done in the semi-arid tropics of central India, the Sahel of West Africa, the subhumid savannahs of sub-Saharan Africa and the highlands of East Africa, mainly in Ethiopia and Kenya. Examples of such studies in the IARCs were chiefly, but not only, from ILRI, ICRISAT and the Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT) as shown in Table 15.4.

Grazing and mixed systems present many complex interactions. Bourn and Wint (1994, pp. 4–5) reviewed 20 aerial and ground surveys of livestock and land use carried out between 1980 and 1991 in Mali, Niger, Sudan, Chad and Nigeria, covering a broad range of grazing and mixed smallholder systems. The surveys found many common elements: (i) positive relationships between plant and animal biomass; (ii) positive relationships between livestock distribution and land-use intensity, rural settlement density and mean annual rainfall (Bourn and Wint 1994, p. 6); (iii) weak seasonal effects on animal biomass in arid and humid climates, implying less seasonal animal mobility in both; (iv) stronger seasonal effects on animal biomass in the '750–1250 mm rainfall band' (Bourn and Wint 1994, p. 9), implying more animal mobility; (v) a declining threat from tsetse and trypanosomiasis because of 'agricultural expansion, deforestation and the removal of wildlife' (Bourn and Wint 1994, p. 15); and (vi) in Nigeria, probable undercounts of 25% of domesticated livestock populations compared with official figures, indicating that the hypothesized conflict between crop and livestock production had been overstated.The principal research goals on mixed systems with comparatively weak integration between crop and animal production were as follows:

- To define constraints to higher productivity in the power, soil nutrient, feed production and animal management components of mixed farms.
- To introduce or improve animal draught power with a research focus on higher work output through health and feed interventions.
- To improve nutrient cycling by using manure on crops.
- To feed crop residues and higher-quality planted forages to ruminants.
- To introduce dairying and small-ruminant fattening into mixed farms.
- Ultimately to raise livestock and crop productivity jointly by exploiting positive interactions between the two components.

Some examples of feasible technical changes in mixed enterprises included the following:

- Applying seed/fertilizer packages.
- Shifting the livestock enterprise mix to dairying and intensive stock raising (poultry, pigs, small ruminants) components.
- Improving feed production by planting forages or by treating crop residues in densely populated areas (semi-arid tropics of India, Ethiopia, northern Nigeria, and cotton-producing areas of West Africa), whether for animal traction, dairying or on-farm fattening.

Table 15.4. Mixed crop–livestock systems studies, various years.

Study	Region/period	Country/ subregion	Climate	Farming systems	Scale of research	Animals	Main crops	Biotic factors	Abiotic factors	Technologies
Von Kaufmann et al. (1986)	West Africa, 1979–1986	Nigeria, Kaduna	Arid to semi-arid	MRH	Household, territory	Cattle	Pearl millet, sorghum, maize, cassava	Soil, water, health, feed	Rainfall, temperature	Subsistence dairy
Wilson (1986)	West Africa, 1978–1986	Mali	Arid to semi-arid	MRA, MIA	Household, territory	Cattle, camels, sheep, goats	Pearl millet, cowpea	Soil, water, health, feed		
Powell (1986a,b)	Sub-Saharan Africa, 1980s–1980s	West Africa	Arid to semi-arid	MRA, MIA	Household, territory	Ruminants	Pearl millet, sorghum, maize, cassava	Soil, water, microbes	Rainfall, temperature	Animal traction
				MRH				(Primary studies)	Water, fire (?)	Mixed farming without animal traction
								(Primary studies)		Manuring crops
								Nutrient cycle	Altitude (Primary studies)	Animal fattening Grazing reserves
Pingali et al. (1987)	Sub-Saharan Africa	Many	Semi-arid	MRA, MIA	Sub- Saharan Africa	Ruminants	Maize, cotton, pearl millet, sorghum, paddy, cassava, cowpea	Grazing, feed		Animal traction
			Subhumid	MRH						Tractor mechanization Mineral fertilizer
			Highlands Humid Highlands	MRT MRH						
Gryseels (1988); Gryseels and Anderson (1983); Getachew Asamenew et al. (1993)	East Africa, 1970s early 1980s	Ethiopia	Highlands	MRH, MRT	Territory	Draft oxen, cattle, sheep	Wheat, barley, teff, faba	Grazing, feed	Rainfall, temperature, frost risk	Dairy

Reference	Study	Location	Agroecology	System	Unit	Livestock	Crops	Pest	Climate	Technology
Norman *et al.* (1988)	Southern Africa and West Africa, 1970s–1980s	Botswana	Arid to semi-arid	MRA	Household	cattle	Sorghum, cowpea, watermelon, maize, groundnut		Heat, aridity	
		Debre Berhan	Cool highlands	MRT	Household	Dairy, work oxen, sheep				Animal traction
		Nigeria Debre Zeit	Subhumid to cool highlands	MRH MRT			Millet, sorghum Teff, wheat, faba			Land management
Walker and Ryan (1990)	South Asia, 1975–1990	India, semi-arid tropics	Semi-arid to subhumid	MIA, MRA	Household, village	Work oxen	Paddy, pearl millet, sorghum, pigeonpea, chickpea	Soil, feed	Water	Mechanization, high-yielding varieties, fertilizer water harvesting, tractorization
Bartholomew (1988)	West Africa, 1984–1989	North-west Mali	Semi-arid	MRA, LGA	Households	Cattle, work oxen	Mixtures of millet and cowpea	*Raghuva* spp.	Rainfall, temperature	Animal traction, manurefor crops
McIntire *et al.* (1992)	Sub-Saharan Africa	22 countries in sub-Saharfan Africa	Semi-arid	MRA, MIA			Maize, cotton, pearl millet, sorghum, paddy, cassava, cowpea, teff, wheat	Grazing, feed	Heat, aridity	Animal traction
			Subhumid	MRH			Sorghum and cowpea	*Stiga hermonthica*	Short growing season	Cattle fattening on farm, animal fattening
			Highlands Humid	MRT MRH			Millet, sorghum			Crop residue use Manure use
Ehui and Spencer (1993)	Nigeria, 1980s	Nigeria	Subhumid to humid	MRT	Households		Cassava, maize, rice, cowpea, yam, melon, plantains			Fertilizer, hand cultivation, tractors

Continued

Table 15.4. Continued

Study	Region/period	Country/subregion	Climate	Farming systems	Scale of research	Animals	Main crops	Biotic factors	Abiotic factors	Technologies
Sanders *et al.* (1996)	1970s–1990s	Sub-Saharan Africa, semi-arid tropics	Semi-arid	MIA, MRA	Households		Pearl millet, sorghum, maize, cowpea	Soil, fertilizer, crop cultivars	Water	Irrigation
Bosma *et al.* (1999)	West Africa, 1977–1987	Southern Mali	Semi-arid to subhumid	MRA, MRH	Households, territory	Cattle, work oxen	Maize, cotton, pearl millet, sorghum,paddy			Fertilizer, hand cultivation, animal traction
Hill (1982); Mortimore (2000)	Sub-Saharan Africa	Northern Nigeria	Semi-arid	MRA, MRH						Hand cultivation, fadama irrigation
Dixon *et al.* (2001)	Global tropics	Many	Arid/ semi-arid Humid	MRA, MRH, MRT MIA, MIH, MIT						
			Highland tropics	LGA, LGH, LGT						
Hiernaux and Ayantunde (2004)	West Africa, 1990s and 2000s	Niger	Arid to semi-arid	MRA	Household, territory	Cattle, camels, sheep, goats	Pearl millet, cowpea	Soil, grazing, feed		
Baltenweck *et al.* (2003)	Sub-Saharan Africa, Latin America	Colombia, India, Kenya, Sri Lanka, Nigeria, Niger	Semi-arid	MRA, MIA						(Primary studies)
	South Asia	Subhumid Highlands Humid		MRH, MIG MRT, MIT MRH						

- Diversifying crop production and processing by adding annual cash crops, such as oilseeds, cotton and grain legumes, which would have a secondary effect of providing more feed.
- Cycling nutrients[70] in mixed grain–livestock farms by feeding crop residues to stock and by restoring manure to fields.

Predictions about the evolution of mixed systems strongly influenced the initial international research in the 1970s. New theories of farming systems (e.g. Boserup, 1965; Ruthenberg, 1980; Binswanger and Rosenzweig, 1986) provided a deeper understanding of how tropical agriculture evolved under the influence of population density, market access, information costs and incentives.

The first prediction was that nomads would settle to become crop farmers. This prediction depended on the view that sedentarization was desirable because it was more productive and would allow better provision of social and infrastructure services to the former nomads. Some mixed-systems research therefore sought to identify the policies and technologies that would reduce the transition costs of the inevitable sedentarization.

Related to the settlement prediction was a later view from the characterization literature. Thornton *et al.* (2002, maps 16a and 16d) contended that there would be major long-term changes in growing periods and in locations of dense livestock and human populations related to climate. The combined effects of these changes would be to shift the West African rangeland units into mixed systems and to eliminate mixed highland systems in East and southern Africa. Jones and Thornton (2009) noted that climate change might push marginal, low-productivity farmers in West Africa into livestock activities, thereby increasing pressure on rangelands.

A second prediction was that closer integration of crops and livestock would be more productive than separate enterprises. Integration would allow more efficient use of resources – animal power, manure and crop residues – that were underused when crops and livestock were managed separately. Many development projects, and their associated research components, acted on this prediction and attempted to accelerate this integration (McIntire *et al.*, 1992, pp. 4–5).

A third prediction was that smallholdings would gradually consolidate into larger commercial enterprises because such units could exploit economies of scale in technologies and management. This prediction was a stimulus to mechanization research, which varied among regions, being stronger in Asia and Latin America than in Africa.

This evolutionary model influenced the three principal themes of research on mixed systems: (i) mechanization; (ii) soil fertility management; and (iii) feeding systems. A fourth theme – improved animal health – was viewed as necessary to achieving results in the other components.

MECHANIZATION. Animal traction had been practically universal among smallholders in the semi-arid tropics of India and in highland Ethiopia for centuries. It had begun to grow rapidly across sub-Saharan Africa in the 1970s. Despite the infrequency of use of animal traction in most of tropical Africa, it was believed that land-abundant areas within sub-Saharan Africa had the potential for mechanization with animals. Mechanization would allow an expansion of cultivated areas and a concomitant increase in crop yields. The efforts to realize these potential gains made farm mechanization with animals an important part of research at ILCA, and to a much lesser extent of ICRISAT, from the 1970s and to the mid-1990s[71].

Mechanization research started from three assumptions:

1. Animal traction was the core component of mixed farming and could create productive interactions among other components that would not occur if those components were separate; Jahnke's (1982, pp. 134–140) summary of livestock development problems in tropical Africa is an example of this view.
2. Animal draught power could increase the cultivated area per worker, could stimulate diversification into more profitable crops and, by improving the quality and timeliness of farm tasks, could raise yields per unit of land.
3. Better animal nutrition could allow more power from livestock and hence extend the hypothesized benefits of area, cropping pattern and yield.

The second assumption – that animal traction would produce substantial area, yield and cropping-pattern benefits – led to many studies of constraints to animal power. These studies often failed to find adoption of animal traction, even where livestock disease was manageable and where adequate feed was available. Pingali *et al.* (1987) explained the mixed adoption of animal traction across sub-Saharan Africa in terms of labour use and fallow type; they concluded that the driving force for mechanization with animals was not output benefits but labour savings in areas of annual cultivation where the transition from forest or bush fallow to grass fallow had taken place and where heavy soils created additional demand for power over what hand hoes could provide.

Pingali *et al.* (1987) complemented a literature review with original farm interviews about the gains from animal traction. They found that area benefits were positive (Pingali *et al.*, 1987, pp. 99–101) and averaged about 25% per person; that yield gains (animal-cultivated fields over hand-cultivated fields for the same crop) were often zero because the quality of tillage with animal traction was not better than that with hand hoes; and that impacts on cropping-pattern diversity were important only where cotton and groundnut had been introduced.

Animal and machine power was introduced into farming systems as a function of population density, given the need to cultivate the same plots repeatedly to suppress weeds, and in response to better market access from proximity to cities, higher population density areas and the introduction of cash row crops, notably cotton and groundnut. The presence of trypanosomiasis, long held to block draught power by restricting cattle production, was shown to be a secondary constraint in the humid and subhumid areas where other climate and population factors weakened the demand for animal power. The core conclusion – the introduction of animal traction into farming systems was a long-term response to growing population and cultivation density, rising wages and the introduction of cash crops (Pingali *et al.*, 1987; McIntire *et al.*, 1992) – greatly weakened the research emphasis on animal draught power in mixed rain-fed systems where animal power was absent or nascent.

The second assumption was that poor animal nutrition constrained draught power. This assumption was tested in many experiments examining animal breed and type (dairy cows or oxen) and feed type (quantity and quality of additions to basal diet of crop residues) at sites in Mali, Ethiopia, Niger and semi-arid India (Renard, 1997). The ILCA research in Mali summarized their findings as: '...dry-season supplementation and weight gain would not improve work output and would be unlikely to increase the amount of land cropped or crop production' (ILCA, 1994, p. 134). The lead scientist for the Malian trials under experimental conditions concluded that work output during the brief 2-week ploughing season '...seem[s] to be unrelated to an animal's body energy reserves at the start of work' (Bartholomew 1988: p. 59). An experiment using dairy cows for traction in Ethiopia found that supplementation allowed additional work while (almost) maintaining the milk output and reproductive performance of the cows (ILCA, 1994, pp. 134–136). Further work (ILRI, 1998, pp. 178–183) in Ethiopia compared working cross-bred dairy cows with non-working dairy cows and traction with local oxen alone, plus improved management of feed and animal housing. The working cross-bred treatment did not produce higher incomes compared with the non-working cross-bred treatment or the local oxen treatment. An ILRI experiment on a semi-arid experiment station with sandy soils in Niger measured energy expenditure of working bulls and oxen (Fall *et al.*, 1997), feed intake and the effects of body condition on work; two important conclusions were that roughage intake did not increase during work and that weight losses during work did not cause reductions in power output (Fall *et al.*, 1997, Chapter 6)[72]. Station and field research on animal power in sub-Saharan Africa did not generally find that nutrition was a serious constraint to adoption or to optimal use of animal power.

ANIMAL POWER AND MIXED FARMING IN SUB-SAHARAN AFRICA.   The view that animal traction had a leading role in developing mixed systems in sub-Saharan Africa was examined by McIntire *et al.* (1992, pp. 47–72), following the study by Pingali *et al.* (1987). McIntire *et al.* (1992) found that components of mixed farming – feeding crop residues to stabled or mobile animals, manuring crops, and investing in dairying and on-farm fattening – existed in many sites without

animal traction. They concluded that using animals for power was not a necessary condition for mixed farming. An example was found in a field study of mixed smallholders in south-eastern Burkina Faso, where Delgado (1980) found that sample farmers practised some elements of mixed farming (manuring, crop residue grazing, fattening animals on farm) but not animal traction.

The mechanization research at ILRI with the greatest development impact was that leading to the broad-bed and furrow maker (BBM), as recounted by Rutherford (2001, 2008). Rutherford's 2008 analysis found a rate of return to ILCA/ILRI research and development of the BBM to be in the order of 0.1%. This was much higher than the negative return found in the 2001 study, the difference being attributed to the greater availability of credit, farmers' adaptation of the BBM tool to their circumstances, and the resulting area and yield effects from greater experience with the tool.

ANIMAL POWER AND MIXED FARMING IN THE SEMI-ARID TROPICS OF INDIA. ICRISAT began work on mixed irrigated and rain-fed cropping systems in the semi-arid tropics of central India (Jodha *et al.*, 1977). These systems were in a hot and usually dry climate, with a single monsoon season, and consisted of small family farms growing ICRISAT mandate crops (sorghum, pearl millet, groundnut, chickpea and pigeon pea) and others (irrigated paddy, cotton, castor and vegetables), usually with bullock power. The chief livestock research component was on the role of animal power for management of Vertisols, cultivation, transport and processing with some work on crop residues. Other national and international research in South Asia concentrated on food crops, on technical changes in irrigation, and on mechanization compatible with smallholdings; livestock research concentrated on animal traction and smallholder dairying (e.g. Singh, 1990, pp. 204–232, on rural poverty in South Asia; Walker and Ryan (1990, on the semi-arid tropics of India).

The centrepiece of ICRISAT's limited livestock work in India were the village-level studies (Walker and Ryan, 1990). These studies allowed a better understanding of the roles of livestock in the semi-arid tropics of South Asia and led to a reorientation of mixed-system smallholder research. This reorientation conceded that public research on mechanization either added too little to farmers' knowledge of crop management – the case of most animal traction research – or could be done better and faster through adaptations in the private sector – the case of most tractor research. Herbicides were proposed as an alternative to animal or tractor mechanization (Le Moigne, 1979, pp. 219–220), but herbicides have only recently become competitive in countries where rural wages have risen rapidly; if herbicides have replaced hand weeding in sub-Saharan Africa, it would be a recent development.

In 40 years of national and international work on animal traction in West Africa, there have been no significant technical changes induced by research findings that are clearly distinguishable from the changes induced by rising population density, cheaper market access and external economies arising from lower implement production costs. The arguments of Pingali *et al.* (1987) and McIntire *et al.* (1992) derived from the evolutionary models of Boserup (1965) and Ruthenberg (1980), and the mixed findings of station and field studies of animal power, effectively ended the era of projects seeking to introduce animal power as a necessary component of mixed farming.

SOIL FERTILITY MANAGEMENT. Low soil fertility was long understood to be a major cause of the lagging productivity of tropical agriculture. Significant work was started in the 1960s and 1970s, in Africa, South Asia and Latin America, on soil fertility management with different emphases for the systems found in each region. Soil fertility work had substantial scientific impact on all continents, but its development impact varied greatly by region, farm type and source of water for cropping.

The Africa soil fertility focus was on nutrient cycling in mixed systems because of the prediction that animal manures were 'slack resources' that could be used more efficiently where crops and animals were managed on the same farm[73]. The integration of crop and animal production would occur in part through nutrient cycling through linked mechanisms: the 'exchange' of plant residues from crops to animals, and the 'exchange' of manure and urine from animals to crops.

Nutrient cycling was studied by Powell *et al.* (1996). The orientation of ILCA/ILRI work on nutrient cycling was on smallholder farms,

where the cycle was soil to food crop to animal to soil and crop vegetation[74].

Feed systems

All characterization research found feed scarcity, in quality and in dry-season quantity, to constrain the livestock component whether animals were used for milk, power or meat production. Three interventions, with increasing levels of management costs, were proposed to unbind this constraint: (i) crop residue management; (ii) sown forages, including alley farming; and (iii) ley farming.

CROP RESIDUE MANAGEMENT. Crop residue management – harvesting, storing, chopping, making hay, field grazing or the many other possibilities – was found to be quite common but has been difficult to improve through research. ILCA's compilation of research on 'Plant Breeding and the Nutritive Value of Crop Residues' (Reed *et al.*, 1988) cited no successful examples of improvement of crop residues in the tropics (nor did the book by Renard, 1997), through plant selection or breeding, or by chemical or urea treatment beyond chopping or other practical methods that farmers can already use (see Chapter 14, this volume). The Walker and Ryan (1990) book covering a decade of on-farm research in the semi-arid tropics of India noted that the unit value of fodder in the study villages was sometimes as high as that of grain, but found few examples of crop residue improvement or of planting of specialized fodder crops to replace crop residues in ruminant diets, even where the fodder value of crop residues was high for dairy production or for animal power.

SOWN FORAGES AND LEY FARMING. Sown forages and ley farming have usually failed in the African tropics. Chapter 13 (this volume) reviews attempts to introduce sown forages into mixed systems in Africa, with reference to the success of pasture grasses in Latin America, while Chapter 14 (this volume) covers multidimensional crops. Nordblom *et al.* (1992, 1994), in analysing a Syrian site, identified land cost as the most direct reason for the failures of sown forages in the tropics. The available alternatives – weeds, field boundaries, crop residues and browse – are cheap and of high enough quality that their benefits surpass those of sown forages (Sumberg, 2002; McIntire and Debrah, 1987).

Where ley farming did emerge, it did so almost exclusively in 'unregulated' form (Ruthenberg, 1980). Where it does exist, it evolved as part of smallholder dairying in temperate highland areas where cross-bred European–African cattle could be raised, rather than from progressive adoption by sedentarized pastoralists. One limited success was achieved around Kaduna, in subhumid central Nigeria, where *Stylosanthes hamata* was introduced as 'fodder banks' in mixed systems (von Kaufmann *et al.*, 1986). Despite the technical promise of fodder banks, their long-term area and yield effects have not been precisely estimated in Nigeria or elsewhere in West Africa. Other obstacles to ley farming were seed costs and farm size (Christiansen *et al.*, 2000, p. 191, and the papers cited therein for the Mediterranean; Ruthenberg, 1980, for East Africa; Tiffen *et al.*, 1994, pp. 164–166, for Kenya; Powell, 1986a for central Nigeria).

Nordblom *et al.* (1994) reviewed field and station studies of a rotation of wheat and *M. sativa* with sheep grazing in north-west Syria. They found historical adoption of *M. sativa* as a pasture crop to be limited in West Asia and North Africa. Their modelling work showed *M. sativa* to be 'less profitable than traditional rotations' and its adoption to be sensitive to farm size, milk prices and soil nutrient carryover effects to the following wheat crop.

FODDER TREES. Fodder trees started with the purpose of adding nitrogen to leached or otherwise infertile soils, thereby improving the soil nutrient stock while contributing nitrogen to cereal and tuber intercrops. The field model of this idea is 'alley farming' – typically planting rows of nitrogen-fixing trees between rows of food crops, such as maize or cassava. Several synthetic works established the basic science of the alley farming model (Kang *et al.*, 1990; Sanchez, 1995; Giller, 2001), followed by many subsequent applications and extensions (Sumberg *et al.* 1987; Jabbar *et al.*, 1996). Promising work was done on economic and environment benefits of silvopastoral systems in Latin America (Ibrahim *et al.*, 2010, p. 189–196).

One extension of the alley farming model was to use nitrogenous browse as a supplementary feed for small ruminants, given the lack of CP

available in grasses or crop residues in the humid tropics. This extension was successful in raising soil nitrogen stocks, in lifting intercrop yields and in providing higher CP content to livestock (Kang *et al.*, 1990, pp. 340–345), while being profitable in an economic sense (Kang *et al.*, 1990). Experiments with livestock were done at two ILCA sites in Nigeria, on alley farming using nitrogenous trees in the humid zone near Ibadan and using leguminous forages (without alleys) and manure recycling at the subhumid site near Kaduna. The latter had greater impact potential because it took place in an agroclimate with lower trypanosomiasis pressure and less heat and humidity, allowing higher ruminant density and productivity.

Jabbar *et al.* (1994) showed that continuous alley farming would be more profitable than alley farming with short fallows or farming with fallow but without the alleys nitrogen-fixing trees. Reynolds and Jabbar (1994) showed that the major benefit of supplementing free-roaming small ruminants in West Africa with the foliage of leguminous trees (*Leucaena* and *Gliricidia* spp.) was an increase in survival, and that the forage was best directed at late-pregnant and lactating females. In East Africa, cross-bred dairy cows showed a significant response in milk production to supplementation with *Leucaena*.

The International Centre for Research on Agroforestry (ICRAF) estimated that 'fodder shrubs have been widely adopted in East Africa, by an estimated 205,000 smallholder dairy farmers by 2005' (Place *et al.* 2009). There is no reliable estimate of direct tree yields or of their indirect effects on crop or livestock yields.

ANIMAL FATTENING ON FARM. On-farm animal fattening was studied as a familiar technology with potential for improvement by using slack resources, especially crop residues and other cut fodder, with local animal breeds. Research themes included: (i) the productivity of supplementary feeds to crop residues and cut grasses; (ii) the introduction of new feeds, notably tree and herbaceous legumes; and (iii) the timing of fattening and sales. Examples of performance trials are given by Bartholomew (1988) and those cited in McIntire *et al.* (1992, pp. 135–164). The emergence of many small peri-urban fattening units, for ruminants and for poultry,

has been rapid in this century but is a function of income growth, urbanization and falling intermediation costs, and does not appear to be related to technical packages developed by research.

Conclusions

What were the impacts of LSR, done mainly by ILRI and its predecessors, on the scientific and development problems of grazing and mixed livestock systems in Africa? How did new knowledge improve productivity or equity in the principal livestock systems?

Scientific impact

LSR has had a strong scientific impact in pastoral and mixed systems. This scientific impact was notable in: (i) dismantling the 'mainstream view' of pastoralism and replacing it with a new model of pastoralism that is biologically and economically more credible than the mainstream view, which has been antiquated for 50 years; (ii) classifying and mapping systems; (iii) estimating productivity parameters to develop bioeconomic models, which have been used particularly in modelling climate change effects; and (iv) applying the network research model to the study of trypanotolerance at disparate field sites.

A NEW VIEW OF PASTORALISM. The core of the 'mainstream view' was that African herders kept too many animals for cultural reasons and that such overstocking caused overgrazing. The systems studies and related work destroyed this view. A first attack on the 'mainstream view' was the demonstration that animal productivity per hectare in the grazing systems was not uniformly worse, and was sometimes better, than that of ranching systems. Such research further demonstrated that herd structures did not consist excessively of older males kept for sentimental reasons or held against risks beyond their optimal sale age[75]. The age/sex compositions of herds did not consist of 'excess' males, as the 'mainstream view' had contended, given the milk production objectives of herders and the low marginal costs of feed and labour needed to maintain male stock to a roughly optimal sale age.

A second part of the 'mainstream view' was that pastoralists' management practices determined stocking rates. The 'mainstream view' held that maintenance of stocking rates above biologically sustainable values led to overgrazing and eventually to destruction of the range. The rise of 'non-equilibrium' models of pasture dynamics (led by Ellis and Swift, 1988) fortified the new view by stating how pasture dynamics depend on abiotic factors and not primarily on the decisions of pastoralists themselves.

A third tenet of the 'mainstream view' was that crops and livestock would inevitably face a general land conflict as population density and cultivation density rose. This hypothetical conflict would reduce grazing areas and, with fixed pasture yields for given rainfall, would reduce livestock production. The attack on this tenet came from the practical fact that cereal and legume crops in the semi-arid and subhumid zones, which house the majority of African ruminants, produce crop residues that are valuable as feed. The growth of crop production, even in areas marginal for arable farming and even in the absence of feeding grain directly to animals, allowed more livestock production, not less, by the indirect channel of additional crop residues.

It should be acknowledged here that part of the scientific impact achieved through the new view of pastoralism derives from the older work of anthropologists, notably the work of Dupire (1972), Monod (1975), Dyson-Hudson and Dyson-Hudson (1969), Oxby (1975) and Stenning (1994), among others. That work, in East and in West Africa, laid an empirical foundation for the new view of pastoralism which recognized the rationality of extensive grazing (as clearly stated by Barbara Grandin in 1987 in an early ILCA paper on Maasailand).

Sandford (1983a, pp. 11–18) best summarized the refutation of the 'mainstream view'. He argued that the 'mainstream view'[76] of grazing systems was wrong, anticipated the non-equilibrium critique and asserted that policies to reduce overgrazing were misguided because the evidence for overgrazing was weak. Sandford (1983a) contended that:

- definitions of overgrazing – changes in vegetation from an undisturbed state ('climax vegetation') to a disturbed one, or loss of productive capacity over time – were not rigorous enough to permit recommendations of alternative management practices to stop overgrazing;
- estimates of overgrazing were biased upwards because measures of animal numbers and of pasture quantity and quality were sparse or inaccurate;
- the 'mainstream view' of the dynamics of overgrazing – a movement from undisturbed vegetation subject to grazing to disturbed vegetation of lowered grazing capacity – was contradicted by observations of pastures whose productivity had been improved by heavy grazing; and
- there was a logical inconsistency in positing overgrazing where stocking rates were highest while simultaneously assuming that such high stocking rates were infeasible on pastures degraded from overgrazing.

The critique of the 'mainstream view' led to a new development path for pastoralism. The new path allowed herd expansion while promoting public investments around grazing areas and regulating conflicts over land and water. This new development path proceeded by:

- improving animal health by controlling disease, mainly rinderpest and trypanosomiasis;
- defending grazing lands by laws and regulations; new laws and regulations reduced conflicts between herding and farming groups and in so doing limited the costs of violence;
- introducing water interventions to raise productivity per animal by reducing trekking times;
- introducing planted forages, as arable crops or as browse trees and shrubs, and supplementary feeds *targeted to a subset of the herd or flock*, such as sedentary milk herds or small ruminants for fattening; and
- accommodating mixed land use of crops, livestock and wildlife.

The studies of Pratt and Gwynne (1977), Ruthenberg (1980), Sandford (1983a), Le Houérou (1989), Solomon Bekure *et al.* (1991), Coppock (1994), Blench (2001) and Lesorogol (2008) projected variants of that generic path. A detailed development pathway for pastoralism was drawn for the Borana system of southern Ethiopia (Coppock, 1994, pp. 272–295; on water, pp. 202–209).

MAPPING SYSTEMS. The outstanding scientific achievement of the various LSR studies, carried out by ILRI and many partners from 1975 to the present, has been to develop a new view of grazing systems that can generate better policies for rangeland management. This view started from the observation that direct efforts to improve rangelands – pasture and breed improvement and grazing restrictions – had failed. It continued with the contention that rangelands could become more productive if herders benefitted from public investments in human and animal health, water, transport and markets, communications and social protection. The findings of rangeland scientists about the potential of arid areas did not differ greatly from those of earlier scientists in terms of raising biological potential, but they did differ in terms of defining an appropriate sequence of policy and public investment to achieve that potential.

Landmark papers – Coppock (1994) for the Borana system in southern Ethiopia; Solomon Bekure *et al.* (1991), for Maasailand in Kenya; Wilson (1986) in north-central Mali; Wagenaar *et al.* (1986) in the Niger Delta of Mali; von Kaufmann *et al.* (1986) in subhumid central Nigeria; and Hiernaux *et al.* (2009) in semi-arid western Niger – not only contributed to knowledge about these areas but also established methods of studying them and induced changes in related research and development programmes.

The major system papers over the past 20 years – Seré and Steinfeld (1996); Thornton *et al.* (2002); Otte and Chilonda (2002); Kruska *et al.* (2003); Robinson *et al.* (2011, 2014), plus the many papers on climate change as discussed in Chapter 16 (this volume) – modernized the methods for defining production systems and reduced the estimation errors for areas, animal numbers and feed balances. This research has clearly had an impact on scientific understanding (Class I) even if it is impossible to estimate the development benefits of this type of research. Work in this century on livestock and the global environment has had a similarly large Class I effect (see Chapter 16, this volume).

The specific scientific achievements were as follows:

- Estimating the economic and environmental weight of livestock systems.

- Development of better survey and analytic tools for estimating system scale and potential across continents.
- Creating methods to compare and reconcile national statistical estimates and remote sensing estimates.
- Reducing errors in estimates of woodland, wildlife, crop and grazing areas, permitting closer analysis of actual and potential resource conflicts.
- Better projections of animal numbers across climates and countries, which eventually produced better estimates of global environmental effects[77] and, very recently, refinement of Tier 2 estimates of greenhouse gas emissions from livestock.
- Planning investments in irrigation, grazing, protected areas, disease management, vector behaviour and control, predator control and wildlife interactions.
- Understanding seasonal effects on plant and animal biomass, wildlife and domestic stock biomass, and animal mobility.

DEVELOPMENT CONSTRAINTS IN AFRICAN LIVESTOCK SYSTEMS. An important scientific impact, from work not always led by ILRI but often done with its support and advice, was in the transversal systems studies. These include the publications of Sandford (1983a)[78] and others on pastoralism; Pingali *et al.* (1987) on animal traction in the farming systems of sub-Saharan Africa, McIntire *et al.* (1992) on crop–livestock integration in sub-Saharan Africa, Thornton *et al.* (2002) on livestock and poverty mapping, Baltenweck *et al.* (2003) for crop–livestock interactions on three continents, Thornton and Herrero (2001) on crop–livestock simulation models, McDermott *et al.* (2010) on sustainable mixed systems and Herrero *et al.* (2012). Moreover, they have added to the scientific and development consensus about what to avoid in grazing systems – introduction of exotic animal breeds, hurried privatization of communal grazing tenure, restriction of mobility and oversowing of pasture in conditions unfavourable to the viability of introduced plants.

PRODUCTIVITY PARAMETERS. The representativeness and accuracy of estimated productivity parameters – such as fertility, mortality, morbidity,

milk production and animal growth – were poor when the older systems studies were launched. The goal of estimating factor and input productivities for the main African livestock systems was completed in the first half of the modern era, as shown in ILCA (1979a) for the subhumid zone of West Africa, Wilson (1986) for Mali, Wagenaar *et al.* (1986) for the interior Delta of Mali, von Kaufmann *et al.* (1986) for central Nigeria, Coppock (1994) for Borana, and Solomon Bekure *et al.* (1991) for Maasailand[79]. Following the work begun in the 1960s and 1970s, the scientific understanding of grazing systems productivity has deepened such that policies and projects can be prepared with comparatively cheap additional background work. One important example is the contemporary use (e.g. de Haan, 2016) of parameters derived from the ILCA systems studies in Mali (Wilson *et al.*, 1983; Wilson, 1986). The policy recommendations of de Haan (2016) depend in part on data and analysis from earlier field studies.

A related use of the data – to apply the estimated input–output parameters in systemic models that can simulate technical, policy and management changes – has scientific validity but has had little or no productivity impact. Reasonably detailed and accurate policy analyses have used the input–output parameters (Thornton *et al.*, 2006; Nelson *et al.*, 2009; Thornton and Herrero, 2010; de Haan, 2016), but resulting policy recommendations to date have not had measurable and attributable welfare impacts.

BIOECONOMIC MODELS.   A second methodological contribution was the application of bioeconomic models to grazing and mixed systems, using station, field and remote sensing data. Examples are Penning de Vries and Heemst (1975), Cartwright *et al.* (1978, 1982), Konandreas and Anderson (1982), Konandreas *et al.* (1983), Itty (1992), Itty *et al.* (1995a,b,c) and Solomon Bekure *et al.* (1991). The influence of this work on poverty analytics is discussed by Thornton and Herrero (2001); Thornton *et al.* (2002, 2006) and Rich and Perry (2011). This work has achieved much in establishing empirical models and in applying them to targeting and analysing effective treatments. Many applied examples to the field of livestock and climate change are discussed in Chapter 16 (this volume).

A recent book (de Haan, 2016, pp. 79–122) presents an integrated bioeconomic model that uses and extends some of the research discussed in this chapter. This book made the first effort to compare the benefits and costs of technical interventions to preserve livelihoods in East and West African drylands. While it is premature to estimate the economic effects of the model, which depend on application of the proposed interventions by governments (health, market integration and promoting recovery from drought through small ruminants), this book is a landmark contribution to more scientific policy making, which uses many of the historical efforts of ILRI and its predecessors.

THE NETWORK RESEARCH MODEL[80].   A further methodological contribution was the study of trypanotolerance and trypanotolerant animals through a novel international network of scientists (Trail *et al.*, 1979a,b; Murray *et al.*, 1990; ILCA/ILRAD, 1988; Rowlands and Teale, 1994; Itty, 1992). The purpose of ATLN (ILCA/ILRAD, 1988, p. 32) was to provide 'a better understanding of genetic resistance, acquired resistance, environmental factors which affect susceptibility and the efficacy of present control measures, and second by ensuring optimal application of both existing knowledge and recent research findings' (see also Chapter 2, this volume)

ATLN allowed a rapid growth of knowledge about trypanotolerance across 18 countries, mainly in village situations, in the humid and subhumid climates of sub-Saharan Africa. The work included status reports beginning in 1979, the establishment of field sites in the early 1980s and ultimately the production of a series of landmark papers. Published work after more than a decade of the ATLN had established the genetic basis of trypanotolerance, clarified the relationship between the animal's ability to control parasitaemia and to control anaemia, developed novel diagnostic tools and laid the basis for selecting for trypanotolerance in young stock (Murray *et al.*, 1990, p. 381).

Development impact

THE DIRECT DEVELOPMENT IMPACT OF LSR IN PASTORAL AREAS.   The direct development impact of LSR in pastoral areas has generally been weak. It is generally impossible to measure the *ex post*

economic impact of grazing system studies by estimating a function relating output or productivity to research or by using indirect methods, such as analysis of citations. Attempting to map the use and effects of new technologies, as proposed by LSR, is also impossible. For these reasons, we conclude that LSR in sub-Saharan Africa has failed to contribute significantly to technical change.

The tropical examples of how knowledge of pastoralism, as derived from characterization research or from integrated work on station and on farm, have changed technologies, policy and productivity are from ranches in Latin America. Despite more than three generations of research in pastoral systems of sub-Saharan Africa, no productivity effects have been observed corresponding to those achieved in soil fertility, pasture management or beef breeds in Latin America.

The chief development impact of grazing systems studies since the 1960s has been to defend the economies and rights of pastoral peoples. This defence, which is an indirect effect of research and extension, has taken the form of grazing rights legislation and consultation with pastoral peoples on their economic, demographic and political interests. Such legislation may have contributed to higher productivity in some grazing situations, but this impact cannot be measured without detailed biological, economic and cultural studies (e.g. Lesorogol, 2008, on northern Kenya, which is an unusual study because it used two survey rounds and stratified by 'privatized' and 'communal' tenure).

Part of the defence of pastoralists' rights has been to enforce pastoralists' rights or to stop bad policies (de Haan, 2016, pp. 59–61 and 76–77). An example of this defence is the research finding that old legislation, such as the 1965 Grazing Reserve Law of Nigeria (Waters-Bayer and Taylor-Powell, 1986a) had set aside land for herders use but that the areas actually allocated were much smaller than projected. A recent example of the new rights of pastoralists has been the genesis of new laws and regulations governing pastoralism in West Africa. IEMVT, relying on its long tradition of work in the Inner Delta of the Niger in Mali, proposed a 'Code Pastoral' (Gallais and Boudet, 1980) specifying political, legal and institutional reforms designed to regulate land use and to protect the rights of all users – arable farmers, herders and fishers – in the Delta. In

Niger, Peyre de Fabrègues (1984) advocated a pastoral code to define the rights and responsibilities of herders and farmers, thereby allowing the development and preservation of pastures. The later study of FAO/CIRAD (2013) delineated years of progress in establishing and protecting the legal and administrative rights of West African pastoralists. The FAO/CIRAD (2013) study showed advances in national laws and regulations in Mauritania, Senegal, Mali, Burkina Faso, Niger and Chad, and in international treaties and local administrative practices, all of which have served to protect pastoralist economies against encroachment by arable farming, commercial ranching, urbanization and land grabs by outsiders. While pastoralists' rights are still precarious in much of Africa, research by national and international programmes has contributed to the understanding of pastoralism and to the defence of pastoralists' rights and welfare.

Another successful example is the long tradition of research on the economic aspects of controlling tsetse and trypanosomiasis, to which ILCA/ILRAD/ILRI work has contributed in part over many years (see Chapter 3, this volume). This began with Hans Jahnke's path-breaking work (1974, 1976, 1982), continued through the African Trypanotolerance Livestock Network (ILCA/ILRAD, 1988; Itty and Swallow, 1994), the summary of Swallow (2000), and the detailed investigations by Shaw (2004) and Shaw *et al.* (2015), for example. This work has allowed the definition of control models and has provided valuable advice to extension services on the application of those models.

Other possible exceptions are usually not applicable to livestock whether in grazing or in mixed systems. These include: (i) research in which crops, not livestock, were the principal treatment; (ii) the finding of positive returns to new livestock technologies using *ex ante* rather than *ex post* techniques (Bryant and Snow, 2008; Kristjanson *et al.*, 1999a, for a trypanosomiasis vaccine; Kristjanson *et al.*, 1999b, for genetic enhancement of cereal crop residues; Thornton *et al.*, 2003, for dual-purpose crops); (iii) efforts to adapt research in temperate countries, where there is a long history of research, data and controlled conditions for estimation and attribution of treatment effects; and/or (iv) research on tropical ranches under more controlled conditions and in more favourable climatic conditions at larger scale.

THE WEAK IMPACT OF LSR ON PRODUCTIVITY IN GRAZING AREAS. This weak or nil impact is often attributable to poor experimental design. For example, the treatments studied had no effect, because the treatment effect was not measured correctly or because the original research was not designed with economic impact in mind. In some instances, treatments spread through extension and hence the research effect could not be separated from the extension effect. This conclusion about the weak impact of technology innovations applies more forcefully to grazing systems than to mixed systems, where crop research has had a significant indirect effect on animal production via the pathway of higher grain and crop residue output. One notable failure of grazing systems research was testing treatments under unrepresentative conditions; the prominent example of this failure was grazing reserves or group ranches that were too small or that lacked adequate water or land for stock movements.

An important example of LSR's effect on animal health is the development of the infection-and-treatment method vaccine against ECF, as discussed in Chapter 6 (this volume)[81]. The targeting of this method to specific types of livestock production in East and southern Africa has resulted from the work of Brian Perry, Adrian Mukhebi and colleagues on the epidemiology of *Theileria*.

LSR has generally failed to contribute to successful project preparation and management in grazing and mixed systems (Wanyoike and Baker, 2013). The contribution of research to the development impact of pastoral projects funded and/or managed by the International Fund for Agricultural Development (IFAD) or FAO, as measured in a sample of 194 projects from Latin America, East Africa, the Middle East and North Africa, was not significant.

Components of higher plant productivity under ranching conditions – fencing, rotational grazing, notably pasture improvements using legumes or exotic grasses, mineral fertilizers and use of exotic animal breeds – and attempts in projects to introduce them usually failed.

Mixed systems

Proposed development pathways in mixed crop–livestock systems had the common objective of integrating crops and livestock with, in some instances, specialization in dairying. The logic behind specific technical interventions – adapting animals for farm mechanization, using crop residues as feed, recycling soil nutrients through application of manure or crop residues and introducing high-yielding dairy cattle – was that on-farm resources were underused and could be made more efficient if managed in an integrated crop and livestock enterprise.

Farm mechanization

One core assumption of LSR was that a lack of adapted tools and quality feed for draught animals blocked crop–livestock integration (Le Moigne, 1979). This assumption was investigated by ICRISAT in India and in West Africa and by ILCA in Ethiopia and West Africa along two lines – developing new farm tools and improving the condition of work animals. Neither the tool line nor the work conditions line produced widely adopt innovations by farmers beyond the intensification response to the increasing value of draught power at higher cropping intensities. Station work on tools did not produce successful innovations and was ultimately abandoned in the 1980s by ICRISAT and in the 1990s by ILCA/ILRI. Station research on feeding draught animals was more successful in that a positive effect was observed on work capacity, but this result did not translate into adoption because alternatives to crop residues for supplemental feeding of work animals were too costly.

The books by Pingali *et al.* (1987) and McIntire *et al.* (1992) prompted a rethinking about agricultural mechanization in Africa, including views on animal nutrition as a factor in stimulating demand for work animals. The authors of these publications found many sites where animals were commonly used for tillage and cultivation, even with feed being scarce in the same sites. They also found many sites with adequate feed, in terms of quality and seasonal availability, with little or no draught animal power in use. They concluded that livestock nutrition was not a significant constraint to the adoption of animal traction in sub-Saharan Africa and that research on the topic should accordingly be limited.

The sustained growth in farm mechanization in sub-Saharan Africa over the past 30 years is strong evidence that mechanization, with

tractors or animals, does not face insurmountable biological or cultural obstacles and has not blocked growth. The present consensus is that animal traction is a viable path for higher farm productivity, but that research has done, and can do, little to widen that path. Where conditions for the use of animal draught power do not exist – because of low cropping intensity, a domination of bush fallow, animal disease and/or poor market access – then research on health and feed can do little to expand animal draught power. The same lack of demand would, of course, occur if there is a weak yield, area or cropping-pattern effect attributable to animal power on farm, but research to strengthen these effects has not succeeded where the systems conditions are unfavourable. Even as seed and fertilizer packages became more widely used, beginning around 1990 (Walker and Alwang, 2015), they could be used without animal traction and hence did not require or induce greater crop–livestock integration.

An exception to generalizations about agricultural mechanization is the simultaneous introduction of animal power with a cash row crop, such as cotton in the subhumid zone of West Africa, groundnut in the sandy soils of Senegal, Mali, Niger and Nigeria, or maize in the subhumid savannah. In such areas, simple extension programmes, combined with profitable crop production packages, have promoted mechanization without significant new research.

CROP RESIDUES. There is scant evidence of any research impact on animal nutrition, livestock productivity or on soil quality despite the effort invested in feed in mixed (and pastoral) systems. Proposed improvements in feed resources have tended to fail to be completely adopted and have only been partially adopted (see Chapter 13, this volume, for an explanation of adoption failures of planted forage grasses and legumes in the tropics). Ley farming, in the Mediterranean or in the highlands of East Africa, generally failed because farm size and environmental conditions were unfavourable to this technology for anything other than specialized dairy production. The failure of such proposed improvements in communal systems contrasts with the success in ranching, where private land tenure and access to markets, finance and veterinary care made investment in primary productivity more remunerative.

A major indirect effect on livestock productivity occurred via the adoption of higher-yielding crop cultivars. Although the Walker and Alwang (2015) record of area and yield increases of improved cultivars did not discuss effects on fodder or by-product yields in any of the species studied, Indian experience with major cereals (rice, wheat, maize, sorghum and pearl millet) has shown such effects to be important (Blümmel *et al.*, 2013, 2014; see also Chapter 14, this volume). A related effect, although not well measured or related to research or extension investments), was the expansion of irrigation and the associated growth of double or triple cropping, allowing higher fodder output per season and longer periods of fodder abundance.

THE LEGACY OF INADEQUATE CROP RESIDUE RESEARCH. The older work found that crop residues were important shares of animal diets in the livestock systems studied by ILRI, ICARDA and ICRISAT, and in South Asia (Reed *et al.*, 1988; Kelley *et al.*, 1993; Renard, 1997)[82]. Recent studies in sub-Saharan Africa (e.g. Hiernaux and Ayantunde, 2004) have confirmed this pattern. Crop residues have always been a significant share of ruminant feed intake on small mixed farms; there is significant growth potential from better use of crop residues, and it is likely that the increase in crop residues associated with higher grain production has stimulated livestock production.

IARC research has done too little on crop residues as feed, despite their importance for smallholder livestock throughout sub-Saharan Africa, West Asia and North Africa, and South Asia. A recent and major example of this shortcoming is the Africa book by Walker and Alwang (2015), which does not report crop residue yields[83] or relate them to grain yields. While the allocation of crop residues between crops and animals was a major research theme at ILCA, in the semi-arid tropics and the Ethiopian highlands, and to a lesser extent at ICARDA in Mediterranean climates, the impact of this work on livestock systems productivity has been weak. *The failure to devote adequate research to crop residue quality, and its relation to the harvest index, is the single most important gap in African livestock research.*

NUTRIENT CYCLING. The extensive soil fertility research for mixed farms in sub-Saharan Africa has had an indirect and weak development impact. Nutrient cycling in mixed systems has been studied by Powell *et al.* (1995) for sub-Saharan Africa, and Boddey *et al.* (1996) for Brazil and Colombia. This is not because mineral fertilizer use has not grown; there has been significant growth of fertilizers and other modern inputs in sub-Saharan agriculture since the mid-1970s. First, most of the stimulus for mineral fertilizer use has come from economic growth and market development in many African countries, which had both demand and supply effects on fertilizers applications (Townsend, 1999; Morris *et al.*, 2009). A second stimulus has been intensification of farming systems under the pressure of population growth and greater market access. An indirect effect of research has been on the recent growth in areas sown with new plant varieties, especially of maize, which has stimulated fertilizer use.

What blocked the translation of scientific impact into development impact?

The contradiction of strong scientific impact and weak development impact was seen in both pastoral and mixed systems. This contradiction had several causes: (i) the difficulty of raising primary productivity in arid and semi-arid regions; (ii) the small farm mandate of the international centres, especially in sub-Saharan Africa; (iii) the persistent misapplication of models from other agricultural systems; (iv) policy bias against agriculture; and (v) lack of background data at the outset.

LOW PRIMARY PRODUCTIVITY IN ARID AND SEMI-ARID AREAS. The translation of knowledge into productivity has largely failed in the dry areas. One strong indicator of this failure is that there have been few sustained investments in plant production (e.g. de Haan, 2016). Hypotheses about the share of primary productivity in the yield gap between actual and potential yield, for both grazing and mixed smallholder systems, proved fruitful in terms of scientific impact but less so in terms of economic impact. New planted forages have not been generally successful in the African tropics, with the chief exceptions of cut and carry forages in highland dairying systems and nitrogenous trees in the humid tropics. The straw components of multidimensional crops have been highly successful as by-products of research on cereals, but breeding programmes targeted at changing plant architecture to lower the harvest index have not done well. An indirect effect of the failure to raise the quantity and quality of feed production was the limited profitability of animal fattening because of the high costs of feed. If the profitability of fattening is changing (e.g. de Haan, 2016), it is more the result of higher incomes shifting demand than it is to research reducing production costs.

THE IARC MANDATE. The mandate of the international centres in sub-Saharan Africa and South Asia – to concentrate on small undercapitalized farms that used few purchased inputs and not on large specialized ranches, tree crop estates or well-capitalized arable farms[84] – explains some of the failure to observe a higher development impact of systems research. This is not a criticism of the mandate – it is a statement of one of its inevitable consequences – nor does this mean that the international centres should have concentrated on larger, more capitalized farms; it means that the choice of the small mixed farmer as the principal IARC client necessarily reduced returns to research because the mandate area is more difficult. The long-term success of private animal breeding research in the USA, for example, is a complement to public research in the USA that has no analogue in sub-Saharan Africa.

FACTOR PROPORTIONS AND THE MISAPPLICATION OF EXTERNAL MODELS. One obstacle to applying research results in sub-Saharan Africa was the misapplication of principles from ranching systems in the USA, Australia, New Zealand and Latin America. These principles – commercial orientation, private land tenure, pasture improvements and limited animal mobility – were generally not applicable to African pastoralism. A confirmation of this was the finding, long ago, that African rangeland systems were already efficient in terms of live-weight production per hectare, as shown by Cossins (1985) comparing East Africa and Australia, and Breman and de Wit (1983) for the USA, Australia and Mali. Other examples of technology transfer failure include planted forages and fencing. Despite

their efficiency at low cash investment and high labour input, the African pastoral economies have not grown as fast as other sectors in the same economies; this is not because of a failure to apply research results but rather from the inability to generate research results that raise productivity in arid and semi-arid climates.

A contributor to weak research impact has been the persistence of errors in defining problems. Beginning with the fundamental error of ILCA – that technologies existed in 1975 that could raise productivity of African livestock – the pattern continued for decades and was seen as recently as the recommendation of Little and Dube (2011) for species and breed diversification in pastoralism. This recommendation has failed because breed selection and upgrading for cattle in the African tropics has long been blocked by heat, thirst, disease and insects; none of these adverse factors has been removed by research (with again the notable exception of the eradication of rinderpest in 2011). Beyond breed diversification, cross-breeding in cattle has been unsuccessful in grazing and mixed systems. The only major success is the use of higher-yielding dairy animals in the cooler highlands of East Africa. The reason, as shown in experiments and in the opinions of the herders, was that exotic races were more susceptible to heat, thirst and disease.

Contrasting factor proportions – historically low labour:land ratios in some parts of sub-Saharan Africa and much higher ratios in others – produced contrasting obstacles to research. It may be argued that rural labour scarcity has disappeared in Africa with the doubling of rural population density over the past two generations, but this is not the way to look at labour scarcity. Labour scarcity is a function of relative wages. If urban productivity, and the purchasing power of urban labour, are higher than the corresponding rural values, then labour will be scarce in rural areas even if rural population density has grown. If rural technologies lag behind urban ones, then so will rural productivity, producing the appearance of rural labour scarcity.

POLICY BIAS AGAINST AGRICULTURE. The long history of bias against market agriculture in Africa is well documented. Macro-policies were unfavourable to technologies that were profitable under experimental conditions (e.g. exchange-rate policies would have discouraged the production of tradable beef and encouraged production of non-tradable milk).

Lack of complementary policies and extension effort reduced the development impact of technologies. An example is trypanosomiasis control. In the absence of a vaccine against this disease, an integrated campaign was needed to apply the knowledge derived from systems research – drug use, management of resistance, vector control and management of trypanotolerant stock – and practically all elements of such an integrated campaign have been difficult to sustain because of fiscal choices made by African countries.

LACK OF BACKGROUND DATA AT THE OUTSET. System information – soils, rainfall, LGP, land-use mapping and productive capacity – only became generally available 10–20 years after independence in sub-Saharan Africa[85]. It took many years for such information to spread and to be usable to policy makers and producers; lack of information about resources would have limited uptake of technologies adapted to specific resource types.

The lack of background data at the outset of the systems studies was aggravated by some features of older research. Many older studies were too qualitative, had data quality problems, notably small sample sizes, and demonstrated failure to conduct or use station research jointly with field studies. In sharp contrast to the African situation 50 years ago, environmental data in 2020 is much more widely and cheaply available, and lack of such data can no longer be adduced as a reason for costly research delays.

This chapter has found few examples of *ex post* economic analysis of grazing systems research and development in sub-Saharan Africa. Such analysis rarely shows value in LSR because the data were not collected or because returns were negative where the treatment effect was nil or even negative[86]. Where there were data on inputs and outputs needed to estimate productivity, it is difficult or impossible to establish a functional link between research effort and productivity at the level of the decision-making unit of the farm or the policy unit of the sector. Lastly, in most grazing systems, detailed studies are not needed to show that research has failed to raise productivity (whether by increasing output or by lowering

input costs) and hence the necessary work to make productivity research estimates has never been done.

DATA PROBLEMS IN LIVESTOCK STUDIES. Many livestock studies had data problems that vitiated their use in technology or policy analysis. Many studies were done over periods that were too short to capture interseasonal and interannual variability because longer studies were thought to be too costly. Given the interannual variability in rainfall and feed supply, observations of even as long as 5 years produced noisy estimates of productivity and its determinants. Even where the biophysical data were of adequate quality to allow economic analysis (e.g. the Nigeria study by von Kaufmann *et al.*, 1986, or the Mali studies of Wilson, 1986, Wagenaar *et al.*, 1986, and Penning de Vries and Djiteye, 1991), their samples across units and time were usually too small to make reliable parameter estimates for periods longer than 2 years. Even where data were of adequate coverage, problems of selection bias, definition of the control or relevance of the treatment made data analysis inconclusive at best.

LSR WAS SPARSE AND TOO OFTEN QUALITATIVE. There are few examples of rigorous productivity estimates in LSR, even of single livestock technologies. One example is *A History of Farming Systems Research* (Collinson, 2000), which has 12 chapters and more than 50 authors on dozens of topics under the general theme of farming systems research in the tropics, covering work from 1960 to the late 1990s. The book has only three empirical studies of animal production: goat mange in Kenya (pp. 130–137), and alpaca and dual-purpose cattle in Peru (pp. 341–354). It fails to mention ILRI and its predecessors, while devoting only a few pages (pp. 110–111) to on-farm research with livestock.

The ICRISAT compendium on 'Socioeconomic Constraints to Development of Semi-arid Tropical Agriculture' (Ryan and Thompson, 1980) published some 5 years after ICRISAT's founding has more than 40 papers, which focus almost entirely on crops. There is one section of the paper on animal traction for smallholdings, one chapter referring to milk production, scant mention of forage crops and one paper (Le Moigne, 1979) on specific problems of on-farm research with livestock or with animal-powered implements.

Another prominent example of a lack of quantitative work is Sandford's (1983a) landmark book on pastoralism in the third world, which has no quantitative analysis of technologies, such as grazing management, pasture improvement, animal breeding, calf supplementation, water investment or public infrastructure. Early quantitative work, such as the cattle model of Konandreas and Anderson (1982) or the Thornton (1987) model for Colombia, and others tended to have short lives and apparently were not applied to generate or to induce gains in productivity.

DISCONTINUATION OF LONG-TERM BIOECONOMIC STUDIES. Work after the merger of ILCA and ILRAD has largely dropped integrated long-term studies, with the exception of the work in Fakara and the Kenyan dairying studies of the mid-1990s. Despite the changes in population density, cropping intensity, market access, animal numbers, herd composition and infrastructure (transport, communications, water and energy) and urbanization since the 1980s, the only recent integrated work in African grazing systems is that of Homewood and Rodgers (2004) and Homewood (2008) for East Africa, Lesorogol (2008) for northern Kenya, FAO/CIRAD (2013) for the Sahel and some chapters in Catley *et al.* (2013). The decline in long-term field research has stopped the generation of adequate data on research and productivity and has therefore prevented comparisons over time. Replacements with *ex ante* projections over very long periods will continue to give uncertain results and therefore will continue to be unreliable policy guides.

The Future

The long-term data requirements of livestock systems studies are made more urgent by secular changes in crop and animal productivity imposed by climate shifts. Therefore, for mixed and pastoral systems alike, it will be necessary to conduct new field data collection and analysis while respecting the hypothesis testing requirements of climate change models, especially with respect to parasitology and resistance to abiotic stresses, notably heat and water scarcity. The long-term effort to sustain and use the ICRISAT

village-level studies in India should be a model for LSR in sub-Saharan Africa. The fact that we are unable to make reliable estimates of the economic return to agricultural research, and especially to livestock research, in sub-Saharan Africa means that a new dedicated effort is required over many years; this effort will be expensive.

Pastoral systems

Governance research should be extended in pastoral areas with the explicit political goals of defending the land rights of pastoralists and preserving minimum areas for these groups.

Long-term data collection and analysis should be restarted for pastoral systems in northern Kenya, southern Ethiopia and in parts of Mali, Niger and Sudan. Special efforts must be made where the conflict between wildlife and domestic livestock is acute, in both economic and biological terms; this is pointedly true along the entire length of the Rift Valley. Such

data collection needs to be linked to verifying predictions of climate change and disease distribution models as a way of contributing to policy debates and of estimating the costs of policy measures.

Mixed systems

Efforts should be made to strengthen or restart long-term data collection and analysis in densely cultivated areas, such as northern Nigeria, the East Africa highlands and the river basins in the Sahel.

Acknowledgements

Notes

[1] ILRI refers to its predecessors, the International Livestock Centre for Africa (ILCA) and the International Laboratory for Research on Animal Diseases (ILRAD), unless otherwise noted. The English acronym ILCA is used in place of the French acronym CIPEA (Centre International pour l'Elevage en Afrique).

[2] One member of ILCA senior management in the 1980s, on his first visit to a Nigerian research station, was informed that cross-bred dairy cattle often suffered from heat stress in the tropics; he suggested that they be put in air-conditioned stalls 'as the Saudis do'.

[3] The expressions 'grazing systems', 'pastoral systems' and 'pastoralism' are used interchangeably to refer to farming systems in which: (i) ruminants are the main stock and are raised largely for subsistence; (ii) open rangelands, including browse from trees and shrubs, are the principal source of feed; and (iii) herds are mobile, across places, seasons and years. The use of 'pastoral' here is distinguished from the term 'pastoral farming' used in parts of the USA, Canada, Argentina, Brazil, Australia and New Zealand, which is a form of private commercial livestock production in which the animals are not mobile and often feed on sown enclosed pastures.

[4] Discussion of *Livestock's Long Shadow* (Steinfeld *et al.*, 2006) is in the chapter on climate and tropical livestock production (Chapter 16, this volume).

[5] Chapter 16 (this volume) discusses the relationship between climate change and tropical livestock production.

[6] We use 'characterization research' and 'farming systems research' interchangeably. Most characterization work fits into the Zilberman and Heiman (2004) classification of policy studies as Class 1 (provision of economic information) or Class II (devising innovations).

[7] Risk management and system resilience goals were infrequently stated in earlier livestock research at IARC, although there are exceptions (Binswanger, 1980, for mixed farming in the semi-arid tropics of Central India; Anderson and Dillon, 1992, for the global drylands).

[8] We refer to research under the controlled conditions of research stations and ranches as 'experiments' and to research under on-farm conditions as 'surveys' or as 'farming systems research'.

[9] The creation of farm typologies was a staple of farming systems research in the francophone countries and such typologies were, in theory, used to target extension messages.

[10] LGP is the 'period in days during a year when precipitation exceeds half the potential evapotranspiration' (FAO, 2014).

[11] There are some Köppen cold arid climates (Bwk) in southern Africa but there is very little IARC livestock research on them.

[12] Mongolia and Central Asia are not tropical but their livestock systems are often characterized by aridity and nomadism, so they are appropriate comparisons with tropical systems in these respects.

[13] There are two higher-elevation livestock types in West Africa: the Mandara mountains bordering Nigeria and Cameroon (Requier-Desjardins, 2011), and the Fouta Djallon of Guinea.

[14] Global estimates of livestock systems scale were unreliable until the path-breaking work of Seré and Steinfeld (1996), which became the base of subsequent classifications. While Seré and Steinfeld included non-ruminants in their classification, we concentrate only on ruminants.

[15] Seré and Steinfeld (1996) presented two systems – landless livestock monogastric production system; and landless livestock ruminant production system – which are not discussed here.

[16] Estimates of farm incomes are unavailable at earlier dates.

[17] An example of spatial heterogeneity from highland Kenya is given by de Steeg *et al.* (2009). An example of managerial heterogeneity is given by Norman *et al.* (1979, p. 57) who found 230 distinct crop mixtures grown in the semi-arid tropics of northern Nigeria.

[18] 'Mixed farming' and 'agro-pastoral' are used interchangeably throughout this book.

[19] A tropical livestock unit or TLU is 'equivalent to one bovine of 250 kg live weight'. Typical conversion factors in sub-Saharan Africa are: cattle = 0.7 TLUs, sheep and goats = 0.10 TLUs, pigs = 0.20 TLUs and chicken = 0.01 TLUs.

[20] East and southern Africa includes Angola, Burundi, Ethiopia, Kenya, Madagascar, Malawi, Mozambique, Rwanda, South Africa, Tanzania, Uganda, Zambia and Zimbabwe. West and Central Africa here includes Burkina Faso, Cameroon, Chad, Côte d'Ivoire, Ghana, Mali, Mauritania, Niger, Nigeria and Senegal; the other West and Central Africa nations of Guinea, Guinea-Bissau, Liberia, Sierra Leone and Togo have done little work with ILRI and its predecessors.

[21] The countries surveyed were Bangladesh, Ecuador, Ghana, Guatemala, Madagascar, Malawi, Nicaragua, Nigeria, Nepal, Pakistan, Panama and Vietnam.

[22] Catley *et al.* (2013), including studies of the Republic of Sudan, Tanzania, Ethiopia and Kenya, was inconclusive on changes in inequality. Devereux (2006, p. 75) reported a Gini coefficient of 0.74 for income among pastoralists in the Somali Region of Ethiopia.

[23] Alene's calculation depends on the weighting structure of the productivity data. An alternative weighting structure gave only a 0.1% annual productivity increase (Alene, 2010, p. 229).

[24] The study by Wilson (1986, p. 14) over 6 years in semi-arid north central Mali argued that the 'degree of dependence on the animal raised' was the primary criterion, not mobility, which he contended was 'contingent' on the degree of dependence on animal products in food consumption and in income. In practice, high dependence on animal products in consumption and income is always associated with mobile grazing in Africa.

[25] Global environmental effects are estimated in Chapter 16 (this volume) on 'Ruminant Livestock and Climate Change in the Tropics'.

[26] Tribe *et al.* (1973), whose authors included at least one future ILCA Board Chair, dismissed African pastoralism as lacking the capacity for rational management (see pp. 14, 23, 24 and 53). The report alleged that such incapacity caused overgrazing (p. 11) and called for large-scale public intervention to manage livestock movement, marketing, soil, water and vegetation (pp. 23–24).

[27] The first Board chair of ILCA declared the standard view of African rangelands in 1975 (Hodgson, 1975, p. 19): 'The productivity of the animal population [in Africa] is low and inefficient. A significant cause is the low and deteriorating productivity of the rangelands.'

[28] Leaving aside Arctic and high-altitude grazing.

[29] '…of the 80 herbaceous tropical arid zone species of forages which have been tried at Niono (550 mm) in Mali in 1977–1980, not one single species became established and amenable to produce a grazing impact' (Le Houérou, 1989, p. 149).

[30] Le Houérou (1989, p. 149) mentioned the successful implantation of *Acacia tortilis* and *Acacia senegal* near M'Bidi, Senegal.

[31] Hodgson's address to the 1975 Sub-Saharan Africa Rangelands Seminar, which was the first major international scientific meeting of the new ILCA, explicitly declared the 'cultural' reasons for the supposed overgrazing and supposed low productivity of rangelands.

[32] As stated in the Swynnerton Plan for Kenyan agriculture, as summarized by de Wilde (1967, p. 4, pp. 174–187) for Kenya, Smith (1976, pp. 110–151) and Thurston (1987). The biased and ultimately

unproductive notion of pastoralist mismanagement was insightfully criticized by ILCA/ILRI scientist Ralph von Kaufmann (von Kaufmann,1976).

[33] Grigg continued to say, correctly, that it would be unwise to enforce sedentarization of pastoralists.

[34] Many distinguished scientists were involved in the Borana work including Jean-Claude Bille, Assefa Eshete, Michel Corra, C.S. Kamara, Mark Nicholson, Jess Reed, Solomon Desta and Andrea Woodward.

[35] Recent work (de Haan, 2016) introduces subclasses of LGA and livestock grazing (LG) semi-arid and LG sub-humid, which would apply to parts of the Borana study area.

[36] Toutain and Boudet (1980, pp. 427–432) mentioned historical restrictions on cutting browse from *Acacia albida*, imposed either by the traditional authorities in eastern Niger, by the French colonists, or by the government of independent Mali in the 1960s, following the colonial model.

[37] ILCA abandoned a study of Afar pastoralists in eastern Ethiopia for security reasons in the 1970s.

[38] One example of the information available to the Maasailand researchers is von Kaufmann (1976) covering pastoral problems and proposed solutions in Kenyan rangelands up to the mid-1970s.

[39] 'Agro-pastoralists' in West Africa usually means Fulani farmers who practised a mix of settled rain-fed farming and seasonally nomadic grazing. In some instances (Blench, 1999, for northern Nigeria; Waters-Bayer and Taylor-Powell, 1986b) such groups had been settled for many years. In others (Benoit, 1979, for western Burkina Faso), herders had recently settled or were in the process of settling as recently as the 1970s.

[40] This book is an outstanding work that is regrettably barely cited in Google Scholar and not cited at all in Scopus. It made a major contribution to the scientific literature, notably through the work of Wolfgang Bayer, David Bourn, M.A. Ibrahim, Salisu Ingawa, J.A. Maina, E O. Otchere, Mark Powell, Mohammed Saleem, Ellen Taylor-Powell, Ralph von Kaufmann, Ann Waters-Bayer and William Wint.

[41] Ellis and Swift (1988) stressed that herders could recover well from droughts of one year, but that longer dry periods would cause greater losses of animals, work and income, forcing herders into other jobs.

[42] Grigg's observation is correct in that the ranches did fail, but his explanation of the failure is wrong.

[43] The studies by Fratkin *et al.* (1994) and Galaty (1994, p. 189) did not quantify the losses in productivity and equity from enforced sedentarization, but it is clear from these works that such losses were substantial.

[44] Mortimore (2000, p. 4), in three states in northern Nigeria, found a decline in agricultural land (cropped) of 8.4% from 1976–1978 to 1993–1995, of which –12.4% was woodlands, +1.3% was grassland and +3.0% was degraded.

[45] This was decades after the British had taken much of the Maasai grazing land, which had narrowed the resource base of the group ranches before they were ever constituted.

[46] See Rutten (1992) on the individualization of ownership in Kajiado district of southern Kenya from 1890 to 1990.

[47] The technical reviews by King (1983) and Sandford (1983a) concerned cattle for meat and dairy. Sandford (1983a, p. 49) noted a lack of information about water use by draught animals in highland Ethiopia.

[48] Homewood and Rodgers (2004, p. 252) reported from Tanzania that energy loss incurred by trekking for water was the 'single biggest constraint to milk production'.

[49] The books of Smith (1992), Fratkin *et al.* (1994); Scoones and Wolmer (2002), Behnke and Scoones (1993), Homewood (2008), Bollig *et al.* (2013) and Catley *et al.* (2013) do not mention water experiments, on station or in the field. The range and herd modelling in Behnke and Scoones (1993) did not use water as an objective or a constraint, nor did that of Konandreas and Anderson (1982). Mengistu *et al.* (2007) observed successful adaptive physiological mechanisms in Ethiopian Somali cattle when subjected to intermittent watering.

[50] This statement does not apply to Latin America, where the market potential of beef had stimulated much earlier research on soils, pastures, livestock disease and animal breeds for commercial ranching.

[51] Examples are Monod (1975) and papers cited in Sandford (1983a).

[52] Chapter 13 discusses the research impact of quality improvements in crop residues for mixed systems, mainly in semi-arid India and in semi-arid and subhumid West Africa.

[53] The book by Pratt and Gwynne (1977), while limited geographically to East Africa, covered more than 30 years of work and made careful reference to rangeland studies in the USA and Australia.

[54] Feed quality was a major theme in the early CIAT Beef Program (CIAT, 1973).

[55] The papers cited by Macharia *et al.* (2011) confirm their findings: station results are positive, field trials are mixed, adoption data are rare and benefit–cost analysis is absent. The study by Nicholson and Mengistu (2016) confirmed the lack of adoption of forage legumes in grazing systems and on mixed farms in Kenya and Ethiopia using surveys in 2014 and 2015.

[56] Chapter 11 (this volume) covers the African range ecology work of ILCA, ILRI and partners. Successes with planted forage grasses in Latin America were mainly on large commercial farms in Brazil and on some smallholder areas in central America, as discussed in Chapter 12 (this volume).

[57] *Medicago sativa* (known as alfalfa in the USA and lucerne in much of Europe) is the most common temperate forage legume but is rarely planted in the semi-arid and subhumid tropics.

[58] Detailed papers on these diseases are in the respective chapters of Part I. Screw worm was accidentally introduced into Libya from the new world in the late 1980s and was eradicated with sterile insect techniques and quarantine measures by the mid-1990s. The eradication of screw worm in Libya and the global eradication in 2011 of rinderpest, a viral disease of cattle and some ungulates, are special cases and are not discussed here.

[59] Konandreas and Anderson (1982, pp. 3–5) reviewed earlier models, including that of CIAT for ranching in Latin America and that of Texas A&M University (Cartwright *et al.*, 1982).

[60] Norton (1975, pp. 313–322) wrote that it would be 'unwise to apply our understanding of American deserts directly to the Sahel' because of differences in stocking rates, climate and flora.

[61] The bibliography in Penning de Vries and Djiteye (1991) cites many individual studies of soils, water, plants and animals, but few analysed these elements jointly over time, at the same site, or applied simulation models to validate and project the field results; a significant exception is Hiernaux and Ayantunde (2004).

[62] The IFPRI IMPACT model was not detailed enough in 2009 to project outcomes for individual livestock systems of any type (Nelson *et al.*, 2009).

[63] It is not possible to calculate an IRR for the 'milking with supplementation' strategy from the original paper, but it appears from Cartwright *et al.* (1978, p. 60, Table 5.4) that it would be positive.

[64] Water was not a major cost of cattle production in the Inner Delta of the Niger River in Mali and hence the studies there had at least one large difference from other work in semi-arid West Africa. Wagenaar *et al.* (1986, p. 5) found that, 'Throughout the year, the herds are watered at least twice daily.'

[65] Coppock (1994, p. 196) referred to 'grain imports' but his context implied not 'imports' in the sense of purchases from foreign suppliers but 'imports into the grazing system' in the sense of purchases from domestic and/or foreign suppliers.

[66] Jahnke (1982, p. 143) estimated that roughly 275,000 km^2 had been cleared of tsetse in Nigeria, Zimbabwe, Tanzania and Uganda between 1947 and 1978 in a total endemic area of 10.3 million km^2 in sub-Saharan Africa (see Box I.1 in the Introduction in this volume).

[67] Vetter (2004) summarized the origins of the equilibrium model, the critique by advocates of the non-equilibrium model and the situations in which one or both might apply.

[68] Dixon *et al.* (2001) defined eight groups, of which six are relevant here; the others are coastal artisanal fishing and urban agriculture.

[69] Walker and Alwang (2015, p. 210) found that fewer than 10% of maize scientists in East and southern Africa were from 'social science' or 'farming systems'. They also found that more than 60% of scientists in 20 crops were in plant breeding, plant pathology, molecular biology and tissue culture (p. 378).

[70] The term 'conservation farming' has been introduced more recently as a model of nutrient cycling (e.g. Dixon *et al.*, 2001, pp. 51–52).

[71] Farm mechanization with power tillers and tractors was part of the research portfolios of the International Rice Research Institute (IRRI; Chancellor, 1998), and of ICRISAT at times. The goal of this research was to accelerate field tasks by replacing animals to achieve higher cropping intensity. IRRI and other centres also studied mechanization of water supply, threshing and milling, but this work typically involves engines rather than animal power.

[72] Some loss of potential impact from the Niger study was due to using a sample size of only seven animals in its trial of energy expenditures, and to sampling animals who weighed roughly one-third more than those animals typically found on farms in western Niger (Fall *et al.*, 1997).

[73] There was little soil fertility work 'on farm' in the pastoral areas.

[74] CIAT's orientation was on improving soil fertility by adding mineral fertilizers and raising the pH of acid soils without returning manure to the soil in a systematic way. The CIAT work had a major development impact on the acid soils of the Latin American savannahs, estimated to be more than 250 million ha in Brazil, Colombia and Venezuela alone (Lynam and Byerlee, 2017, p. 83) and is one of the principal successes of natural resource management work from the international agricultural research centres.

[75] The cattle age/sex pyramid for the Malian Delta in Wagenaar *et al.* (1986, p. 10) showed the ratio of females to males increased sharply after the age of 3–4 years. The cattle age/sex data for Mali (Wilson, 1986, p. 36) found higher female:male ratios in herds not used for animal draught; in herds used for draught power, the

female:male ratios were roughly equivalent in one sedentary herd for milk and draught and much less than 1 in another sedentary herd. The female:male ratio in the Maasailand study (Solomon Bekure *et al.*, 1991, p. 83) ranged from 1.86 (rich households) to 2.23–2.30 (poor households) with a mean of 1.97. The ratio of females:males was greater than 3 before the 1983 drought in southern Ethiopia and about 4 in 1985 after the drought (Coppock, 1994, p. 168)

[76] The foreword to Pratt and Gwynne (1977, p. vii) illustrated the 'mainstream view': '…in the last few decades, stock numbers have increased so much that extensive areas have been severely overgrazed and now have an extremely low annual productivity, far below that which the land is capable of producing under good management'.

[77] Examples are Thornton *et al.* (2006), Thornton *et al.* (2009) and Thornton and Herrero (2010).

[78] The books of Katherine Homewood (notably, Homewood and Rodgers, 2004; Homewood, 2008), on East African pastoralism, although not ILRI work, are in the same tradition.

[79] An exception is parts of East and southern Africa, where ILCA and ILRAD did little apart from early cattle modelling on Botswana (Konandreas and Anderson, 1982) and the epidemiological work of Brian Perry and colleagues in the second half of the 1980s.

[80] Network models have also been used in animal traction, forages, animal genetics and economics.

[81] The exception to this generalization about the lack of a productivity effect from livestock research in sub-Saharan Africa is the eradication of rinderpest (Roeder and Rich, 2009). Even for rinderpest, the modern research effect was limited to a policy for delivery systems. The vaccine was developed long before eradication was declared in 2011 and the role of systems research in the campaign was very small.

[82] There is a long history of crop research in the USA, Canada and Australia on the value of crop residues as a soil amendment. A review by Wilhelm *et al*. (2004) on removal of stover in the Maize Belt in the USA found studies covering nearly 70 years.

[83] Chapter 13 (this volume) reports rough estimates of the contribution of improved cultivars of dryland cereals (maize, pearl millet and sorghum) to animal feed availability for India and some countries in sub-Saharan Africa. Walker and Alwang (2015, pp. 32, 228 and 232) made occasional reference to straw as feed but did not report data on crop residues as feed, changes in harvest index in modern varieties or changes in feed quality of crop residues.

[84] There was a focus on large farms at CIAT in research on rice cultivars, beef ranching, forage grasses and acid soil management.

[85] This had been available for decades in the livestock systems in South Asia and parts of Latin America. The ILCA (1975) proceedings of 'Inventaire et cartographie des Pâturages Tropicaux Africains: Actes du Colloque Bamako' was a landmark in compiling and publishing this information.

[86] The chapter by Evenson (2001) in the *Handbook of Agricultural Economics* cited one estimate on pasture research among more than 100 estimates of returns to research, and fewer than five papers on livestock in a global total of more than 100 papers on crops and livestock.

[84]This had been available for decades in the livestock systems in South Asia and parts of Latin America. The ILCA (1975) proceedings of 'Inventaire et cartographie des Pâturages Tropicaux Africains: Actes du Colloque Bamako' was a landmark in compiling and publishing this information.

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16 Ruminant Livestock and Climate Change in the Tropics

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Contents

Executive Summary

The problem

The temperature and humidity changes associated with climate change will have direct and for the most part adverse effects on tropical animal productivity. Related changes in pasture and feed productivity will have further indirect adverse effects on productivity. Collectively, these effects will become increasingly negative as climate change progresses, reducing incomes to both specialized and mixed livestock producers and possibly reducing the incomes of consumers.

At the same time, livestock production activities contribute to climate change. In the early 2000s, livestock production accounted for 18% of global greenhouse gas (GHG) emissions, with enteric emissions about 25% of the total, emissions from manure a further 24% and conversion of forests to pasture another 34%. Livestock also have negative environmental effects on water availability and quality, biodiversity and other ecosystem services.

A recent study showed per capita consumption of animal products is likely to increase by about 50% for low-income countries and about 10% for higher-income countries between 2010 and 2050. This demand growth implies rising livestock GHG emissions unless cost-effective mitigation options can be found. Options to reduce emissions include both supply and demand-side changes. On the supply side, technical mitigation options can reduce emissions per unit of output substantially, but their economic feasibility varies by location and is generally understudied. On the demand side, changes in dietary patterns can reduce meat consumption and therefore GHG emissions but mechanisms to generate widespread change are not clear.

Adaptation to climate change will become more challenging with growing GHG concentrations. At some point in this century, and in some regions, temperature and humidity increases will make production biologically impossible. Well before that point, the adaptation costs are likely to outweigh economic benefits of producing livestock in many current producing regions.

ILRI research

The work of the International Livestock Research Institute (ILRI) on livestock and climate change began with studies of livestock water use (King, 1983; Sandford, 1983), agroecology, and drought (Henricksen and Durkin, 1986) before evolving into crop growing period models. Deeper global research efforts were stimulated by the publication of *Livestock's Long Shadow: Environmental Issues and Options* by Steinfeld *et al.* (2006), which was the first book to comprehensively address the environmental costs of livestock. Steinfeld *et al.* (2006) found that, while livestock contributed significant shares of national income, employment and protein supply, it also had adverse effects on water and air quality, contributed to deforestation and to loss of other ecosystem services, and generated 18% of anthropogenic GHG emissions.

A second major impetus for ILRI research was the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC), published in 2014 (IPCC, 2014). AR5 was the first IPCC assessment to evaluate climate change and livestock interactions. ILRI researchers played important roles in this

evaluation and extended their contributions in subsequent work.

This chapter provides an overview of both the scientific and the development impacts of ILRI research on climate change. Scientific impact is measured by advances in research methods and in research output, such as publications that advance our understanding of climate change and options to manage it. Development impact is about making a direct and positive contribution to welfare, directly or indirectly. In the case of climate change, development impact activities would include adoption of adaptation and mitigation methods. Scientific impact is relatively straightforward to measure with bibliometric approaches. Measuring development impact is much more challenging because it often develops through long chains of causality; for example, an adviser to a policy maker in a country reads a key academic reference that draws on a data set on country-specific livestock systems that was generated using a simulation model. Hence, assessments of development impact tend to be somewhat anecdotal in the absence of studies of adoption of new methods generated by research.

Research spending and bibliometrics

It was not possible to separate ILRI spending on climate change from other spending in detail, but we do know that the climate research is the product of a small number of scientists and hence the budget share would be small in relation to the total. The productivity of climate change research, as shown in the Altmetric (www.altmetric.com/; accessed 7 March 2020) and bibliometric analyses, is quite high and suggests that the field is seriously underfunded when considering the importance of the problem, the scale of other international efforts and the productivity to date of ILRI research in this area.

Scientific impact

The key scientific impacts of ILRI research on climate change arose from the development of two models – MarkSim and RUMINANT – and the use of these models to generate a range of data sets that are now widely used in the scientific literature. Scientists in these activities have published extensively in prestigious scientific journals and their papers are widely cited.

Models

MarkSim is a stochastic weather generator developed at Centro Internacional de Agricultura Tropical (Jones and Thornton, 2000) in the 1990s with ILRI input. It is used to downscale climate outputs from global climate models temporally to daily weather data and spatially from large grid sizes of 2° latitude/longitude or more down to a few kilometres.

The RUMINANT model, initially developed in the mid-1990s, was used to predict feed intake, nutrient supply and methane (CH_4) emissions. These numbers are then aggregated to systems, countries, regions and continents using animal population projections, allowing refinement of GHG emissions estimates related to animal production.

Data sets

Data sets produced by MarkSim and RUMINANT have been used by a wide range of researchers as well as by the model developers themselves.

Scientific results

Scientific results include the following:

- Initial and periodic revisions of estimates of area, production, livestock numbers and feed sources by systems in the tropics.
- Impacts of climate change on livestock productivity and production from changing temperature and humidity, growing period shifts, and pest and disease distributions.
- Identification of adaptation options.
- Estimates of GHG per animal and per system.
- Estimates of mitigation possibilities (e.g. percentage changes below the trend of different climate scenarios).
- Feed quality and its GHG impact in the tropics.

Development impact

The two main development impacts have been: (i) appropriate animal selection, breeding and management techniques to reduce GHG per unit of output in the OECD countries; and (ii) modelling

of supply and demand management options, even if not yet broadly applied, which may have policy effects on GHG mitigation and ultimately on global warming.

Capacity development and partnerships

The principal capacity development impact of the modelling work originating at ILRI has been a wide range of partners who now use the models, or the data sets generated from them. Some of these partners have been involved in model development, validation and application; others have been trained to use the models for their own research needs. The creation of a website that generates MarkSim results for any arbitrary location extends the reach of the models dramatically.

The second has been the development of data and models under tropical conditions and their applications. An example is the Mazingira Centre at ILRI, which develops the capacity of national and regional scientists to study interactions between livestock and climate.

The future

The future for ruminant livestock is more certain on the demand side because of expected rising incomes in developing countries and the high income elasticity of demand for animal products. It is projected that demand for all animal products will grow globally, although there will be composition effects as demand shifts among animal types and as competition from plant sources of protein grows.

The future on the supply side is uncertain in part because of the interactions between climate change and animal agriculture. Information on mitigation of, and adaptation to, climate change is inadequate in the tropics compared with what is known about the temperate zone. The research agenda stated here will require more detailed information on existing systems, on the potential for technical changes that contribute to adaptation and mitigation, on modelling such changes as new GCM outputs become available, and on policy changes that have the potential for significant adaptation and mitigation.

Livestock productivity

The following questions need to be addressed:

- What are the productivity impacts in tropical livestock given temperature and humidity levels in producing regions under a range of climate scenarios?
- How will climate change effects on livestock pests and diseases spill over into effects on livestock productivity?
- What types of livestock systems are most resilient to changes in both mean changes and variability of temperature and humidity? One system in particular, confined animal feeding operations (CAFOs), is likely to grow rapidly in the tropics. How vulnerable are CAFOs to climate change?
- How cost-effective are existing adaptation options?
- What are the biological limits to adaptation? Are they likely to be reached in important producing areas?
- What are the potential effects of climate change on the use of livestock as a risk-management asset?
- Will climate change alleviate or exacerbate livestock's negative effects on water quality and quantity and on ecosystem services?

Mitigation and supply- and demand-side efforts

Outstanding questions in this area include the following:

- Are there technical and cost-effective options for reducing GHG emissions from existing livestock systems?
- What kind of changes to existing systems would achieve cost-effective mitigation?
- What policy activities could contribute to adoption of mitigation technologies?
- What demand-side actions would be needed to have a substantial reduction in emissions and in what regions of the world?

Introduction

This chapter explores our understanding of the evolving interactions between climate change and ruminant livestock in the tropics. It analyses the research done by ILRI and its partners in

improving this understanding and in contributing to solutions for mitigation of GHG emissions and adaptation to climate change. The focus is mostly on ruminants and, within this category, on cattle. The chapter first reviews the scientific and development impacts of ILRI and partner research before suggesting research priorities on climate change and tropical animal production.

ILRI's predecessors did little on the global environmental costs of tropical animal production. ILRI's research on livestock–climate change interactions began with the growing period modelling of Jones and Thornton (2000, 2003) and the studies of McDermott *et al.* (2001), Jones *et al.* (2002) and Thornton *et al.* (2002). Climate change research at ILRI was stimulated by the publication of the Food and Agriculture Organization of the United Nations (FAO) book *Livestock's Long Shadow: Environmental Issues and Options* (Steinfeld *et al.*, 2006), which sought to '...assess the full impact of the livestock sector on environmental problems, along with potential technical and policy approaches to mitigation'. Steinfeld *et al.* (2006) found that in the first decade of this century, livestock (including cattle, poultry and pigs) contributed 40% of agricultural gross domestic product, employed 1.3 billion people and provided one-third of humanity's protein intake. However, livestock production also had major negative environmental effects – polluting water and altering water flows, contributing to biodiversity loss and increasing air pollution as GHGs and other noxious gases. Steinfeld *et al.* (2006, p. 112) estimated that, in the early 2000s, livestock production accounted for some 18% of global GHG emissions and for more than 80% of agricultural emissions. Extensive livestock systems contributed about 13% of global GHGs and intensive systems contributed about 5%. The major livestock sources were enteric emissions (25% of the total), conversion of forests to pasture (34%) and manure (about 24%) (Steinfeld *et al.*, 2006, p. 113, Table 3.12). More recent estimates have revised these shares downwards, but livestock still is a major contributor to global GHG emissions.

A second impetus for new research on tropical livestock was the IPCC's Fifth Assessment Report (AR5; IPCC, 2014). AR5 was the first IPCC assessment to evaluate climate change and livestock interactions in some detail. It assessed the literature on livestock adaptation to climate change in addition to mitigation challenges and

opportunities. The research undertaken by ILRI after *Livestock's Long Shadow* became a major source of research outputs used in AR5. ILRI researchers were invited to participate in the IPCC GHG emissions taskforce in 2009 on improving GHG livestock emissions estimates. This work led to collaboration with the International Institute for Applied Systems Analysis (IIASA) and its GLOBIOM model, a multi-market model with 30 regions covering the globe and coverage of some 18 or 27 commodities. This collaboration allowed a better disaggregation of livestock numbers and feed sources by system, especially in the tropics. A similar arrangement exists with the IMPACT multi-market model of IFPRI, with 158 regions and 60 commodities.

After a brief overview of livestock systems and their resource use, this chapter addresses three areas: (i) climate change impacts on ruminant livestock; (ii) adaptation of livestock systems to climate change; and (iii) options to reduce GHG emissions.

Livestock Production Systems and Resource Use

Following Seré and Steinfeld (1996) and Kruska *et al.* (2003), Robinson *et al.* (2011) updated the most common classification for tropical livestock production. Level 1 in this classification described livestock production systems using land characteristics. Level 2 linked potential to actual livestock production and accounted for other enterprise options by referring to specific combinations of crops and livestock. Level 3 addressed the intensity and scale of production by incorporating management practices. The resulting classification has nine land-based systems and two landless systems. The land-based systems have three climate categories – arid, humid and temperate – and three agrosystem categories – pastoral, mixed rainfed and mixed irrigated. The notation is LGA (livestock/grazing/arid), LGH (livestock/grazing/humid) and LGT (livestock/grazing/temperate and topical); MRA (mixed/rainfed/arid and semi-arid), MRH (mixed/rainfed/humid) and MRT (mixed/rain-fed/temperate and tropical); and MIA (mixed/irrigated/arid), MIH (mixed/irrigated/humid) and MIT (mixed/irrigated/temperate and tropical). Map 2 (p. xviii) shows the nine systems in Africa.

Table 16.1. Livestock farming system extent and cattle numbers in Africa and Latin America, 2000. (Adapted from Robinson *et al.*, 2011.)

Farming system	Region[a]	Area in 2000 (million km²)	Population in 2000 (million)	Cattle in 2000 (million TLUs)
Agropastoral and pastoral	Central and South America	5.4	40.5	64.2
	East Asia	5.5	41.3	12.7
	South Africa	0.5	19.2	6.2
	South-east Asia	0.2	2.2	1.7
	Sub-Saharan Africa	13.4	80.2	36.7
	West Asia and North Africa	10.2	111.7	8.5
	Total	35.2	295.1	129.9
Mixed extensive	Central and South America	3.5	100.7	67.2
	East Asia	1.7	195.4	20.3
	South Africa	1.6	371.9	72.0
	South-east Asia	1.2	85.3	10.2
	Sub-Saharan Africa	5.1	258.7	55.5
	West Asia and North Africa	0.9	87.2	5.3
	Total	14.0	1099.2	230.6
Mixed intensifying potential	Central and South America	2.4	221.2	69.4
	East Asia	2.3	938.5	34.4
	South Africa	1.8	844.6	109.5
	South-east Asia	1.1	347.2	13.8
	Sub-Saharan Africa	1.5	168.2	11.7
	West Asia and North Africa	0.6	154.4	6.0
	Total	7.3	2674.1	244.9
Other	Central and South America	8.8	125.8	41.8
	East Asia	1.5	104.2	9.8
	South Africa	0.4	69.5	8.7
	South-east Asia	1.9	40.4	7.1
	Sub-Saharan Africa	4.1	109.2	6.8
	West Asia and North Africa	0.2	31.3	1.4
	Total	16.9	480.4	75.5

TLU, tropical livestock unit.
[a]Regional groupings of countries are as listed in Thornton *et al.* (2002).

Land

Table 16.1 provides statistics from Robinson *et al.* (2011) for the areas of cattle-based livestock systems, estimates of the numbers of animals, and human population by regions of Africa and Latin America in 2000. The report provides similar tables for pig and chicken systems in Asia.

Agropastoral and pastoral systems have by far the greatest area with 35.2 million km², of which sub-Saharan Africa and West Asia and North Africa are dominant. Mixed crop–livestock systems occupy 23.8 million km², of which sub-Saharan Africa and Central and South America dominate. Human and cattle population density are greatest in 'mixed intensive' systems in

Central and South America and in South Asia, which would therefore have the greatest need for adaptation to climate change.

An updated data set on ruminant meat and milk production by region and within region by systems is shown in Fig. 16.5.

CAFOs are part of the Seré and Steinfeld (1996) system and have been an important source of production of cattle, poultry and swine in higher-income countries for many years. FAO estimates that 80% of growth in the livestock sector now comes from these industrial production systems, and this growth is likely to continue. CAFOs are increasingly important in lower-income countries, especially for poultry, which now accounts for 23 billion of the 30 billion farm animals,

but lack of data makes it impossible to map them accurately outside the USA and Europe. ILRI has done little research on CAFOs but these should be a topic for future work related to climate.

Water quantity

One estimate is that livestock production accounts for almost 30% of water use in agriculture, most of which is water in crop production for feed (Mekonnen and Hoekstra, 2010). Some research has contested this concept of water use. Peden *et al.*, (2007) contend that the majority of feed and fodder is rainfed, not irrigated; they propose an alternative notion, that of livestock water productivity 'defined as the ratio of livestock's beneficial outputs and services to water depleted in their production' (Haileselassie *et al.*, 2009). Haileselassie *et al.*, (2009) found that livestock and water crop productivity were comparable in rainfed systems of Ethiopia.

Water quality

Livestock reduce water quality principally by manure runoff. Manure runoff increases both faecal contamination of water, a major disease transmission mechanism where water treatment is inadequate, and nutrient loads, which have adverse human health effects and indirect effects on concentrations of harmful organisms (e.g. algae blooms). Pesticides such as sheep-dipping chemicals, and bacterial and protozoan contamination of soil and water are other concerns regarding water quality (Hooda *et al.*, 2000). CAFOs present both potential benefits and threats to water quality. CAFOs confine livestock waste, reducing the possibility of water contamination over wide areas. However, failure of a containment facility can discharge large quantities of waste in a matter of hours, overwhelming regular waste-management approaches (Mallin and Cahoon, 2003).

Air

The most important air pollutants from livestock are emissions of GHGs. These are discussed in detail in the section below on mitigation. CAFOs, especially those that utilize feed concentrates based on maize and soybean meal, generate noxious odours that affect the quality of life in the immediate area and can be hazardous to human health. In addition, the manure generated can be a large source of the GHGs nitrous oxide (N_2O) and CH_4.

Ecosystem services

Ecosystem services affected by livestock are of two main types: (i) services provided by forests that are lost as forested areas are converted to pasture or crop production for feed; and (ii) changes in grasslands that reduce a range of services, from water quality and quantity availability to biodiversity. Quantifying deforestation is difficult because few countries collect the needed data but de Sy *et al.* (2015) estimated that, of deforestation identified in the 2010 FAO Forest Resource Assessment, pasture was the dominant driver of forest area change (71.2%) and related carbon loss (71.6%) in South America, followed by commercial cropland (14% and 12.1%, respectively).

Changes in grassland ecosystem services are driven by managed changes in species mix to improve nutrient quality (see Chapter 11, this volume). Driscoll *et al.* (2014) used data from eight countries on six continents to show that few governments regulate conventionally bred pasture grasses to limit threats to these natural areas, even though these are bred with characteristics typical of invasive species and environmental weeds. Proença *et al.* (2015) reported on a production model that addresses some of these concerns about grassland ecosystem services. The system of sown biodiverse permanent pastures rich in legumes has been successfully implemented in Portugal on farms in Mediterranean climate areas as a response to the low levels of productivity and feed quality obtained in semi-natural pastures. It consists of a mix of mostly local grasses and legumes, each mixture tailored to local environmental conditions to best cover the available environmental niches. The system combines higher pasture productivity with soil carbon sequestration, reducing atmospheric carbon dioxide (CO_2) providing the potential for increased farm income from payments for soil carbon sequestration.

Climate Change Impacts on Ruminant Livestock

Climate change affects livestock both directly and indirectly. The direct effects arise from higher temperature and humidity that slow animal growth and increase susceptibility to disease. A recent study by Rose *et al.* (2014, p. 219) argued that 'changes in climate' may have a 'major impact on the seasonal transmission of gastro-intestinal nematodes in livestock', based on evidence from temperate and tropical conditions. Indirect effects are felt from the higher feed prices that are likely as crop and pasture productivity is reduced, changes in nutrient composition of feeds and pastures occur, and climate affects livestock and wildlife pests and diseases.

AR5 highlighted that research on climate change impacts on livestock production systems was relatively limited at the time of its writing. 'In comparison to crop and fish production, considerably less work has been published on observed impacts for other food production systems, such as livestock or aquaculture, and to our knowledge nothing has been published for hunting or collection of wild foods other than for capture fisheries' (Porter *et al.*, 2014, p. 494). Figure 16.1 shows one-seventh the number of citations in Porter *et al.* (2014) on livestock compared with crops (even fewer on fish and far fewer on pests and diseases).

The major livestock-related climate impact messages from AR5 were as follows:

- Temperature is an important limiting factor for livestock, for both meat and milk production.
- Climate change will increase water stress on livestock systems, affecting the water resources available for livestock via impacts on runoff and groundwater.
- Pasture response to climate change is complex. Increases in CO_2 concentration, temperature and precipitation will affect pasture productivity and quality directly and also have important indirect effects on plant competition, seasonal productivity and plant–animal interactions. For example, projected increases in temperature and the lengthening of the growing season should extend forage production into late autumn and early spring in temperate zones. Increases in CO_2 will tend to benefit C_3 species; however, warmer temperatures and drier conditions will tend to favour C_4 species. Often rangelands benefit from a combination of both types of grasses as rainfall and temperature vary throughout the year.
- Host and pathogen systems in livestock will change their ranges because of climate
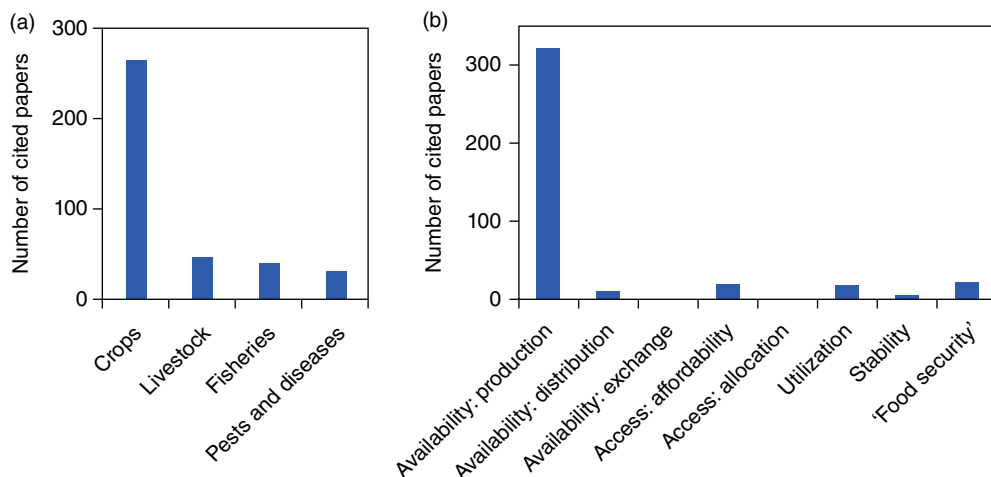
Fig. 16.1. Livestock coverage in the 'food security and food production systems' chapter of AR5, Working Group II. (a) Subsectors, and pests and diseases; some citations are not mutually exclusive among categories (e.g. a few crop–livestock citations are included in both subsectors). (b) Food security dimensions. The category 'Food security' covers food security in general terms. (From Campbell *et al.*, 2016.)

change. Species diversity of some pathogens may decrease in lowland tropical areas as temperatures increase. For example, temperate regions may become more suitable for tropical vector-borne diseases such as Rift Valley fever and malaria. Vector-borne diseases of livestock such as African horse sickness and bluetongue may expand their range northwards to the northern hemisphere. Changing frequency of extreme weather events, particularly flooding, will also affect diseases.

Table 16.2 gives AR5's projected impacts of climate change on livestock in the tropics. At the deadline for accepted papers for AR5 (August 2013), detailed summaries of impacts on livestock systems with or without adaptation were not available. Summaries addressing the interactions between crop and livestock enterprises were also not available.

An important topic not covered in AR5 is how climate change might affect the risk-management role of livestock. Particularly in poor tropical countries, livestock is an enormously important risk-management asset for hundreds of millions of people. The impacts of increasing climate variability on downside risk and on the inter-annual stability of livestock production are not well studied. Jones and Thornton (2009) provided some quantitative assessment of effects of climate change on livestock's risk-management role. It is highly likely that the effects will be negative (Thornton and Herrero, 2015).

Climate change will affect all living organisms, including livestock pests and diseases. The effects might be positive or negative for livestock productivity depending on the biological susceptibility of the species to changes in temperature and humidity. The effects are likely to be location specific and to vary over time as climate changes become more pronounced.

This research is in its infancy, but ILRI researchers have been contributing to it since

Table 16.2. AR5 livestock impacts in the tropics. (Adapted from Porter *et al.*, 2014.)

Region	Subregion	Climate change impacts	Scenarios
Africa	Botswana	Cost of supplying water from boreholes could increase by 23% due to increased hours of pumping, under drier and warmer conditions	A2, B2, to 2050
	Lowlands of Africa	Reduced stocking of dairy cows, and a shift from cattle to sheep and goats, due to high temperature	
	Highlands of East Africa	Livestock keeping could benefit from increased temperature	
	East Africa	Maize stover availability per head of cattle may decrease due to water scarcity	
	South Africa	Dairy yields decrease by 10–25%	A2, 2046–2065/2080–2100, ECHAM5/MPI-OM, GFDL-CM2.0/2, MRI-CGCM2.3.2
Central and South America	Andean Mountain countries	Beef and dairy cattle, pigs, and chickens could decrease by between 0.9% and 3.2%, while sheep could increase by 7%	To 2060, hot and dry scenario
	Colombia, Venezuela and Ecuador	Beef cattle choice declined	To 2060, milder and wet scenario
	Argentina and Chile	Beef cattle choice increased	Future climate change
	Pernambuco, Brazil	Milk production and feed intake in cattle strongly affected	Future climate change

the beginning of this century. McDermott *et al.* (2001) looked at the potential effects of climate change, human population growth and expected disease control activities on tsetse distribution and trypanosomiasis risk in five agroecological environments in sub-Saharan Africa up to 2050. They found that the combined effects of these changes would be to contract areas under trypanosomiasis risk continent-wide with the greatest decrease in the impacts of animal trypanosomiasis in the semi-arid and subhumid zones of West Africa.

More recently, Olwoch *et al.* (2008) examined effects of climate change on the range of the tick-borne disease East Coast fever in sub-Saharan Africa using a species distribution model. They showed increases in East Coast fever suitability in the Northern Cape and Eastern Cape provinces of South Africa, Botswana, Malawi, Zambia and eastern Democratic Republic of the Congo. The range shifts are due to changes in temperature minima and maxima and in January and July rainfall.

Bett *et al.* (2017) reviewed case studies on the epidemiology of infectious diseases. Some of the studies showed a positive association between temperature and expansion of the geographical ranges of arthropod vectors, while others had a negative association.

Samy and Peterson (2016) used ecological niche modelling with a comprehensive occurrence data set to map the current distribution and explore the future potential distribution of bluetongue virus globally under a range of climate scenarios. Under future climate conditions, the potential distribution of bluetongue virus was predicted to broaden, especially in Central Africa, the USA and western Russia.

CGIAR research on climate change impacts in livestock systems

In the early 1990s, Philip Thornton of ILRI and Peter Jones of CIAT began two lines of research on climate change impacts and adaptation: (i) development of models to transform output from climate models into weather data useful in impact studies; and (ii) models of livestock system performance under climate change.

Weather data in climate analyses

An early step in research on climate change and its impacts was the release of MarkSim, a stochastic weather generator developed at CIAT in the 1990s in partnership with ILRI (Jones and Thornton, 1993, 1997, 1999, 2000).

The livestock system classification of Seré and Steinfeld (1996), further refined and developed by Kruska *et al.* (2003), is driven partially by the length of growing period (LGP). The MarkSim model has since been used to refine models of LGP. The early use of future LGP surfaces was by McDermott *et al.* (2001), who investigated the effects of climate, human population and socio-economic changes on tsetse-transmitted trypanosomiasis to 2050. Another application of LGP surfaces was published as part of the study on 'Mapping poverty and livestock in the developing world' (Thornton *et al.*, 2002), which had 479 Google Scholar citations to April 2020.

Several projections have been made of how livestock systems might evolve by 2050 as climate change affects LGP. Kristjanson *et al.* (2004) projected LGP shifts and livestock system changes in West Africa. They forecast declines in LGP across most of West Africa, with many marginal cropping areas becoming even more marginal by mid-century and with rangeland systems disappearing entirely in a few countries. Jones and Thornton (2009) (97th percentile in Scopus citations) highlighted the possible livelihood impacts of climate change across Africa, hypothesizing that as cropping became more marginal in semi-arid zones, farmers would turn to more livestock keeping.

MarkSim techniques were refined by Thornton *et al.* (2006) on 'Mapping climate vulnerability and poverty in Africa.' 'Hotspots' of climate change, identified via LGP changes projected to the middle of the 21st century for different global climate models and emissions scenarios, were combined with social indicators to identify priority livestock systems for policies to reduce vulnerability and poverty. The study concluded that many vulnerable regions are likely to be adversely affected by climate change in sub-Saharan Africa, notably the mixed arid–semi-arid systems in the Sahel, the arid–semi-arid rangelands in eastern Africa, the Great Lakes and coastal regions of eastern Africa, and all systems in southern Africa. Some

of the maps and data from Thornton *et al.* (2006) were used directly in the IPCC's Fourth Assessment Report (Boko *et al.*, 2007; IPCC, 2007) and the paper had been cited in Google Scholar more than 325 times to April 2020.

Further analyses using MarkSim followed the 2006 study. Projections of cattle trypanosomiasis were redone to 2030 for one of the UK Government's Foresight Projects (Thornton *et al.*, 2006). Systems impacts were analysed in Turkana District, Kenya (Notenbaert *et al.*, 2007). Impact studies were undertaken on pastoral and agropastoral systems in East and West Africa for the CGIAR's Systemwide Livestock Programme (Thornton *et al.*, 2008), and on the agricultural sector in East and Central Africa for the Association for Strengthening Agricultural Research in Eastern and Central Africa (ASARECA; van de Steeg *et al.*, 2009). Box 16.1 summarizes research utilizing MarkSim analysis and data generation. This list indicates the scope and nature of analyses completed, with impacts on crop and livestock productivity, pest incidence, changes in land use, CH_4 emissions and poverty. Rassmann and Schuetz (2017) highlighted wider studies using MarkSim, including a study on the possible future spread of the Zika virus (Messina *et al.*, 2016) and a projected decline in ice-skating days in Canada, an important recreational ecosystem service in that country (Brammer *et al.*, 2015).

A recent innovation promises to expand MarkSim's usefulness. MarkSim/GCM is a web tool that uses MarkSim to generate location-specific weather data from GCM results used in AR5. The outputs include graphical depictions of the data and creation of a data set that can be imported into the crop modelling software DSSAT. (http://gisweb.ciat.cgiar.org/MarkSimGCM/; accessed 7 March 2020). The second version of MarkSim will be improved over the first version as it will use 55,000 rainfall stations, compared with some 9000 for version 1. It will allow the study of novel climates – climates that will exist in the future that currently do not exist anywhere – in more detail.

Impacts on livestock systems

Thornton *et al.* (2008) reviewed what was known about climate change and livestock and assessed potential priority activities for ILRI. The inventory of climate change impacts (Thornton *et al.*, 2009) listed seven topics – feeds quantity and quality, heat stress, water quantity and quality, livestock diseases and disease vectors, biodiversity, systems and livelihoods, and indirect impacts (human health effects from changing disease burden, worsening heat-related mortality and morbidity). Table 16.3, adapted from Thornton *et al.* (2008), summarizes gaps in our understanding of the impacts of climate change and the role(s) that international research might have in closing such gaps.

Activities were ranked in relation to their importance to ILRI's mandate and the achievability of outputs and outcomes. The top-ranked activities were: (i) identification of feed 'hotspots'; (ii) improved understanding of climate change on livestock systems and livestock keepers' livelihoods; (iii) the development and deployment of assessment frameworks and targeting tools; and (iv) identification and dissemination of adaptation options. In the 10 years since the analysis was completed, considerable progress has been made in activities (ii) and (iii). Less progress has been made on activities (i) and (iv), although new research is under way at ILRI on both of these areas.

ILRI inputs were used in the International Assessment of Agricultural Knowledge, Science and Technology for Development (IAASTD) agricultural scenarios to 2050 (Rosegrant *et al.*, 2009), which projected spatial livestock data. Reception of the IAASTD report at its release was mixed, although it did provide an important analysis of necessary changes in the global food system. ILRI work has also contributed to the analysis of drivers of change in agricultural systems (van Vuuren *et al.*, 2009).

Box 16.2 summarizes key ILRI research outputs on climate change impacts, including reviews of impact and adaptation studies in mixed crop–livestock and pastoral–agro-pastoral systems and a range of adaptation studies using different modelling approaches at varying scales (e.g. household, regional, global). Tables 16.1 and 16.2 highlight the shift from livestock component impact studies to more systems-oriented work that attempts to understand the broader implications of climate change adaptation at different scales. Much of the research of ILRI and its partners is tied to models of sustainable

Box 16.1. Impact of the MarkSim model.

MarkSim has had far-reaching impacts in: (i) modelling crop production; (ii) mapping the relationships among climate, agriculture and poverty; and (iii) modelling system effects of climate change:

Modelling crop production

Impacts of climate change to 2055 on maize yields in Latin America and Africa	Jones and Thornton (2003) (99th percentile in Scopus)
Spatial variation of crop yield response to climate change in East Africa	Thornton et al. (2009) (99th percentile in Scopus)
Rainfall variability, and impacts of climate change on length of growing period	Thornton et al. (2007)

Mapping relationships among climate, agriculture and poverty

Mapping poverty and livestock in the developing world	Thornton et al. (2002)
Mapping climate vulnerability and poverty in Africa	Thornton et al. (2006)
The livestock, climate change and poverty nexus	Thornton et al. (2008)

Modelling system effects of climate change

Effects of climate, human population and socio-economic changes on tsetse-transmitted trypanosomiasis to 2050	McDermott et al. (2001)
Livestock systems changes to 2050 in West Africa	Kristjanson et al. (2004)
Cattle trypanosomiasis in Africa to 2030	Thornton et al. (2006)
Livestock development and climate change in Turkana District, Kenya	Notenbaert et al. (2007)
Impacts of climate change on pastoral and agropastoral systems in East and West Africa	Thornton et al. (2008)
Understanding climate–land interactions in East Africa	Olson et al. (2008)
Spatial distribution of CH_4 emissions from African domestic ruminants to 2030	Herrero et al. (2008)
Influence of climate change and climate variability on the agricultural sector of East and Central Africa	van de Steeg et al. (2009)
Livestock system impacts in the tropics	Thornton and Herrero (2010a)
Climate change and crop production impacts in the Albertine Rift	Thornton (2009)
Possible impacts of climate change on livelihood transitions in Africa – croppers to livestock keepers?	Jones and Thornton (2009)
Adapting to climate change in households in East Africa at the level of the household and the system	Thornton et al. (2010)
Impacts of climate change on migration to 2060	New et al. (2011)
Mapping hotspots of climate change and food insecurity in the global tropics	Ericksen et al. (2011)
Adapting to climate change in mixed crop–livestock systems in developing countries	Thornton et al. (2011)
Agriculture in sub-Saharan Africa in a 4°-plus world	Thornton et al. (2011)
Global livestock production systems	Robinson et al. (2011)
Consequences of climate change for pastoralism in sub-Saharan Africa	Ericksen et al. (2012)
Future climate change and land-use change impacts on East African food security	Moore et al. (2012)
MarkSim as a GCM downscaling tool: AR4 climate model ensembles	Jones and Thornton (2013)
Climate change adaptation in mixed crop–livestock systems in developing countries	Thornton and Herrero (2015)
Climate variability and vulnerability to climate change: a review	Thornton et al. (2014)

Continued

Box 16.1. Continued.	
Impacts on smallholder agriculture in sub-Saharan Africa to 2050	Cooper *et al.* (2014)
Climate change impacts on livestock	Thornton *et al.* (2015)
Carbon and biodiversity costs of converting Africa's wet savannahs to cropland	Searchinger *et al.* (2015)
MarkSim as a GCM downscaling tool: AR5 climate model ensembles and soils data	Jones and Thornton (2015)
Climate change adaptation in the mixed crop–livestock system in sub-Saharan Africa	Thornton and Herrero (2015)
Adaptation paths for vulnerable areas	Cacho *et al.* (2016)
Pastoral farming systems and food security in sub-Saharan Africa	de Leeuw *et al.* (2019)

intensification (Garnett *et al.*, 2013) and climate-smart agriculture (Lipper *et al.*, 2014).

Current knowledge gaps on impacts

As initially identified by Thornton *et al.* (2008), identification of feed 'hotspots' remains a priority. In addition, there is much that is not well understood about the interactions of climate and climate variability with other drivers of change in livestock systems and with population growth, income growth and global trade. Multiple and competing pressures are likely on tropical and subtropical livestock systems in the future, to produce food, to feed livestock and to produce energy crops, for example. While recent scientific assessments such a AR4 and AR5 (IPCC, 2007, 2014) represent an accurate reflection of current knowledge, there remain gaps in their treatment of tropical livestock systems regarding the provision of ecosystems goods and services and the maintenance of livelihoods.

First, more clarity is needed concerning the benefits of livestock, their negative impacts on GHG emissions and the environment, and the effects of climate change on livestock systems. The regional and local variations in public costs and benefits associated with livestock need to be understood before technology and policy options for adaptation and mitigation can be targeted appropriately. Much agricultural impact work is reported at a continental or regional level (e.g. Lobell *et al.*, 2008), but this aggregation masks widespread differences.

Second, while a great deal is known about how livestock keepers manage current climate variability, more information is needed concerning the nature and extent of the trade-offs among crop and livestock enterprises, and between on- and off-farm income sources, as climate variability increases. This may have critical effects on food security; in addition to impacts on food availability, variability may strongly affect the stability of food supplies and vulnerable people's ability to access food at affordable prices (Schmidhuber and Tubiello, 2007). Key to these broad issues will be the refinement of impact models to assess climate variability effects on adaptation and mitigation options at regional and local scales, their effects on livelihoods and the trade-offs that arise among income, food security and environmental objectives.

Grace *et al.* (2015) identified the following knowledge gaps in animal disease and climate change:

- Information on animal diseases. The relatively limited availability of epidemiological (and ecological) observations on animal disease in the tropics constrains our understanding of the climate–disease relationships. Current surveillance detects only a small proportion of livestock and wildlife diseases and is not well linked to human disease surveillance.
- Disease dynamics. There are numerous pathways – direct and indirect – through which climate can influence disease. These drivers are not all equal, and impacts mediated through changes in human population and behaviour may induce effects that are orders of magnitude greater than those mediated through biological pathways.

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Table 16.3. Climate change knowledge gaps and research hypotheses. (Adapted from Thornton *et al.*, 2008.)

Activity area	Knowledge gaps	Research outputs	Regional focus	System focus	Time to outputs	Relative cost	Alternative suppliers of outputs	Feasibility of outputs	Feasibility of delivery (outputs to outcomes)
Feeds: quantity and quality	What are the localized impacts?	Localized impacts and hotspots identified	East, West and South Africa	MRA, LRA	Short	Low	Very few	High	High (e.g. for priority setting)
	Rangelands: primary productivity, species distribution and change due to CO_2 and other factors; estimation of carrying capacities	Rangeland net primary productivity distribution and impacts elucidated	East and South Africa, North-east Asia	LRA/LRH/ LRT	Medium	Medium	ARIs	Medium–high	Medium
	Crops: primary productivity, harvest indexes and stover production, dual purpose crops	Modified crop and residue quality and quantity	East, West and South Africa, South Asia	MRA/MRH/ MRT, MIA/MIH/ MIT	Long	Medium–high	Very few	Medium	Low–medium
	Feasibility of new feeding strategies with existing materials	New feeding strategies developed	East, West and South Africa, South Asia	MRA/MRH/ MRT	Medium–long	Medium	NARS	Medium	Low–medium
	Pests and diseases of feeds	Hotspots identified of key pests, diseases of key feed crops	East, West and South Africa	MRA/MRH/ MRT	Medium	Medium	OIOs	Low–medium	Medium
Water	Evolution of surface and groundwater supply, impacts on livestock	Understanding of changes in surface and groundwater supply, and impacts on livestock	East, West and South Africa, South Asia	LRA/LRH/ LRT, MRA/ MRH/ MRT	Medium	Medium	OIOs	Low–medium	Medium

	Increases in livestock water productivity	Options developed and tested to increase livestock water productivity	East, West and South Africa, South Asia	LRA/LRT, MRA/MRT, MIA/MIT	Medium–long	Medium–high	Very few	Low–medium	Medium
Animal health	Potential changes in the prevalence and intensity of epizootics in livestock	Future changes in prevalence and intensity of epizootics predicted	East, West and South Africa, South Asia	All livestock systems	Medium–long	Medium–high	ARIs	Low–medium	Medium–high
	Impacts of diseases of intensification (e.g. mastitis)	Impacts of 'management' diseases elucidated and options identified	East, West and South Africa, South Asia	MRH/MRT, coast, urban	Medium–long	Medium–high	OIOs	Low–medium	Medium–high
Biodiversity	'Ecological biodiversity': what will happen to numbers of species as systems change?	Impacts on ecological biodiversity elucidated	East, West and South Africa, South Asia	All livestock systems	Medium–long	Medium–high	GCC	Low	Low
	Animal breed biodiversity: which traits might be useful in the future?	Animal breed biodiversity characterized, and a road map developed for future exploitation	East, West and South Africa, South Asia	All livestock systems	Medium–long	High	OIOs	Low	High
	Plant biodiversity: which traits and hence which germplasm might be useful in the future?	Animal breed biodiversity characterized, and a road map developed for future exploitation	East, West and South Africa, South Asia	All livestock systems	Medium–long	High	OIOs	Low	High

ARI, advanced research institute; GCC, global change community; LRA, livestock/rainfed/arid; LRH, livestock/rainfed/humid; LRT, livestock/rainfed/temperate and tropical; NARS, national agricultural research system; OIO, other international organization.

Box 16.2. Impact of ILRI climate research.

Climate research by ILRI and partners has had important scientific impacts on: (i) policy options; (ii) mitigation technologies; (iii) adaptation problems; and (iv) the future of tropical agriculture.

Policy options

Livestock production: recent trends, future prospects	Thornton (2010) (99th percentile in Scopus)
Discussion paper on ILRI's research in relation to climate change	Thornton *et al.* (2008)
A review of the impacts of climate change on livestock and livestock systems in developing countries, current knowledge and gaps	Thornton *et al.* (2009)
Coping with drought and climate change in the pastoral sector in sub-Saharan Africa: policy considerations	Herrero *et al.* (2010)
Livestock and global change: emerging issues for sustainable food systems; a brief summary of the major challenges	Herrero and Thornton (2013)
Livestock contributions to the chapter 'Food Security and Food Production Systems', Working Group II	Porter *et al.* (2014)
Livestock and the environment: what have we learnt in the last decade?	Herrero *et al.* (2015)
Impacts of climate change on the agricultural and aquatic systems and natural resources within CGIAR's mandate: an inventory of what is known	Thornton and Cramer (2012)
How does climate change alter agricultural strategies to support food security?	Thornton and Lipper (2014)

Mitigation technologies

The potential for reduced CH_4 and CO_2 emissions from livestock and pasture management in the tropics; analysis based on systems characterization in the future	Thornton and Herrero (2010b)
The impacts of climate change on livestock and livestock systems in developing countries	Thornton *et al.* (2010)

Adaptation problems

Is proactive adaptation to climate change necessary in grazed rangelands? A study on how these systems may need to adapt	Ash *et al.* (2012)
Adapting smallholder mixed crop–livestock farming systems to climate variability in northern Burkina Faso with crop–livestock interactions	Rigolot *et al.* (2017)
Transitions in agro-pastoralist systems of East Africa: impacts on food security and poverty. Twelve case study sites in the marginal areas, evaluating likely impacts and possible adaptations	Rufino *et al.* (2013)
Evaluating climate-smart adaptation options in mixed crop–livestock systems in developing countries: a largely qualitative approach to targeting and evaluation	Thornton *et al.* (2016)
Climate change and pastoralism: impacts, consequences and adaptation	Herrero *et al.* (2016)
Exploring future changes in smallholder farming systems by linking socio-economic scenarios with regional and household models: an early multi-scale analysis of different drives of change, including climate change	Herrero *et al.* (2014)

The future of tropical agriculture

The future of agriculture (crops and livestock) to 2050	Rosegrant *et al.* (2009)
Drivers of change in agricultural systems to 2050	van Vuuren *et al.* (2009)
A largely qualitative assessment of the likely effects of climate change as a constraint to the growth of the livestock sector	Thornton and Gerber (2009)
Kenya: climate variability and climate change and their impacts on the agricultural sector	Herrero *et al.* (2010)
Implications of future climate and atmospheric CO_2 content for regional biogeochemistry, biogeography and ecosystem services across East Africa	Doherty *et al.* (2010)
Climate change and the growth of the livestock sector in developing countries	Thornton and Gerber (2009)
Impact of climate change on African agriculture: focus on pests and diseases	Dinesh *et al.* (2019)
Using a stakeholder and multi-model process to translate the shared socio-economic paths under climate change for the West Africa region	Palazzo *et al.* (2017)

- Multi-host diseases. The majority of climate-sensitive diseases affect many host species including livestock, wildlife and occasionally humans. This makes them much more difficult to control or eliminate than disease that have only a human or livestock host (for example, when zoonotic tuberculosis is present in badgers it is much more difficult to control than when it is only present in cattle).
- Joint occurrence of climate-sensitive diseases. A review of risk maps reveals that a number of climate-sensitive livestock diseases occur in some common areas given that their emergence and transmission are controlled by similar ecological factors.
- Lack of laboratory and epidemiology capacity. The lack of laboratory and epidemiology capacity is a long-standing problem in developing countries. Much effort and expense has been spent on improving capacity, and best approaches exist but require investment.

Adaptation of Livestock Systems to Climate Change

The AR5 text (IPCC, 2014) on adaptation relies heavily on Thornton *et al.* (2009) for its list of adaptation options. Adaptation options include: (i) matching stocking rates with pasture production; (ii) adjusting herd and watering point management to altered seasonal and spatial patterns of forage production; (iii) managing diet quality (using diet supplements, legumes, introduced pasture species and pasture fertility management); (iv) more effective use of silage, pasture seeding and rotation; (v) fire management to control browse encroachment; (vi) using more suitable livestock breeds or species; (vii) migratory pastoralism; and (viii) biosecurity activities to monitor and manage pests, weeds and diseases (IPCC, 2014, p. 517).

Research in Australia found that combining adaptations can be more beneficial than single adaptations (Ghahramani and Moore, 2013; Moore and Ghahramani, 2013). Options include replacing cattle with small ruminants, reducing stocking rates, better water management technologies and animal health services, and improving tree cover.

Improving livestock genetics is an option. Ortiz-Colón *et al.* (2018) reviewed work from the Caribbean showing that introducing a 'slick hair' gene into Holstein cows by cross-breeding with Senepols may increase heat tolerance and productivity. However, genetic improvements would require substantial investments and would involve long delays before being introduced into production animal populations. Moreover, there would be temperature limits above which adaptation is not possible, even with substantial genetic progress.

Costs of adaptation

There are many possible adaptations in tropical livestock systems for which we lack information on social and private costs and benefits. Dittrich *et al.* (2017) suggested techniques to assess livestock adaptations, such as cost–benefit analysis, portfolio analysis, real options analysis and robust decision making, but their approach suffered from a lack of empirical data to verify the proposed adaptations under tropical conditions.

Weindl *et al.* (2015) is the only study to project adaptation costs by simulating climate impacts on crop and range yields productivity for ten world regions to 2045. If tropical livestock systems shift towards mixed crop–livestock systems and away from grazing systems, adaptation costs would fall in sub-Saharan Africa and Latin America and the Caribbean, while rising significantly in Pacific Asia and South Asia. The Weindl model does not account for climate change effects on livestock disease or on animal reproductive performance and it is likely, therefore, to underestimate adaptation costs.

CGIAR research on climate change adaptation in livestock systems

While there have been extensive international efforts to develop options to adapt to climate change, less has been done with producers on implementation of these options. One innovation with the potential to facilitate adaptation has been agricultural insurance.

The information costs and incentive problems that are characteristic of agriculture have often prevented the emergence of insurance markets in rural areas (Binswanger and Rosenzweig, 1986). As information costs have fallen, the use of insurance for agricultural risk management has become more common in developed countries for staple crops (e.g. maize, wheat) and to a lesser extent for other crops and livestock. Insurance, by managing the effects of shocks, allows farms to invest more profitably in non-shock periods (Alderman and Haque, 2007; Barnett *et al.*, 2008; Mahul and Stutley, 2010). Insurance also facilitates complementary markets, such as those for credit, inputs and production methods (Alderman, and Haque, 2007; Carter *et al.*, 2007) by diffusing risks. Insurance can potentially help farmers to manage climate risk by allowing them to use new adaptation strategies, while reducing the adverse effects of current shocks (Collier *et al.*, 2009).

Index insurance has emerged as a possible solution for overcoming supply-side constraints to rural insurance markets and for extending access to agricultural insurance. The Index-based Livestock Insurance (IBLI) work is one form of that solution. By basing insurance policies on easily observed indices, such as precipitation or temperature, that are covariate with rural income and wealth risks, index insurance can potentially resolve the information costs and incentive problems inherent in rural financial markets and allow provision of insurance coverage at a fraction of the costs of loss-based polices (Chantarat *et al.*, 2013; Jensen and Barrett, 2016).

There is some limited empirical evidence of the effects of IBLI. Households with IBLI coverage reduced their herd size and increased investments that made the remaining animals more productive (Thornton and Herrero 2010; Gerber, *et al.*, 2011; Jensen *et al.*, 2017). Such impacts are consistent with economic theory, whereby insurance coverage substitutes for informal insurance mechanisms, oversized herds in this case. Insurance releases households from some risk constraints so that they can invest in productivity-increasing technologies, such as animal health care. In terms of climate change adaptation, insurance reduces sensitivity to drought and lowers the costs of adaptation.

A challenge to any insurance approach is cost. While it is conceptually possible for an insurance scheme to self-finance, and many private insurance programmes do so in other markets (e.g. life, automobile, health insurance) because of long experience identifying actuarial risks, agricultural insurance markets have proven difficult for the private sector to operate profitably because of the spatial nature of agriculture. The spatial nature of farming makes it costly to monitor risks and identify losses that trigger payment. Furthermore, climate change is likely to change the risk portfolio in unknown ways, making insurance management more difficult.

Knowledge gaps on adaptation

Thornton *et al.* (2008) summarized the knowledge gaps in adaptation and followed a priority-setting process to identify adaptation activities by their importance to ILRI's mandate, the clarity of ILRI's role, the presence of other providers, the achievability of outputs and outcomes, and the cost and approximate time to output. The gaps were as follows

- Adequately detailed estimates of the impacts of climate change on livestock systems with or without adaptation.
- The impacts of increasing climate variability.
- Information on costs and benefits of adaptations at given sites and seasons. This applies particularly to mixed systems, in which the interactions between crops and livestock can sometimes be managed to advantage. The challenge is to target packages of adaptation options that are locally appropriate and amenable to scaling up.

Some of the major gaps were addressed in the decade since Thornton *et al.* (2008). One example was the impacts of climate change on rangeland net primary productivity (Boone *et al.*, 2018). Several assessment models and targeting tools were developed and a special issue of *Agricultural Systems* (Volume 151, February 2017) was devoted to this topic. However, while these studies provide insights into what the impacts of climate change are likely to be, they do not provide much general guidance on priority adaptation activities as these are context specific.

A review by Ash *et al.* (2012) gave mixed results about the need for 'proactive adaptation' in rangelands; while 'incremental, autonomous adaptation [would be] sufficient to deal with the gradual expression of climate' it is not known how autonomous adaptation can manage more rapid climate change in the absence of new research and more supportive public policies.

Adaptation in mixed crop–livestock systems

Thornton and Herrero (2015) highlight four research needs for appropriate adaptation options among mixed crop–livestock enterprises in sub-Saharan Africa:

1. Biophysical models are needed to represent interactions among crops and livestock to make evaluations of mixed systems more robust. Most biophysical modelling has been done on the primary cereals (particularly maize, rice and wheat) and legumes (groundnut and soybean), but more work is needed on lesser-studied crops, such as trees and other perennials.

2. Whole-farm models are needed because of the complex interactions of financial and physical resources in smallholder households. Trade-offs between benefits and costs of adaptation recommendations are inevitable and must be quantified with a whole-farm perspective. Whole-farm modelling, especially in tropical Africa, is constrained by a systemic lack of time-series data. The explicit inclusion of human nutrition with its appropriate metrics is also essential.

3. Use of future scenarios is needed to capture the nuances of smallholder systems in the context of larger economic and biological changes. Some smallholder systems will intensify production and survive; others will become redundant as smallholdings are aggregated into larger, more intensive and more specialized systems.

4. Better metrics are needed to estimate vulnerability to climate change among smallholders and to define measures of successful adaptation, such as sustainability and reduced variability of income.

Adaptation in pastoral systems

Pastoralists have long adapted to a highly variable climate (see Chapter 15, this volume).

However, the most recent epoch in which global temperature was as high as it is now was more than 100,000 years ago. The experiences of pastoralists in recent millennia may therefore prove inadequate for adapting to current changes in levels and variability of temperature and humidity. For example, Thornton and Herrero (2010a) simulated an increase in drought frequency to once every 3 years and found that this higher frequency decreased livestock densities below desirable levels. In some places, adaptation will be possible through species changes, increased market orientation or the increased ability of pastoralists to manage climate risk.

Increasing population densities can rapidly modify the accessibility to land, water and feed that makes pastoralism a viable livelihood strategy (Hobbs *et al.*, 2008). Rising incomes are affecting consumption patterns and modifying expectations, with lasting impacts on traditional socio-cultural value systems and kinship networks. In some places, adaptation will be possible via farming system intensification through increased market orientation and increased ability of pastoralists to manage climate-related risks. In others, adaptation may need to be more transformative, including social innovations and changes in behaviour, institutions and cultural norms. Opportunities exist for improving development outcomes in pastoral systems, through combinations of policies and institutional and technological alternatives that will vary with context and through time as the future climate change envelope becomes less uncertain (Ericksen *et al.*, 2012). Understanding what is possible, what is not, and where will be critical for effectively improving the livelihoods of pastoralists and their rangelands (Herrero *et al.*, 2016).

Research is also needed on how policy can support the scaling of interventions that can contribute to food and nutritional security and poverty reduction under climate change. ILRI is already contributing to this agenda via work on IBLI and cash transfers and research on effective governance mechanisms that can promote adaptation. A recent collaboration with the World Agroforestry Centre called Local Governance and Adaptation to Climate Change (LGACC; http://www.worldagroforestry.org/project/local-governance-and-adapting-climate-change-

sub-saharan-africa-lgacc; accessed 8 March 2020), for example, combined research on rangeland governance with research on processes that promote adaptation. The team was able to draw conclusions about the complementarity between governance, rangeland management and climate change adaptation (LGACC, 2018).

Mitigation of Greenhouse Gas Emissions from Livestock

The livestock sector is a major source of GHG emissions, primarily CH_4, CO_2 and N_2O. Emissions arise from five components – ruminant digestion, excretion of manure and urine, feed production, land conversion to pasture and transport/processing.

Projections from the beginning of the 21st century to mid-century suggest that per capita meat consumption between 2010 and 2050 could increase by about 50% for low-income countries and about 10% for higher-income countries (Nelson et al., 2018, Supplementary Fig. 4). Low- and middle-income countries have a 62% share of total global production, rising to 72% by 2050 (Thornton, 2010). The GHG mitigation challenge is how to satisfy a growing livestock product demand while reducing GHG emissions.

Estimates of emissions from livestock

Estimates of GHG emissions of livestock products vary considerably; emissions per unit of protein are highest for beef and dairy and lower for pork, chicken meat and eggs (de Vries and de Boer, 2010; Gerber et al., 2013) due to their different feed and land-use intensities. Beef production can use up to five times more biomass to produce 1 kg of animal protein than dairy. Emissions intensities for the same livestock product also vary largely among different regions of the world (Herrero et al., 2013). Europe and North America have lower emission intensities per kg of protein than Africa, Asia and Latin America.

Estimates of the contribution of livestock to GHG emissions depend on estimation methods and data sources. AR5 reported a range of total agricultural emissions estimates of between 4.25 and 5.25 $GtCO_2eq$/year (Smith et al., 2014, Fig. 11.4). Estimates of emissions from enteric fermentation were just less than 2 $GtCO_2eq$/year, implying that cattle were responsible for 40–50% of agricultural emissions. Figure 16.2 reports early 21st century estimates of anthropogenic GHG emissions and livestock's share. In this figure, livestock's share of total emissions is 14.5%, with 27% from CO_2, 29% from N_2O and 44% from CH_4. Figure 16.3 shows the spatial distribution of livestock GHG emissions around the turn of the century.

National research on livestock emissions has been growing rapidly in response to the United Nations Framework Convention on Climate Change (UNFCCC) requirement of national emissions inventories. Patra (2012) estimated CH_4 and N_2O emissions from Indian livestock. Svinurai et al. (2018) provided estimates of enteric CH_4 emissions in Zimbabwe. What is not clear is how comparable the country-specific results are. The Standard Assessment of Agricultural Mitigation Potential and Livelihoods (SAMPLES) project (http://samples.ccafs.cgiar.org; accessed 8 March 2020) of which ILRI researchers are a part is designed to facilitate this cross-country comparability (Rosenstock et al., 2016).

Mitigation via supply- and demand-side options

Supply-side activities to reduce GHG emissions from ruminant livestock production can be classified as: (i) targeting reductions of enteric CH_4; (ii) managing manure to reduce N_2O emissions; (iii) sequestering carbon in rangelands; (iv) implementation of better animal husbandry practices; and (v) land-use practices to sequester carbon. Excluding land-use practices, Herrero et al. (2016) found that these options have a global mitigation potential of 2.4 $GtCO_2eq$/year. These estimates are in the same range as those proposed by Gerber et al. (2013) of 1.8 $GtCO_2$-eq/year, although strategies will vary by production system (Rivera-Ferre et al., 2016).

The AR5 review of mitigation options in agriculture (Smith et al., 2014) found that:

> Studies based on integrated modelling show that changes in diets strongly affect future GHG

Global total GHG anthropogenic emissions
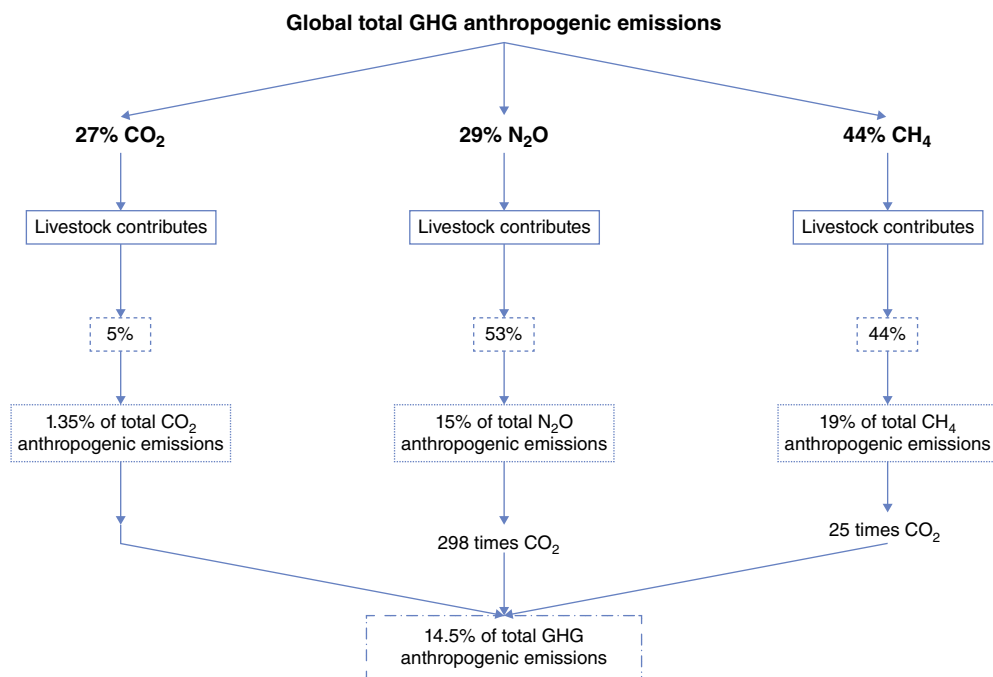
Fig. 16.2. Global total GHG anthropogenic emissions and livestock's share. (From Rojas-Downing *et al.*, 2017, based on analysis for the early 21st century in Gerber *et al.*, 2013.)
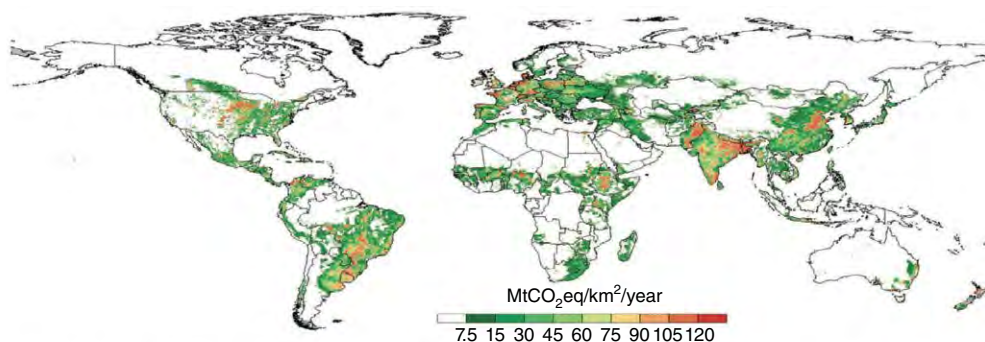
Fig. 16.3. GHG emissions from global livestock, 1995–2005. (From Herrero *et al.*, 2016.)

emissions from food production... Technical mitigation options on the supply side, such as improved cropland or livestock management, alone could reduce [emissions from 15.3 $GtCO_2eq/year$] to 9.8 $GtCO_2eq/yr$, whereas emissions were reduced to 4.3 $GtCO_2eq/yr$ in a 'decreased livestock product' scenario and to 2.5 $GtCO_2eq/yr$ if both technical mitigation and dietary change were assumed. Hence, the potential to reduce GHG emissions through

changes in consumption was found to be substantially higher than that of technical mitigation measures.

Supply-side options

Supply-side efforts have focused on reducing the GHG burden of livestock through increases in productivity. Capper *et al.* (2009) showed that

US dairy production in 2007 used only 21% of the animals, 23% of the feed, 35% of the water and 10% of the milk that had been required in 1944 to produce 1 billion kg of milk. Emissions from dairy cattle fell in consequence, with CH_4 emissions only 43% and 56% of N_2O emissions in 2007 relative to 1944. Overall, the carbon-equivalent footprint of 1 billion kg of milk in the USA in 2007 was 34% of that in 1944. Similar evidence was found by Gerber *et al.* (2011) who identified four reasons for the reduction in emissions from dairy systems as they intensify: (i) higher-quality diets; (ii) higher proportions of feed energy and protein used for production and not maintenance; (iii) higher nitrogen efficiency; and (iv) a concentration approach to reducing unit emissions through genetics and animal health.

Gerber *et al.* (2013, p. xiii) provided a global review of mitigation potentials to reduce GHG emissions from ruminant and non-ruminant livestock. They found that a '30% reduction of GHG emissions would be possible, for example, if producers in a given system, region and climate adopted the technologies and practice currently used by the 10% of producers with the lowest emission intensity'.

The technical changes modelled in Gerber *et al.* (2013) are due to productivity gains from higher digestibility feeds, herd health interventions and genetic selection for animals with higher milk productivity. It is not clear whether the technologies producing these gains are profitable.

Weindl *et al.* (2017) compared supply- and demand-side scenarios in carbon dynamics to 2050. They mapped the results of two demand scenarios – a continuation of trends in global diets, including levels of animal products, and a gradual change in diet projections to lower shares of animal-based calories in diets, with 15% as the upper limit in 2050 for calories from livestock and fish – and four supply scenarios, ranging from current levels of productivity in low-productivity animal systems to slight to low to moderate productivity gains. Changes in diet would produce substantial reductions in CO_2 burden at all levels of productivity change, ranging from −40% to −57%. Changes in productivity without changes in diet would increase the CO_2 burden substantially. The highest abatement of carbon emissions (63–78%) can be achieved if reduced consumption of animal-based products is combined with sustained productivity gains in plant production, but the economic feasibility of the latter is uncertain.

Scherer and Verburg (2017) compared supply- and demand-side options under the label of 'climate-smart agriculture'. Adaptation measures under climate-smart agriculture can involve technological advances, new farming practices, and changes in food origin and supply chain management. Unlike Weindl *et al.* (2017), Scherer and Verburg (2017) did not use an integrated global model, so their findings are weaker with regard to demand-side measures. Their findings were that: (i) emissions reductions are possible with demand measures, such as a vegan diet or local sourcing, but their economics are very uncertain and site-specific; and (ii) supply-side measures can also have mitigation effects, but the latter are probably less effective than demand measures.

Ripple *et al.* (2013) argued for both supply- and demand-side options, citing modelling of a food tax proportional to the mean GHG emissions per unit of food sold. Shields and Orme-Evans (2015) argued that a mitigation strategy of intensifying production would not be socially sustainable because of its adverse effects on animal welfare.

Valin *et al.* (2013) reported results from GLOBIOM modelling of productivity increases in crops and livestock. They found that closing yield gaps by 50% for crops and 25% for livestock by 2050 would decrease agriculture and land-use change emissions by 8% overall, and by 12% per calorie produced. However, the outcome is sensitive to the technological path and which factor benefits from productivity gains: sustainable land intensification would increase GHG savings by one-third when compared with a fertilizer-intensive pathway. Improvements in the crop or livestock sector have different outcomes: crop yield gains would bring the largest food provision benefits, whereas livestock yield gains would bring the largest cuts in GHGs.

N_2O is a powerful GHG that is emitted as a consequence of the use of both organic and inorganic nitrogenous fertilizers. Some quantity of applied nitrogen is not taken up by the plants and is lost to ground water and the atmosphere. In the early part of the 21st century, it was discovered that the roots of many plants release

substances that inhibit nitrogen release. The process is called 'biological nitrification inhibition'. Early research focused on the tropical pasture grass, *Brachiaria* spp., and researchers have since looked into the possibility of enhancing biological nitrification inhibition in wheat, barley and rye (Subbarao *et al.*, 2009; Moreta *et al.*, 2014; Byrnes *et al.*, 2017; Karwat *et al.*, 2017; Subbarao *et al.*, 2017; Nuñez *et al.*, 2018; Teutscherova *et al.*, 2019).

Mitigation research in livestock systems

A key contribution to both ILRI and other researchers in the study of livestock emissions was the development of the RUMINANT model, as first described by Herrero (1997) and subsequently by Herrero *et al.* (2013), with reference to Sniffen *et al.* (1992) and AFRC (1993). It is used to predict feed intake, nutrient supply and CH_4 emissions. These numbers are then aggregated to systems, countries, regions and continents using the population projections.

The main mitigation research at ILRI began just after the publication of *Livestock's Long Shadow* (Steinfeld *et al.*, 2006), building on earlier research at ILRI on five factors – digestion, manure, feed production, land conversion and transport/processing – that contribute to ruminant-related GHG emissions. The goal was to develop spatially disaggregated livestock system data and better information on differential impacts and emissions by system, species, region, technology and country.

Herrero *et al.* (2008) published the first study estimating emissions from African domestic ruminants. This study combined country-level calculations of changes in livestock production due to population densities and climate change with spatially explicit distributions of CH_4 emissions. The classification system built upon earlier ILRI efforts to better classify and map livestock production systems (Kruska *et al.*, 2003; Kruska, 2006), accounting for differences in land areas, population densities, numbers of livestock and diets for ruminants. Climate change was modelled as changes in LGP using the MarkSim model, which resulted in changes in area under different production systems (Thornton *et al.*, 2006). For animal population changes, national projections were made assuming that production and productivity

increase to meet demand and using data from FAO on livestock species and diet composition and Food and Agriculture Organization Corporate Statistical Database (FAOSTAT) population projections. For the latter, Africa was divided into regions to be more specific about diets by production system and season variation, along with the level of intensification. To move from diets to CH_4 emissions, they used the RUMINANT model. The results showed the importance of the assumptions about population growth and changes in densities, as these drove the projected increase in total CH_4 emissions, estimated to be 42% between 2000 and 2030. Emissions intensities differed between production systems, but all were estimated to increase by 2030. Total emissions varied by region, with the Horn of Africa estimated to be the largest emitting region. Cattle contributed over 80% of emissions across the continent. These findings were in line with other studies. Steinfeld *et al.* (2006) estimated emissions from Africa to be about 13% of the global total of enteric CH_4; Herrero *et al.* (2008) estimated the contribution to be about 10%. The differences are due largely to assumptions and inherent uncertainties in emissions factor estimates, which suggested the need for more research to have better CH_4 emissions estimates and targeting of interventions to reduce emissions.

In 2009, the IPCC GHG emissions taskforce invited ILRI's contribution to the emissions factor database. ILRI's contributions included both biological research into emissions from cattle production systems (e.g. Pelster *et al.*, 2016) and a long-term collaboration with the GLOBIOM model at IIASA.

Thornton and Herrero (2010b) estimated the potential for four interventions to reduce GHG emissions from livestock: (i) adoption of improved pastures; (ii) intensification of ruminant diets; (iii) changes in land-use practices; and (iv) changing breeds of ruminants. They estimated reductions in emissions intensities, per unit of milk or meat, and reductions in numbers of animals (e.g. from improved productivity), as well as carbon sequestered through the land management options. Restoration of degraded rangelands had the highest mitigation potential, followed by agroforestry, which both sequesters carbon and improves diet quality (and hence animal productivity). Improving breeds and

grain supplementation had the lowest mitigation potentials. The total of all interventions combined was a range of 6–12% reduction in current livestock-related emissions (depending on assumptions about adoption rates).

Herrero *et al.* (2016) assessed three interventions: (i) technical and management interventions; (ii) intensification and the associated structural changes of livestock systems; and (iii) moderation of demand for livestock products. All such interventions have the technical potential to mitigate emissions from livestock, but their economic potential may be far smaller due to adoption costs on the supply side and a lack of effective policies for promoting healthy levels of consumption of livestock products (Fig. 16.4).

In 2013, a special issue of *Proceedings of the National Academy of Sciences USA* was published, representing several years of intensive work to improve the modelling of heterogeneity in livestock system characteristics and their evolution, using spatially explicit data sets and different assumptions by region about future growth. Herrero *et al.* (2013) focused on differences among systems in land-use intensities and GHG emissions. They concluded that these differences showed potential for improvements in all tropical livestock systems, given their low productivity. This study produced an innovative data set on biomass use, production, feed efficiency, excretion and GHG emissions for 28 regions, eight livestock production systems, four animal species and three livestock products (Figs. 16.5–16.7).

The special issue of *Proceedings of the National Academy of Sciences USA* used the first biologically consistent, spatially disaggregated global data set of the main biophysical interactions among feed use, animal production and GHG emissions. It highlighted three points: (i) feed-use efficiencies are a key driver of productivity and therefore of GHG emissions per unit of output; (ii) grasslands are a critical resource, which provide almost 50% of plant biomass for animals; and (iii) mixed crop–livestock systems produce over 60% of animal production across the world.

CH_4 from enteric fermentation is the largest source of non-CO_2 emissions, with cattle accounting for 77%. Developing world regions contribute 75% of the global emissions from livestock, and sub-Saharan Africa is a global hotspot for high emissions intensities, driven by low animal productivity per unit of land and low-quality feeds, which extend the growing periods of animals raised on grasslands or crop residues.

Herrero *et al.* (2016) updated the 2013 analysis with new data on livestock production systems and on differences between technical mitigation potential and economic potential. First, they reviewed the major studies of GHG emissions from livestock, including both IPCC emissions guidelines as well as life cycle assessments, focusing on uncertainties in the estimates. They estimated that over the period 1995–2005, annual global GHG direct and indirect emissions from livestock were 5.6–7.5
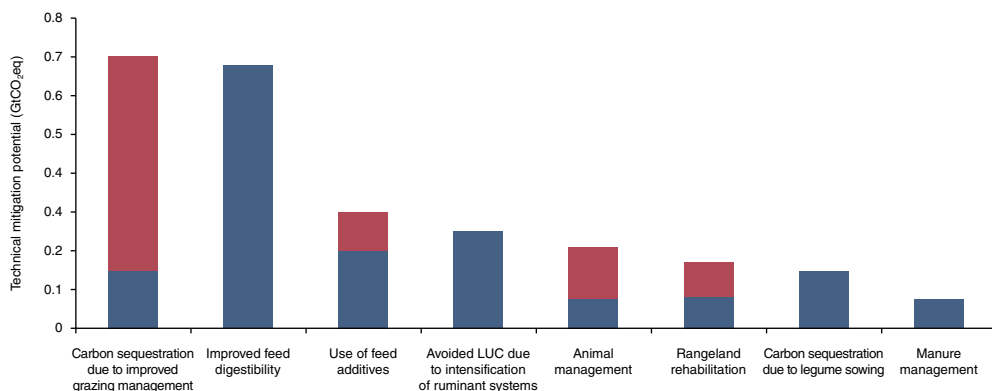
Fig. 16.4. Mitigation potentials of supply-side measures. Red represents the range for each practice, where available. LUC, land-use change. (From Herrero *et al.*, 2016.)
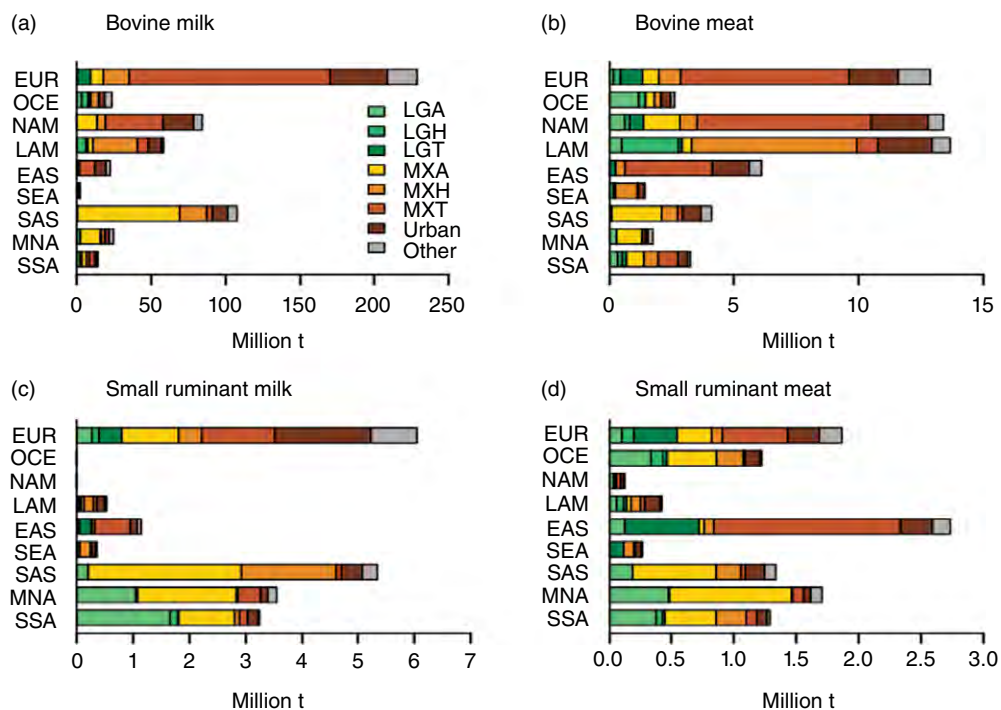
Fig. 16.5. Bovine meat (a) and milk (b) production and small ruminant milk (c) and meat (d) by region. EUR, Europe; OCE, Oceania; NAM, North America; LAM, Latin America and the Caribbean; EAS, Eastern Asia; SEA, South-East Asia; SAS, South Asia; MNA, Middle East and North Africa; SSA, sub-Saharan Africa; LGA, livestock/grazing/arid; LGH, livestock/grazing/humid; LGT, livestock/grazing/temperate; MXA, mixed/arid; MXH, mixed/humid; MXT, mixed/temperate; Other, other systems; Urban, urban systems. (From Herrero *et al.*, 2013.)

$GtCO_2eq$. They then estimated emissions reductions potential for several supply options, concluding that these practices could help mitigate between 0.01 and 0.5 $GtCO_2eq$/year or about two-thirds of livestock emissions. The supply options included feed additives, improved feed digestibility, manure management, soil carbon sequestration in grasslands, animal productivity and health, and avoided deforestation due to intensification

Demand-side options, discussed in greater detail below, comprise a new agenda that has gained traction in Europe and North America in response to concerns that livestock production uses a disproportionate amount of land, emits significant GHGs and can have negative health effects. The study assessed the potential for mitigation over the range of GHG taxes of US$20, US$50 and US$100/$tCO_2eq$. The 2030 mitigation potentials for these taxes were projected to

be 175, 200 and 225 tCO_2eq. For measures targeting soil carbon sequestration in grazing lands, higher mitigation levels of 250, 375 and 750 tCO_2eq/year were found.

Most emissions results to date have been derived from studies of temperate livestock and extrapolated to the tropics. Without more accurate data, existing models used to calculate emissions from smallholdings are more likely to give unreliable estimates and, in turn, are less useful for policy in the tropics (Rufino *et al.*, 2014; Kim and Kirschbaum, 2015). In 2013, ILRI began collaboration with the Karlsruhe Institute of Technology in Germany to measure the global environmental impacts of livestock production, in particular GHG emissions, in order to derive better estimates under tropical conditions (e.g. Zhou *et al.*, 2014a, near Lake Victoria; Zhou *et al.*, 2014b, for a wheat–maize rotation in subtropical China; Pelster *et al.*, 2017, for
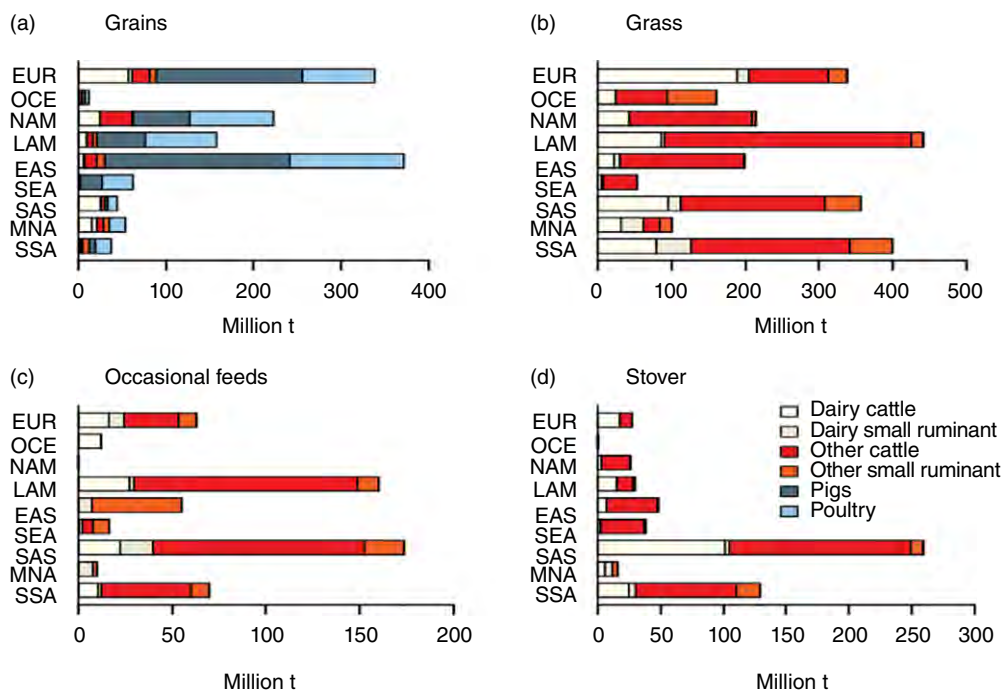
Fig. 16.6. Regional estimates of feed production for grains (a), grass (b), occasional feeds (c) and stover (d). See Fig. 16.5 for abbreviations. (From Herrero *et al.*, 2013.)

cattle and tree fodder in Kenya; Rosenstock *et al.*, 2016, for croplands in Kenya and Tanzania).

In 2012, ILRI researchers engaged with the CGIAR Research Programme on Climate Change, Agriculture and Food Security (CCAFS) flagship on Low Emissions Agriculture began collaborating on SAMPLES. Rosenstock *et al.* (2013) described the SAMPLES protocol for improving data quality and quantity from tropical smallholdings. This protocol was based on five innovations: (i) systematic data collection; (ii) informed sampling from emissions hotspots; (iii) quantifying emissions at several spatial scales, including whole farm and landscape; (iv) using a multi-criteria approach to link GHG emissions reductions with productivity gains; and (v) offering cost-differentiated measurements, depending on user needs.

ILRI established a modern environmental laboratory in 2014. The Mazingira (Kiswahili for environment) Centre is the only facility in Africa with the capacity for accurate measurements of GHG emissions from soils, manure and ruminant digestion, using field and laboratory measurements and analysis (https://mazingira. ilri.org; accessed 8 March 2020).

The Mazingira facility responds to several analytical challenges. Little is known about current baselines (e.g. Hickman *et al.*, 2014 found only 20 studies on N_2O and NO fluxes from agriculture in sub-Saharan Africa). Second, existing models have not accounted for all of the processes through which livestock emit GHGs (Rufino *et al.*, 2014). Third, time is needed for measurements to start and for data quality to be evaluated. An initial SAMPLES study provided 'the most comprehensive study in Africa to date' of annual *in situ* CO_2, CH_4 and N_2O emissions from soils in a mixed crop–livestock system in western Kenya (Pelster *et al.*, 2017). The authors found that land classes did not make much difference in fluxes, nor did management because input use was so low. The lack of a management effect is probably representative of most smallholdings in Africa, but the land class effect has not been widely tested. A second study found that land use and soil texture influenced GHG fluxes, although this study measured fluxes in the laboratory rather than *in situ* (Wanyama *et al.*, 2018). Pelster *et al.* (2016) measured emissions from excreta from cattle fed diets representative of
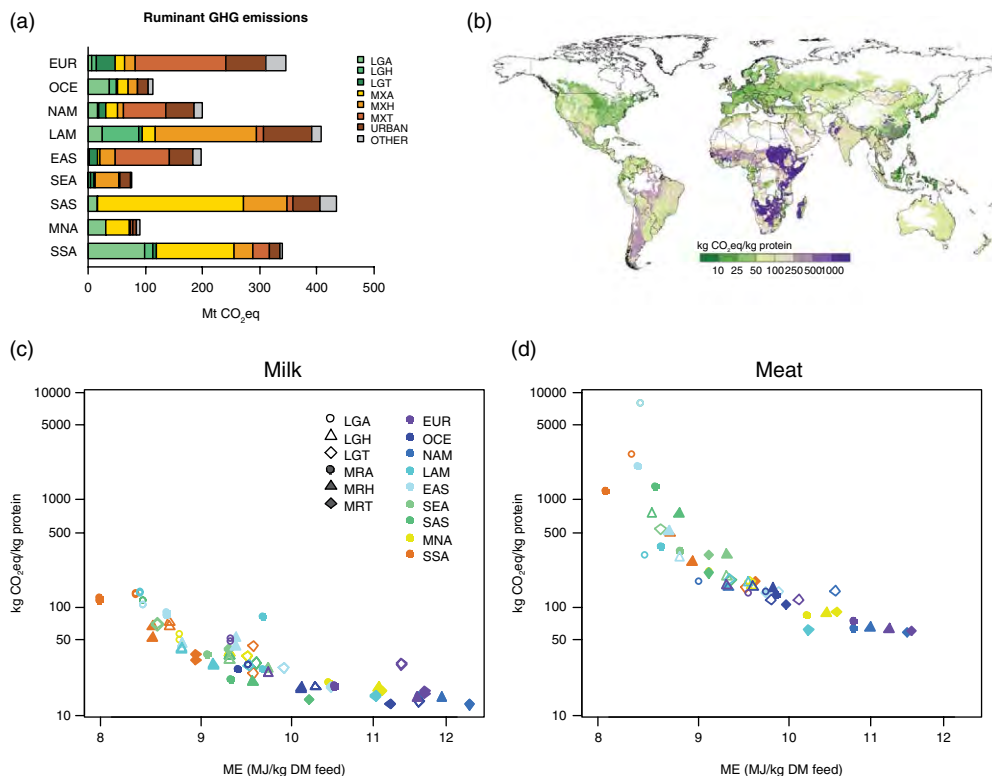
Fig. 16.7. Global non-CO_2 GHG emissions from ruminant livestock. (a) Non-CO_2 GHG emissions from global ruminant livestock (cattle, sheep, and goats) by production system and region. (b) Spatial distribution of non-CO_2 GHG emissions from ruminants (kg CO_2eq/kg edible animal protein). (c, d) Relationship between diet quality of ruminants and the non-CO_2 GHG emission intensity for edible animal protein from ruminant milk (c) and meat (d). DM, dry matter; see Fig. 16.5 for other abbreviations. (From Herrero *et al.*, 2013.)

East African conditions and found that CH_4 and N_2O emissions were lower than current IPCC estimates. The lower emissions were apparently due to the low nitrogen content of the excreta, reflecting the low nitrogen content of animal diets in the sample.

Another problem in establishing tropical emissions baselines is seasonal variability in feed quality and supply. Goopy *et al.* (2018) defined a method based on animal energy requirements, derived from field measurements of live weight, milk production, locomotion and feed digestibility. Emissions factors for annual CH_4 production were produced for three locations in western Kenya (Ndung'u *et al.*, 2018; Onyango, 2018). In all locations, the emissions factors per unit of live weight by type of animal and agroecology differed from the current IPCC estimates due to

variation in live weight, feed sources and feed availability.

Previous studies have shown that improving dietary quality and quantity results in live weight gains, which reduce emissions intensities per unit of live weight. Feed quality is the key factor influencing CH_4 production from ruminant digestion as shown in a meta-analysis of animal experimentation data (Hristov *et al.*, 2013)[1]. Blümmel *et al.* (2009, 2013) studied the potential to reduce GHG emissions in India. Although the research emphasis was on use of crop residues to improve productivity, the India work found that a collateral benefit could be reductions in GHG emissions intensities per unit of output, and possibly a reduction in total emissions per herd, if productivity gains allowed a reduction in herd sizes.

Demand-side options

Much has recently been written about demand-side interventions (Garnett 2009; Smith *et al.*, 2013; Valin *et al.*, 2013). Springmann *et al.* (2017) estimated the mitigation benefits of a tax on foods whose production is GHG intensive and where current consumption levels in some countries have negative health effects (Fig. 16.8). They found a double benefit from this policy approach – a substantial reduction in GHG emissions, and health-promoting outcomes in middle- and high-income countries. Average GHG taxes on food commodities (based on an emissions tax of US$52/t$CO_2$eq) were highest for animal-sourced foods, such as beef (US$2.8/kg), lamb (US$1.3/kg), and pork and poultry (US$0.3/kg each), which corresponded to 40%, 15%, 7% and 9% of the mean global producer prices of these commodities.

Springmann *et al.* (2018) showed that between 2010 and 2050, as a result of expected changes in population and income levels, the environmental effects of the food system could increase by 50–90% in the absence of technological changes and dedicated mitigation measures. The same study also found that no single measure is enough to keep these effects within all planetary boundaries simultaneously, and that a combination of measures is needed to sufficiently mitigate the projected increase in environmental pressures.

Havlik *et al.* (2014) found that sustainable intensification of livestock production systems might become a key climate-mitigation technology. However, livestock production systems vary widely, making the implementation of climate-mitigation policies a costly challenge. They projected that by 2030 autonomous transitions towards more efficient systems would decrease emissions by 0.74 GtCO_2eq/year, mainly through avoided emissions from the conversion of 162 million ha of natural land. A moderate mitigation policy targeting emissions from both the agricultural and land-use change sectors with a carbon price of US$10/t$CO_2$eq could lead to an abatement of 3.22 GtCO_2eq/year. Livestock system transitions would contribute 21% of the total abatement, intra- and interregional relocation of livestock production another 40% and all other mechanisms would add 39%. Mitigation policies targeting emissions from land-use change are five to ten times more efficient – measured in 'total abatement calorie cost' – than policies targeting emissions from livestock only.

Revell (2015) used a partial equilibrium model of beef, poultry, pig and sheep meats for the major regions of the world to explore scenarios that might reduce meat consumption and GHG emissions. He concluded that economic and population growth to 2050 without any mitigation measures would lead to a 21% increase in per capita meat consumption and a 63% increase in total consumption and GHG emissions by 2050. However, the mitigation projections from the scenarios generated only a 14% reduction in cumulative emissions from the baseline 2050 projections, insufficient to meet the 2050 target of a 50% reduction in global GHG emissions.

Schader *et al.* (2015) explored the scope for sustainable livestock production by modelling the effects of a third strategy in which animal feeds that compete with food production are reduced, and in an extreme scenario, animals are fed only from grasslands and by-products from food production. While the extreme scenario largely reduces animal protein per capita by some 70%, it could provide adequate energy and proteins and reduce environmental impacts compared with a 2050 reference scenario as follows: GHG emissions −18%, arable land occupation −26%, nitrogen surplus −46%, phosphorus surplus −40%, non-renewable energy use −36%, pesticide-use −22%, and freshwater use −21%.

White and Hall (2017) used the total removal of animals as the extreme boundary to potential mitigation options and required the fewest assumptions to model the yearly nutritional and GHG impacts of eliminating animals from US agriculture. Although modelled plants-only agriculture produced 23% more food, it met fewer of the US population's requirements for essential nutrients. When nutritional adequacy was evaluated by using least-cost diets produced from the foods available, more nutrient deficiencies, a greater excess of energy and a need to consume a greater amount of food solids were encountered in plants-only diets. In the simulated system with no animals, estimated agricultural GHG decreased (28%) but did not fully counterbalance the animal contribution of GHG (49% in this model). This assessment suggests that removing animals from US agriculture would reduce agricultural GHG emissions but
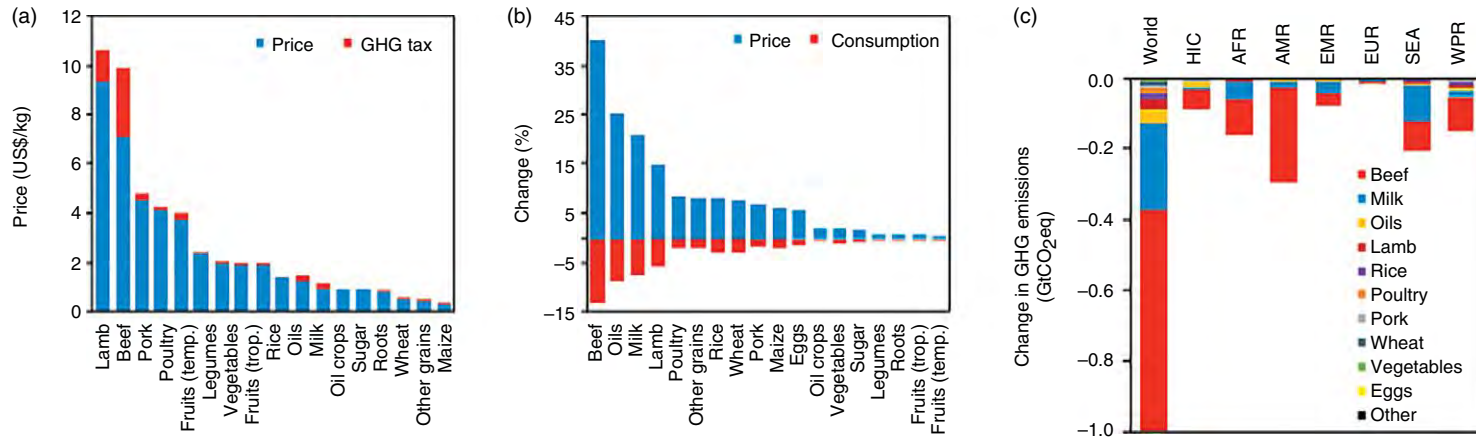
Fig. 16.8. Impacts of GHG taxes on food prices, consumption and GHG emissions. (a) Prices and GHG taxes by food commodity. (b) Percentage changes in price and consumption by food commodity. (c) Change in GHG emissions by food commodity and region. Regions include high-income countries (HICs) and the low- and middle-income countries of Africa (AFR), the USA (AMR), the Eastern Mediterranean (EMR), Europe (EUR), South-east Asia (SEA) and the Western Pacific (WPR), and an aggregate of all regions (World). Impacts are for a tax scenario in which GHG taxes are levied on all food commodities. (From Springmann *et al*., 2018.)

would also create a food supply incapable of supporting the US population's nutritional requirements.

The Future

Future climate research priorities for tropical livestock have three components – mitigation, adaptation and policy.

Research has established the mitigation potential of technical changes in the systems responsible for most GHG emissions from production animals. The best-understood systems are dairy and beef, which account for about 70% of GHG emissions from world livestock supply chains (Gerber *et al.*, 2013, p. 18). Other work by Gerber *et al.* (2011), on intensive dairying in a temperate climate, has established ranges of possible mitigation gains and the components – feed, genetics, health and management – of such gains and the output costs of those changes. The lessons of this work are applicable as first approximations to mitigation paths for low-productivity dairying in the tropics, but more *in situ* measurements from tropical systems are needed to sharpen estimates of potential gains. Mitigation work on the supply side must rely less on the assumption that temperate data and models are directly transferable to tropical conditions and instead will require greater focus on new findings under tropical conditions.

The future of mitigation research is to: (i) estimate potential GHG reductions from less well-studied tropical systems, such as extensive beef on pastures, intensive fattening on smallholdings and nutrient cycling in mixed crop–livestock farms; (ii) identify the components – feed quality and management, animal genetics, health, overall herd management, and demand reduction – of potential GHG reductions; (iii) refine estimates of success probabilities from investigations of feed-use efficiency in the tropics; (iv) identify profitability constraints, including policies, to adoption of potential technical changes; (v) 'backcast' projections from published models, notably MarkSim and LGP-based work, into actual data to test the validity of these projections; (vi) strengthen demand-side mitigation research in comparison with supply-side efforts to estimate least-cost paths for emissions reductions

from animal production and animal product consumption; and (vii) extend field tests under tropical conditions of actual emission levels and possible reductions. Examples of the latter are pilot projects for Low Emissions Development options (Ericksen and Crane, 2018; Kashangaki and Ericksen 2018).

There has been less research on climate adaptation in tropical livestock than there has been on mitigation. Additional adaptation research requires a broader view of adaptation beyond technical change, involving changes in behaviour, institutions and culture. Priorities for adaptation studies in tropical livestock systems include the following:

- More effort on the specific tropical problems of heat stress and animal performance, on the genetics of reproduction under greater heat stress, and on pests and diseases that do not exist in temperate climates.
- Improved capacity for surveillance of climate-sensitive diseases, coupled with new diagnostics for these diseases (see Chapters 2, 3 and 5–10, this volume).
- An expanded programme of characterizing, testing and disseminating perennial forage species adapted to hotter, drier and more variable climates (see Chapters 12 and 13, this volume).
- Decision support tools to target adaptation programmes and to monitor their effects, including new measures of adaptation at the household level.

The models underpinning policy recommendations for climate are inherently complex because of the number and scale of the climate, biological and behavioural relationships involved. Policy recommendations from climate research involving animals, in particular, require a closer integration of supply- and demand-side modelling because of the interactions between the two sides:

- More research is needed on the policy incentives to promote broad adoption of mitigation and adaptation practices in the tropics, given the externality problems involved in both.
- The literature comparing supply and demand measures is limited. Future modelling by ILRI and partners must involve closer

integration between supply and demand components (e.g. Weindl *et al.*, 2017).

- The dependence of arid rangelands on livestock demands an extended research and policy effort that recognizes that technical options are limited (Ericksen *et al.*, 2012; Herrero *et al.*, 2016) for GHG mitigation, for adaptation and for raising productivity even (see Chapter 11, this volume, on the difficulties of raising productivity from arid rangelands). Improved technical and institutional support for rangeland management is needed to identify sustainable land management practices and to promote them. Related to this would be assistance to such risk-management interventions as IBLI.

- In mixed crop–livestock systems, we also have not assessed the impacts of production shifts away from ruminants towards poultry on livelihoods and food security.

- Countries also need support to develop protocols and data to monitor and report on their commitments to UNFCCC and to prepare credible investment plans.

Acknowledgements

Note

[1] Most of the studies cited in the meta-analysis of Hristov *et al*. (2013) were conducted on ruminants consuming significant shares of grain in their diets, which is still uncommon in African livestock production compared with other regions.

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17 Economics and Policy Research at ILRI, 1975–2018

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Executive Summary

Goals of economics and policy research

The goals of livestock policy and economics research at the International Livestock Research Institute (ILRI) have been to increase small-holder returns from animal agriculture by: (i) analysing the productivity and targeting of live-stock-based technologies; (ii) identifying policy barriers that lower farm prices, raise input costs or lower the financial, information, and risk costs of new agricultural innovations; (iii) supporting institutions that improve productivity, create assets and improve the performance of value chains; and (iv) creating a policy and regulatory environment that allows animal agriculture to contribute to growth and poverty reduction.

Research spending

International Livestock Centre for Africa (ILCA) spending on economics and policy research was some US$48 million from 1975 to 1994, or 13% of the ILCA total of US$374 million. The sum of livestock systems research, which often had a policy component, plus economics and policy research during the ILCA era was US$120 million or 32% of the 1975–1994 total.

ILRI lifetime spending on economics and policy research has been about US$198 million since 1975, or 11% of the 1975–2018 total of US$1.75 billion. The sum of economics and policy work plus livestock systems research, which nearly always made some policy recommendations, was about US$375 million, or 21% of the 1975–2018 total.

Scientific impacts

The scientific impact of economics and policy research at ILRI and its predecessors, ILCA and the International Laboratory for Research on Animal Diseases (ILRAD), has been substantial:

- Definition of a path from research to development impact known as 'Livestock – A Pathway out of Poverty'.
- Contributions to global knowledge about distortions in agricultural incentives via a wide range of livestock system, value-chain, trade and incentive studies.
- The notable scientific achievement comprising the joint effort of ILRI, the International Food Policy Research Institute (IFPRI) and the Food and Agriculture Organization of the United Nations (FAO) to produce a study of global livestock trends: 'Livestock to 2020: the next food revolution' (Delgado *et al.*, 1999).
- Informed pro-poor regulatory systems for improved dairying in Kenya and Ethiopia, for live-animal marketing in Sudan, and for better structuring and financing of animal health in various livestock systems.
- Using remote sensing and household survey data, development of an index-based livestock insurance product, achieving wide scientific impact through the many well-cited papers produced from that data in Kenya and Ethiopia.
- Developing new methods: incorporating geographic information systems (GIS)-derived variables in econometric analysis, integrating models through farm, sector and global levels, including participatory approaches in field investigations and in the derivation of policy recommendations.

The second scientific impact was to develop technical and economic models derived from original field data that were applicable to policy problems:

- Collected and analysed data needed to support policy measures, including field surveys, modelling with GIS, bioeconomic models and surveys, randomized controlled trials.
- Property rights studies of grazing land, arable land and tree tenure, leading to site-specific policy recommendations in Ethiopia, Kenya and some countries in West Africa. This included demonstrations of the scope and impact of collective action in land rights, livestock value chains and natural resource management.

- Quantification of environmental constraints to growth, including soil erosion constraining higher land productivity in Ethiopia.
- Identification of barriers to women's participation in technology and product markets, notably in Nigeria and Kenya.
- The landmark work on dairy reform in Kenya, which used a combination of an innovative data set, modelling and communications strategy to achieve substantial economic benefits.

Development impacts

ILRI's policy and economics research, with the exception of the Kenya dairy policy effort, had limited identifiable development impact on output or equity. Some indication of development impact can be seen in the following:

- Analytical and organizational contributions to dairy market reforms in Kenya that benefited small producers and poor consumers. The estimated net present value (NPV) of these reforms, in terms of additional producer and consumer benefits minus reform programme costs, was US$230 million.
- Purchases of index-based livestock insurance (IBLI) policies in Kenya at an approximate amount of US$25 million and pay-outs to herders of US$10 million; purchases of IBLI policies in Ethiopia of US$2.5 million and pay-outs of US$370,000; and adoption by the government of Kenya of a national IBLI policy, based on the ILRI/IBLI model, which now provides insurance to 80,000 herder beneficiaries in the risky arid and semi-arid areas of Kenya.
- Identification of measures to promote the supply response after the 'Livestock Revolution' including supporting infrastructure, targeted producer transfers, definition of the conditions for successful collective action, and modernization of sanitary and phytosanitary (SPS) standards.
- Contribution to the design and analysis of reforms of property rights in mixed crop–livestock farming systems in Ethiopia after overthrow of the Derg in 1991.
- Evaluation of the effects of property rights, including traditional informal tenure, on land use, land management and tree tenure as it affected incentives to adopt alley farming practices.
- Contribution to reforms of animal health services in sub-Saharan Africa.
- A national programme to control classical swine fever launched in India following an ILRI study disclosing the economic impacts of the disease in three states in the country's north-eastern region.
- Livestock master plans: the major achievement in influencing public expenditure was production of livestock master plans in Ethiopia, Rwanda and Tanzania and in the state of Bihar, India.
- Capacity development: the main achievement was to link economists and scientists in other programmes and in other institutions through the African Livestock Policy Analysis Network (ALPAN), the African Trypanotolerant Livestock Network (ATLN) and the epidemiology-economics programme started at ILRAD in 1987. The epidemiology-economics work has continued for 30 years (see Chapters 5 and 6, this volume) and has had a strong scientific impact in proposing solutions to animal health problems.

Introduction

This chapter defines policy as the actions of governments and public agencies. Policy actions can include, *inter alia*, the writing and enforcement of laws and regulations; the funding or conducting of research that investigates public actions; the provision of information and other inputs; and the building, operating or funding of productive infrastructure (e.g. laboratories for disease diagnosis) and market infrastructure. In their policy actions, governments typically make use of fiscal instruments such as taxes, subsidies, and wage and price controls, as well as institutional constructs and measures (organizations, rules and regulations).

Two factors drive demand for public policy. The first consists of market failures (typically characterized by inefficient distribution of goods and services), negative externalities (when production and/or consumption imposes external costs on third parties, causing social costs to exceed private costs) or of 'free-riders' (where some individuals consume more than their fair share or pay less than their fair share of the cost of a shared resource). To address such market failures, governments may intervene to correct market distortions to improve efficiency and equity. The second driver of demand for public policy is ambitions to achieve social objectives of efficiency and equity through public goods that maximize society's return and ensure the equitable distribution of returns.

Zilberman and Heiman (2004) placed studies of public policy into three classes:

- Class I: advancing scientific understanding in describing systems and markets, assessing performance of markets, making sectoral accounts and estimating productivity.
- Class II: contributing to technical change that lifts productivity, such as breeding new stock or forage plants.
- Class III: advising on policies to improve efficiency or equity, such as improving external terms of trade, building institutions, investing in public goods, eliminating market distortions and calculating the costs of bad policies.

Studies of scientific understanding and technical change are of a 'diagnostic' nature: they provide information to agents – individuals, firms and sectors – with or without specific policy implications. Such studies may indicate market failures, negative externalities, or free-rider problems and their underlying causes, and suggest interventions as corrective measures. The focus of this chapter is on Class I and III types of policy studies, ranging from diagnostic market performance studies to analyses of the impacts of interventions and polices. Table 17.1 summarizes policy research impacts by policy class and gives specific problems addressed. Table 17.2 gives selected applications of bioeconomic models to policy problems.

Policy Problems

The overall goal of economics and policy research at ILRI and its predecessor ILCA has been to increase smallholder returns from farming with animals. This research has sought to: (i) analyse the targeting and productivity of livestock-based technologies; (ii) identify policy barriers that lower farm prices, raise input costs or increase the financial, information and risk costs of new livestock-related innovations; and (iii) support institutions that improve livestock productivity, create livestock assets and improve the performance of livestock value chains.

The following problems have been the focus of ILCA and ILRI economics and policy research: (i) the historical problem of supply response; (ii) animal health services and productivity; (iii) responding to the 'Livestock Revolution'; (iv) policy and technical barriers to smallholder dairying; (v) livestock and poverty; (vi) markets, institutions and competitiveness; (vii) land tenure; and (viii) livestock master plans. Economic and policy analyses linked to specific technologies are discussed for animal health in Chapters 1–9 and for feed production in Chapters 11–14 (this volume).

The historical problem of supply response

An initial problem of policy research at the founding of ILCA in the mid-1970s was how to stimulate supply through higher productivity. This led to policy research on the structure of production and trade and on the role of incentives in raising production. The research on this problem had very limited impact and has largely been forgotten, mainly because it failed to use ILCA's comparative advantage in farm data access and analysis.

The initial ILCA policy papers analysed subcontinental trends in production, demand and trade, and their drivers (Montgolfier-Kouevi and Vlavonou, 1981; Addis Anteneh, 1984; Sandford, 1985). These studies highlighted that Africa's low livestock productivity and growth rates contrasted sharply with the rapidly growing demand for animal-source foods, which implied an increasing dependence on imports. National

Table 17.1. Livestock policy research impacts by class and problem.

Themes	Policy Class I: providing information	Policy Class II: contributing to technical change	Policy Class III: improving efficiency and equity
The problem of supply response	Scenario modelling after 1995: Thornton (2010), Herrero *et al.* (2010); major impact for ILCA before 1995; Addis Anteneh on public services (1983, 1984, 1991); Thornton *et al.* (2011), Robinson *et al.* (2011) on mapping global livestock	McIntire *et al.* (1992); Pingali *et al.* (1987)	Perry and Randolph (1999) on animal disease; Jones and Thornton (2009) on crop–livestock interactions as affected by climate change
Animal health services	Addis Anteneh (1983, 1984, 1991)	Perry *et al.* (2002) on animal health and poverty; Kristjanson *et al.* (1999) on trypanosomiasis vaccine; McDermott and Arimi (2002) on brucellosis, McDermott and Coleman (2001) on trypanosomiasis control strategies	Perry and Randolph (1999)
Responding to the Livestock Revolution			
Livestock assets, poverty, and financial markets	Thornton *et al.* (2002) on poverty analytics		Thornton *et al.* (2002) on poverty analytics; Giller *et al.* (2011) on targeting technical change
Barriers to smallholder dairying		Holloway *et al.* (2000a) on dairying in Ethiopia	
Land tenure, property rights, and institutions	Verburg *et al.* (2009), Fritz *et al.* (2015) on cropland and field size	Reid *et al.* (2000b) on land use in Ethiopia, Berhanu Gebremedhin on land conservation in Ethiopia, Franzel and Wambugu (2007) on fodder shrubs	Coughenor *et al.* (1985) on pastoral models, Lawry *et al.* (1994); McCarthy *et al.* (1999)
Livestock master plans			
Public investment	Randolph *et al.* (2007) on role of livestock, Thornton *et al.* (2011) on adaptation to climate change	Minor impact	Coughenor *et al.* (1985) on pastoral models, Randolph *et al.* (2007) on role of livestock, Havlik *et al.* (2013) on adaptation to climate change; Shapiro *et al.* (2015)

Table 17.2. Selected applications of bioeconomic models, various years.

Problem/study	Theme and chapter in this volume	Region/country/ climate	Method	Objective function	Treatments	Policy recommendations	Technical recommendations
ECF							
Gettinby *et al.* (1988)	Acaricide resistance/ Ticks (Chapter 10)	Sub-Saharan Africa; subhumid	Process simulation	Minimize acaricide resistance in treated tick populations	Acaricides	Regulate acaricide use	Elucidate genetic basis of acaricide resistance in ticks
Mukhebi *et al.* (1992)	ECF (Chapters 5 and 6)	Kenya; subhumid	Partial budgeting	Financial and economic returns to ITM and tick control; IRR 48%	ITM and acaricides	Monitor benefits and costs of dipping frequency carefully	Joint use of acaricides and ITM
Nyangito *et al.* (1996a,b)	ECF immunization and tick control/ ECF, ticks (Chapters 5,6, and, 10)	Kenya; subhumid	Whole-farm simulation	Financial returns to ITM and tick control	ITM and acaricides	Monitor benefits and costs of dipping frequency carefully	Joint use of acaricides and ITM
	Ticks and their control (Chapter 10)	East Africa; subhumid and humid	Literature review	Financial and biological sustainability of long-term acaricides	Acaricides in rotation and combination	Buffer zones between domestic stock and alternate hosts (wildlife)	Strategic application of acaricides
Cattle productivity							
Cartwright *et al.* (1982)	Beef production/ livestock systems (Chapter 15)	Botswana; arid	Herd simulation	Output and profit maximization	Weaning ages of calves	NA	Manage weaning ages and milk offtake policy
Konandreas *et al.* (1983)	Beef and milk production/ livestock systems (Chapter 15)	Botswana; arid	Herd simulation	Profit maximization of product and input choice	Feed supplementation in cross-bred and indigenous cows	Supplementation economically superior in cross-bred cows; no public policy implications	Feed supplementation

Thornton (1987)[a]	Dual-purpose beef and milk production/ livestock systems (Chapter 15)	Colombia; humid and subhumid	Simulation model from station trials and field surveys	Optimize beef production	Improved grass-legume pastures in dual-purpose systems	None (pending more results on pasture outcomes)	Not specific

Feeds and forages

Powell *et al.* (1995)	Soil fertility management/ livestock systems (Chapter 15)	Several sub-Saharan African countries; subhumid and semi-arid	Survey, station trials, tabular models, deterministic simulation	Yield and financial optimization of organic and mineral soil amendments	Mulching, manuring, mineral fertilizers, crop-residue management		
Elbasha *et al.* (1999)	Planted forages (Chapter 13)	West and Central African countries; subhumid and humid	Survey, herd simulation model, tabular model of forage production	*Ex post* economic surplus; 'research paid for itself'	Planted forages, 'fodder bank' (usually *Stylosanthes* spp.)	Most recommendations technical; policies include providing extension information, credit and subsidized seed	
Kristjanson *et al.* (2001)	Dual-purpose cowpea/planted forages (Chapter 13)	Central and northern Nigeria; subhumid and semi-arid	Survey and tabular model after station trials	*Ex ante* economic surplus; cowpea grain 128–154% of NPV gross benefits; cowpea hay from –28% to –54%	Improved dual-purpose cowpea cultivars	No technical recommendations	No policy recommendations
Kristjanson and Zerbini (1999)	Dual-purpose pearl millet and sorghum/ multidimensional crops (Chapter 14)	105 districts within nine states of semi-arid India	*Ex ante* deterministic simulation	*Ex ante* economic surplus; meat and milk productivity (IRR 26–43%)	Higher straw quality in pearl millet and sorghum	Value incremental traction and manure output, value effects in new areas (e.g. north-east Brazil)	No policy recommendations
Valbuena *et al.* (2012)	Conservation agriculture	12 sites in nine countries in sub-Saharan Africa	Literature and data review	Optimize crop-residue uses among feed and mulch	Mulching versus feeding	Value output and soil quality	Favour conservation agriculture in sites with higher mean biomass production

Continued

Table 17.2. Continued.

Problem/study	Theme/part and chapter in this volume	Region/country/climate	Method	Objective function	Treatments	Policy recommendations	Technical recommendations
Trypanosomiasis							
ILCA/ILRAD (1988)	Trypanosomiasis/livestock systems (Chapters 2 and 3)	East Africa/Kenya coast; humid	Survey and tabular model	Optimize use of trypanotolerant stock	Trypanocidal drugs, sprays, traps, trypanotolerant stock		Choice method of trypanosomiasis control as functions of challenge, livestock system and susceptibility of animals
Itty (1992), Itty *et al.* (1988)	Trypanotolerant livestock and trypanocides	Several sub-Saharan African countries; subhumid	Surveys, herd/flock deterministic simulations	Optimize use of trypanotolerant stock	Vector control, trypanocidal drugs, trypanotolerant stock	Policy choice among treatments as function of land potential and stock density	
Agyemang *et al.* (1997)	N'Dama cattle and milk offtake	The Gambia; subhumid	Herd measurements, deterministic simulations	Profit maximization	Milk offtake of trypanotolerant stock	Private management recommendation of partial milk offtake	
Kristjanson *et al.* (1999)	Trypanosomiasis vaccine/trypanosomiasis (Chapters 2 and 3)	Sub-Saharan Africa; subhumid and humid	*Ex ante* simulation	NPV of net benefits to vaccine	Vaccine	None	
McDermott and Coleman (2001)	Trypanosomiasis (Chapters 2 and 3)	Sub-Saharan Africa; humid and subhumid	Deterministic epidemiological model without prices or costs	Rate of trypanosomiasis prevalence	Curative drugs, vector control, trypanotolerant cattle, vaccine	None	
Reid *et al.* (2000a)	Environmental effects of trypanosomiasis control/tick-borne disease	Sub-Saharan Africa; humid and subhumid	Survey and time-series projections	Rate of change of tsetse infestation as function of population growth	Implicit treatments of population growth and land use intensity	None	None
Dairying							
Nicholson *et al.* (1999)	Dairying	Coastal Kenya; humid	Household surveys	Impact of dairying on income and employment	Breed, feed, management, disease control	Promoting access of smallholders to dairy technology through financial and institutional measures	Not specific

Kaitibie *et al.* (2010a)	Reform of dairy marketing policy	Rural Kenya, mainly highlands	Household surveys, market surveys	Impact of dairy market reforms income and employment	Liberalization of raw-milk trade	Promoting direct sales of raw milk by smallholders and traders	Not specific
Other diseases							
McDermott and Arimi (2002), McDermott *et al.* (2013)	Brucellosis/ veterinary epidemiology (Chapter 5)						
Kimani *et al.* (2016)	RVF/ECF (Chapter 6)	Kenya; subhumid	Simulation of RVF epidemics	Reduce human and animal health effects of RVF measured in disability-adjusted life years	Vaccination and disease surveillance	Enhanced surveillance and earlier vaccination	Enhanced surveillance and earlier vaccination
Vertisol technology and land management							
Gryseels (1988); Gryseels and Anderson (1983); Getachew Asamenew *et al.* (1993)	Improved drainage as part of broad-bed management/ livestock systems (Chapter 15)	Ethiopia; highlands	Farm budget analysis and linear programming model	Profit/ha	Enhanced Vertisol drainage and tillage quality	Extend the technology; reduce cost of the BBM	Target technology to poorly drained areas
Rutherford (2008)	Improved plough for broad-bed management/ livestock systems (Chapter 15)	Ethiopia; highlands	Farm and market surveys, analysis of research and development costs	Estimate return to research in the BBM	Enhanced Vertisol drainage with BBM	Expand credit supply, reduce cost of the BBM	Expand use of BBM for pond construction and field irrigation

BBM, broad-bed maker; ECF, East Coast fever; ITM, infection-and treatment method; IRR, internal rate of return; NA, not applicable; NPV, net present value; RVF, Rift Valley fever.

[a]Thornton (1987) was part of a CIAT effort on modelling beef production, beginning roughly with CIAT (1975).

trends differed significantly and there was significant cross-border trade in live animals among many countries, especially in West and East Africa. In West Africa, the large cities in the coastal region in the south were major centres of meat and milk consumption, while livestock production was concentrated in the arid, semi-arid and subhumid zones in the Sahel to the north. A similar pattern – production in the pastoral and agro-pastoral zones and consumption in the cities – held in East Africa. This policy work established that demand was not a constraint to growth of African livestock and agriculture more generally.

Several early studies, notably Jahnke (1982), observed the poor incentives for all agricultural production in sub-Saharan Africa due to low official prices and overvalued exchange rates as domestic factors, and as a result of dumping and food aid as external factors. The 1970s and 1980s generated extensive study of price incentives in global and sub-Saharan African agriculture culminating in the landmark work of Schiff and Valdés (1992) to which ILCA and ILRI made little contribution.

ILCA contributions on incentives problems were microeconomic. An ILCA paper argued that international trade and pricing policies were particularly important for livestock given the widespread trade in live animals in sub-Saharan Africa (Solomon Bekure and Macdonald, 1985). First, many people derive income from livestock production and these incomes are directly affected by livestock prices. Second, consumers spend an important share of their income on livestock products and this share will rise with economic growth. Third, livestock pricing policies are important to governments because of their implications for incentives, public spending and revenue. The study further argued that 'positive' policies – enhancing effective measures – improved efficiency in live-animal markets where transport costs were high. Examples of such 'positive' policies were gazetting animal trekking routes to reduce costs of crop damage along the routes and establishing water and feeding facilities to reduce weight loss and mortality in transit. 'Negative' policies – eliminating ineffective measures – could also improve the efficiency of livestock markets, such as by eliminating arbitrary or discriminatory licensing of traders and other intermediaries and by

reducing protection to uncompetitive public agencies, such as parastatals, which were producing, trading or processing livestock products. Related studies of import competition in dairy products were inconclusive in terms of policy recommendations (von Massow, 1989).

Two trade studies were conducted around the time of the ILCA/ILRI merger in 1995. The first compared the effects of livestock policies on output, consumption, trade and government revenues in Côte d'Ivoire, Mali, Nigeria, Sudan and Zimbabwe (Williams, 1993). The study found that inflation and exchange rates were key variables in livestock pricing policies, and that some success had been seen in stabilizing real domestic prices. As a result of policy changes in exchange rates and domestic prices since the 1980s, there had been a shift away from taxing livestock producers. These changes had positive impacts on beef production and consumption in all study countries except Côte d'Ivoire, with mixed effects on exports.

The second study reviewed macroeconomic, sectoral and trade policies based on information developed for international farm trade negotiations (Williams *et al.*, 1995). The study focused on ruminant livestock in Africa, Asia and Latin America and on pork and poultry in West Asia and North Africa. It found that, along with macroeconomic, sectoral and trade policies, investments in infrastructure, animal health, and processing and marketing facilities were required to promote efficient resource use and growth in production, consumption and trade. It projected positive effects on livestock product supply from better incentives through trade liberalization, though the effects varied by region, country and commodity.

Markets, institutions and competitiveness

Ruminants

Market participation by smallholders can allow them to expand crop and livestock supply. To identify barriers to wider market participation, ILRI policy research has focused on the structure, conduct and performance of product and input markets with a particular emphasis on market access.

Kebede Andargachew and Brokken (1993) analysed sheep price patterns in the central highlands of Ethiopia to determine the effects of animal and market characteristics and season on price. Weekly price variations were evident in redistribution, intermediate and terminal markets. Animal characteristics (weight, age, body condition, sex and colour), as well as purpose for buying and buying season, were important in explaining price variation. The findings indicated that producers targeted market strategies to gain from coordination of fattening, breeding and trading operations. The study did not find any subtle market inefficiencies that might be addressed by policy beyond the obvious measures of increasing market density and lowering transaction costs by providing infrastructure.

ILRI collaborated in a study led by the Ethiopian Agricultural Research Organization (EARO) in which hedonic price models were used to determine seasonal and intermarket differences in prices of sheep in Ethiopia (Ayele Solomon et al., 2003). There were significant differences in prices among seasons and markets. Seasons in which farmers faced severe cash shortages exhibited the lowest adjusted prices for animals they sold, indicating that, although livestock may provide a fallback position for cash in times of crisis, terms of trade may be worst when farmers need cash the most. In general, there was no clear progression in price of sheep along the primary to terminal market chain ending in Addis Ababa as would normally be expected, except that the farthest market had the lowest price. In the case of goats, the price differences between markets followed to some extent the expected differences between primary, secondary and terminal markets. One possible reason for the different price progression along the supply chains of sheep and goats is that, in general, the Ethiopian highlands are not a major production or consumption area for goats, so supplies come mainly from the lowlands, with the result that the price movement followed the market chain from primary markets in pastoral areas to the terminal market in Addis Ababa. On the other hand, most of the higher-quality sheep originating in both highlands and lowlands are bought by exporters and processors in the intermediate markets so both average quality and price are lower at the Addis Ababa terminal market. The implication is that producers and traders respond to market opportunities, so better transmission of demand and price information will benefit them.

A series of studies of livestock trade in Nigeria found that markets were quite responsive to incentives. Regular supply–demand imbalances, determined by regional comparative advantage, were corrected by live-animal trade from other regions of the country (Jabbar, 1993, 1995, 1998). Seasonal excess demand for small ruminants in southern Nigeria was met by supplies from the north. These findings suggested that production technologies that contribute to a regular increase in supply might be appropriate for smallholders, while seasonal commercial production might be geared to peak season markets.

A series of studies on cattle breed preferences applying hedonic analysis of cattle prices in south-west Nigeria found small but significant price differentials by breed (Jabbar et al., 1995, 1997; Jabbar and Diedhiou, 2001). In these studies, Muturu, a locally adapted West African Shorthorn breed, illustrated the relationship between farmer preferences and market values of cattle breeds. Even though Muturu is known for its superior abilities to resist diseases, particularly trypanosomiasis, and is productive under high humidity, heat stress, water restriction and poor-quality feed, the Muturu was rated the least desirable for market value and mobility. For producers, the perceived limited marketability, low market value and the need for mobility to market are important components of the returns to raising Muturu. For these reasons, farmers' aversion to Muturu as an investment imply little scope for its in vivo conservation. Eliciting farmers' knowledge about traits of breeds and their relationships to prices can be useful for designing breeding policy and strategy for breed development programmes (Jabbar et al., 1999).

Another study on the spatial integration of livestock markets in Niger found that livestock markets were 'related, but not closely integrated' (Fafchamps and Gavian, 1996). The authors suggested policy options for improving livestock market efficiency by investing in animal transport and lifting official restrictions on animal trade.

Ayele Solomon et al. (2003) surveyed livestock markets and traders in the highlands of

the Amhara, Oromiya and Tigray regions in 2000 and 2001. They showed that the numbers of agents (wholesalers, brokers and retailers) who trade many species had increased significantly since the collapse of the *Derg* regime 1991. This expansion in the numbers of agents, combined with small numbers of inspectors, led to many unlicensed traders, irregular inspections and a scarcity of fencing, feed and water troughs.

Jabbar *et al.* (2008) found that Ethiopian livestock markets were characterized by non-standardized products and lack of public information about quantities and prices. Consequently, livestock trading was largely a personalized business among brokers with regular buyers and sellers; this regularity is a form of social capital used for gathering information, searching buyers/sellers, negotiating prices and enforcing contracts. Business relationships were based principally on trust developed over time, without strong ethnic, religious or family ties. Although most transactions were conducted in the physical presence of parties, contract disputes were common and were typically settled mainly through informal means as formal legal systems were absent or expensive. It was argued that policies to reduce transactions costs and multiple taxes while increasing access to market information would improve trader margins and market performance.

Examining the factors that affect market participation and sales by households, Ehui *et al.* (2003) showed that physical capital (ownership of different species of livestock and landholdings) and financial capital (crop and non-farm income) are the main factors influencing market participation and sales, rather than the distance to markets and towns. These results suggested that constraints to production of livestock and livestock products (e.g. capital to purchase animals, feeds and processing equipment) were the main factors limiting market participation.

Baltenweck and Staal (2007) explored spatial measures of market access for milk and beans in the Kenyan highlands. Measures of market access were used to create spatial price decay functions in relation to transaction costs. The effects of market access differed significantly depending on the traded good. The analysis also demonstrated that spatial price formation could be used to generate more accurate measures of unit distance marketing costs than other approaches and hence indicate priorities for public investments to reduce those costs.

Bahta and Malope (2014) examined the competitiveness of smallholder beef farmers in Botswana using data from randomly selected producers. There was significant inefficiency, with about 74% of the variation in actual profit from maximum profit between farms arising from differences in farmer practices. The mean profit-efficiency level of 0.58 suggested scope to improve beef profitability with current technology. Profit drivers included education, distance to market, herd size, access to information and crop income. The main policy lesson was to improve market access so as to raise profits among smaller producers.

Pigs and poultry

With the merger of ILCA and ILRAD into ILRI in 1995, the mandate of the new institute expanded to include pigs and poultry. A series of ILRI-led studies in Asia beginning in the 1990s identified constraints to smallholder production in non-ruminant livestock.

Lapar *et al.* (2003a) studied a cross-section of smallholders in northern Luzon, in the Philippines. They investigated factors motivating smallholders' decisions to sell products or consume them as functions of transaction costs, labour mobility, capital formation and indebtedness. The strong effect of animal numbers on the participation and selling decisions of farmers suggested that policy interventions may be needed to support smallholder access to input and output markets. The availability of alternative occupation opportunities, however, significantly affected the viability of social and economic prescriptions, and policy makers must be cognizant of these results when targeting objectives for smallholders. Remittances had a positive influence on market participation, suggesting the importance of financial security in enabling smallholders to manage risks and subsistence requirements.

Costales *et al.* (2006) studied how scale affected access to markets by hog producers in southern Luzon, a major hog-producing area in the Philippines. Regional data indicated that between the 1990s and 2000s there had been an expansion of larger hog farms and displacement

of small farms. The study applied a probit model to identify factors that determine participation in hog production and applied a profit-efficiency model to identify the role of transaction cost barriers in smallholder performance. The model results showed that the decision to participate in hog production was positively influenced by the availability of family labour and by the capacity to deal with fixed transaction costs for access to financial resources. Market participation was negatively influenced by higher opportunity costs of family labour due to access to off-farm job markets and by distance to hog markets outside the village. Comparison of contract and independent growers among hog producers showed that most contract growers tended to specialize in fattening pigs to slaughter. In contrast, independent producers tended to combine the production of weaners (piglets) with slaughter hogs or specialized in weaner piglet production. In general, contract growers had larger levels of operations than independent growers. Contract growers exhibited better access to output markets and to good-quality feeds and stock, feed credit, veterinary health services and credit for expansion purposes.

One study analysed contract farming in Bangladesh poultry (Jabbar *et al.*, 2007), while another covered pig farming in Vietnam (Tiongco *et al.*, 2009). The Bangladesh study found three emerging contracts – production marketing, formal input marketing and informal output marketing. The profitability of broiler farms did not differ significantly between contract and independent farms, but it differed between the two sample districts. Contract layer farms performed much better than independent layer farms. These differences were due to differences in the feed conversion ratio, fattening days and sale weight for broilers, and egg production per bird per laying period and length of laying period for layers. Based on a sample of independent poultry farms in five districts, the key reasons for business failure after 1 or more years of operation were identified as high input prices, irregular supply of day-old chicks and poor-quality veterinary drugs. Some input market problems have been solved by contract farming in other contexts, but formal contract farming seems to have offered few opportunities for commercial poultry farmers in Bangladesh.

The study on pig contract farming conducted in four provinces in northern Vietnam showed that there was limited scope for smallholder pig producers to participate in formal contracts; however, smallholders were found to participate in informal contracts with cooperatives and with input/output traders that facilitated their access to pig markets. To understand the drivers of these smallholders to participate in these types of contractual arrangements for pig and piglet production, a multinomial logit model was applied. The results suggested that the significant determinants of smallholders' participation in contractual arrangements are age, proportion of time spent in pig-raising, location, distance to veterinary shops and access to animal health services.

A study on livestock development in Vietnam identified barriers to input and output markets for smallholders (Lapar *et al.*, 2003b). The uncertain quality and high prices of animal feeds, including raw materials for feed processing, the variable quality and high cost of more productive animal breeds, and the high costs of veterinary inputs were found to be the principal barriers in livestock input markets. Constraints to reaching output markets included poor-quality and unsafe meat and meat products, lack of a legal framework and standards, bottlenecks in the distribution channel and limited access to information. In addition, the prevailing marketing system and channels for each type of commodity from farm to market have evolved into a multi-stage system that is characterized by high transaction costs and lack of market integration.

Another study in Vietnam addressed whether national livestock production can remain competitive under rapid demand and import growth (Akter *et al.*, 2004). The study applied a policy analysis matrix to assess the competitiveness of poultry and pig production based on 1999 data from a sample of 2213 farms. Poultry and egg production from cross-bred and exotic breeds were competitive in the north, while egg production with local breeds was uncompetitive in the south due to low productivity and high per-unit cost. Economies of scale in poultry production existed in the north but were not so clear in the south. Domestic prices of outputs and inputs were higher than world prices due to trade protection. In the long run, small poultry farmers might not be able to compete in a more

liberalized economic environment with low-productive local breeds and higher per-unit cost; policy support such as access to credit and inputs for smallholders would be needed to maintain their competitiveness.

Pig production under existing technologies and market conditions was highly competitive, especially with local and cross-breeds in the north and exotic breeds in the south. At the time of the survey, the producers in the south were apparently benefiting due to a greater role of formal market conditions, which favoured cross-breeds and exotic breeds, while in the north, policy interventions made input costs higher and output prices lower. Some economies of scale were demonstrated in pig production, in that medium-sized farms were more cost-effective and small farms were least competitive.

Using the same data set for Vietnam, stochastic frontier production functions were used to assess the effects of market and other factors on technical efficiency, respectively, in poultry (Jabbar and Akter, 2006) and pig production (Jabbar and Akter, 2008) In the developing-country production environment, farm production efficiency is often measured in terms of on-farm resources and producer characteristics. In these studies, it was postulated that input and output market-related factors also influence farm production decisions and hence farm efficiency.

In the case of poultry, in general there are significant differences in the production behaviour and efficiency levels between the north and the south among farms producing different breeds of poultry, between mixed and specialized poultry farms, between household and commercial farms, and among producers located in different agroecological regions. Sale at marketplace rather than at the farm gate, market distance and flock size significantly reduced inefficiency in both regions. Contract farming or sale, the number of visits by extension staff, family labour supply, land size and education levels of households had significantly reduced inefficiency in the north but had no significant effect in the south. The direction and significance of influence on efficiency differ between the two regions for credit use, inputs from government, ratio of home-produced crude feed, producer age and gender of the household head. Therefore, opportunities exist for improving average efficiency through interventions in a number of product and input market domains and household characteristics that may improve access to information, technology and management decisions.

In the case of pigs, there are significant differences in production behaviour and efficiency levels between the north and the south among farms producing different breeds, between mixed and specialized farms, between household and commercial farms, and among producers located in different agroecological regions. Access to better output markets, land size, herd size and education of the household head significantly reduced inefficiency, while access to government-supplied inputs, age of the household head, female-headed households and family-supplied crude feeds significantly increased inefficiency in both regions. The direction of influence on efficiency differs between the two regions for access to credit, proportion of output sold at market rather than at the farm gate and family labour supply. Generally, market-related factors had a more consistent influence on production efficiency in the south of Vietnam, where the experience of market economics is longer than in the north. Policy actions on providing better extension, more timely access to better-quality inputs through the private sector, making credit more easily accessible to smallholders and providing opportunity to sell output at better-priced secondary markets are expected to increase productivity and reduce inefficiency among producers located in different agroecological regions.

In some countries, local products are shielded from international competition by 'natural' factors influencing the purchase of products, such as strong local tastes (or preferences) that favour the local product and the absence (or relative absence) of complementary retail outlets or home appliances suitable for storing and preparing potential imported substitutes (Tisdell, 2009). The desire for fresh meat rather than chilled or frozen meat, the absence of supermarket outlets and limited refrigeration possibilities in homes can limit imports into developing countries of meat supplied by developed countries. This study gave some simple economic analysis of how local producers of livestock benefit from natural protection. Drawing on the results of research completed in Vietnam and other sources, factors that provide natural

protection to Vietnam's pork industry were identified, with particular attention given to their implications for small-scale household pig producers compared with larger-scale commercial pig producers. It was noted that the protection of Vietnam's pig industry was not based on a preference for pork from local breeds but arose for other reasons.

Animal health services and productivity

Policy aspects of animal health research at ILCA concentrated initially on institutions – who provides animal health services, how can services provision be more efficient and what is the scope for private provision? Public agencies were the main providers of animal health services throughout sub-Saharan Africa before 1980. After the introduction of structural adjustment programmes in the late 1970s and early 1980s and given the failure of veterinary services to reach many livestock farmers, the form and pricing of veterinary services became important policy issues. The debate centred on the justification for public financing of animal health services, especially those that could be considered private goods, such as curative services.

Addis Anteneh (1983, 1985) reviewed national information on the financing of livestock services in selected African countries. He found that: (i) services were underfunded with respect to the share of livestock in agricultural gross-domestic product (GDP); (ii) costs were mostly operating budgets and hence capital funding per staff was generally inadequate; (iii) services were largely funded with public resources and foreign aid, not with user charges, which discouraged user participation in service management; (iv) there was potential for more public spending because user charges – head taxes, slaughterhouse fees and taxes – were sometimes greater than public spending on livestock services, indicating that livestock revenue had been diverted to other sectors; and (v) the quality of veterinary services was low because of lack of funding, especially for non-staff variable costs.

A later study on financing livestock services (Addis Anteneh, 1991, Part 7) arrived at similar conclusions: (i) livestock services were again underfunded; (ii) staff costs dominated services to the detriment of non-staff variable costs, such as drugs and fuel; (iii) cost recovery was limited as a share of livestock service budgets; and (iv) private service delivery was weak, partly because of resistance from the public veterinary sector.

Mohammed Mussa and Gavian (1994) reviewed the privatization of animal health services in Ethiopia. They argued that vaccination and vector control are public goods because the benefits extend to the whole economy, while curative services (diagnosis and treatment) of non-transmittable diseases are primarily private goods (although some effects of repeated curative treatments, such as induced resistance to trypanocides or other antibiotics, would become public goods). The policy lesson is that preventative services work better when managed by the state, while privatization is feasible for curative treatments.

The question of payment for public services was studied by Swallow and Woudyalew (1994) who investigated whether communities in south-west Ethiopia would pay in cash and/or labour for trypanosomiasis control. When asked about the maximum amounts of money and/or labour that they would be willing to pay, 59% of households volunteered both money and labour and only 3% volunteered neither. Willingness to contribute money was related to the gender of the household head, the number of cattle held by the household and the participation of the household in a monitoring exercise being conducted by the research organization. Willingness to contribute labour was related negatively to off-farm employment status of the head of the household, and positively to the information available to the respondent about the programme. Apart from direct applicability of these results to increase local involvement of the affected population in the control programme, the study stressed that the methodology used here, when integrated into a participatory research approach, can generate practical results for evaluating the prospects for local participation in the provision of public goods.

Hall et al. (2004) evaluated the welfare effects of herd health programmes on smallholder dairies in central Thailand. Dairy farmers had appropriate incentives to adopt herd health measures; following adoption of control measures, there was an improvement in the efficiency

of policy support to dairying. Following a reduction in disease incidence on adopters' farms, the study found an increase in farm profits.

Outbreaks of Rift Valley fever (RVF) in East Africa in the past prompted a ban by Middle Eastern countries on imports of live animals from that region. Nin-Pratt *et al.* (2003a) evaluated the certification of exported live animals granted in an RVF-free zone, as a case for Ethiopia, as one way of handling RVF and complying with international regulations. The study also examined policies (export tax, sales tax and increased transaction costs) to make producers bear programme costs. The study concluded that implementing an animal health programme in Ethiopia's Somali region was economically feasible and would benefit poor livestock producers. It suggested that increasing taxes on livestock sales offered the best way to fund the health certification plan. This option, in which a transfer from middle and better-off producers to poor livestock producers is implicit, reduces harms to exports and welfare and increases benefits to the poor.

While Ethiopia has been a major supplier of animals to Middle Eastern markets, its market share has varied (Asfaw Negassa and Jabbar, 2008). The reasons included an inadequate supply of good-quality live animals to the export abattoirs in Ethiopia, with some abattoirs operating at less than half their capacity, which raised the average fixed costs per animal and reduced competitiveness in export and domestic markets. Livestock census data revealed very low commercial offtake rates of cattle and shoats from Ethiopia's smallholder farmers and pastoralists. This limited market participation by Ethiopia's smallholders and herders implied that, under the prevailing production and marketing conditions, small-scale farms and pastoral systems were not supplying sufficient numbers of good-quality live animals at competitive prices to make efficient use of the country's meat-processing capacity in its export abattoirs, lowering the competitiveness of Ethiopia's domestic and export livestock markets.

In addition, SPS barriers and animal diseases have traditionally constrained market access. A system dynamics model was applied to examine a proposed SPS certification system. The model's results indicated that the system may not be viable for beef exports to Middle Eastern markets, but the binding constraint was domestic input costs rather than the costs of compliance. Sensitivity analyses revealed that, while investments in feed efficiency and animal productivity would enhance Ethiopia's export competitiveness, the highly competitive nature of international beef markets may still prevent market access by Ethiopia's beef producers (Rich *et al.*, 2008; Rich and Perry, 2009).

Somalia was a traditional supplier of live sheep, goats and camels to Middle Eastern markets. Following the collapse of the Somali state in 1991, a rapid appraisal identified the institutions active in livestock exports (Mugunieri *et al.*, 2008) to understand informal policies. A more detailed study was then conducted with exporters to understand how the Somali origin satisfied import requirements for product quality and cost (Asfaw Negassa *et al.*, 2008). Constraints along the export chains were mapped, and appropriate steps for addressing the constraints were recommended. The recommendations included: a certification system for health and quality; provision of market information, training in market opportunities for traders; formation of trade associations and other collective action forums to share information, capital, and strengthen ability to negotiate; and harmonization of informal and formal taxes and fees in marketing chains.

Sudan (including South Sudan, which became independent in 2011) was an historical exporter of live sheep and sheep meat to the Middle East, but its market share has fallen over time because Sudanese supply failed to meet Middle Eastern standards. A study analysing supply-chain constraints for Sudanese exports of sheep and mutton found that they faced long costly journeys by trekking or trucking, which reduced the animals' health and quality (El Dirani *et al.*, 2009). A high incidence of disease and mortality and low offtake rates among traditional producers limited the supply of high-quality animals. There were elaborate systems of inspection, testing and screening for diseases and other SPS standards in the supply chains, but, because of poor enforcement, too many unacceptable animals remained in the export lots, which led to rejections at destination. Although major markets in Sudan's hinterlands were integrated with the terminal market in Khartoum, as indicated by price cointegration, responses to price shocks

were variable among markets, with some markets more responsive than others and with supply markets responding more quickly and intensely to shocks than terminal markets. Policy recommendations to increase supply of export quality animals were to: invest in health, extension and higher-quality inputs leading to increased offtake rate especially from larger flocks; to reduce rejection rate throughout the long supply chain, increase investment in proper laboratory facilities including equipment and trained manpower; rigorously enforce screening procedures and standards, and enhance coordination among various agencies involved in supporting export oriented production and trading.

Responding to the 'Livestock Revolution'

A third policy problem has been how trade and globalization affected incentives for livestock production in poor countries and what policy could do to mitigate adverse effects or to exploit favourable effects. This problem became more acute at the turn of the century as growing populations, urbanization and rising incomes in developing countries fuelled a rapid increase in demand for animal-source foods, a phenomenon that become known as the 'Livestock Revolution'.

A 1999 collaborative study involving IFPRI, FAO and ILRI, 'Livestock to 2020: the next food revolution' (Delgado *et al.*, 1999) – became known as the Livestock Revolution study, used a global model to analyse changing supply and demand as they affected poverty, nutrition and health, and the environment. From 1971 to 1995, meat consumption in developing countries grew almost three times as fast as in developed countries. It was projected that by 2020, developing countries would be consuming 100 million t more meat and 223 million t more milk than they had in 1993, dwarfing the projected increases in meat and milk consumption in developed countries. Again from 1993 to 2020, per-capita consumption of meat and milk in developing countries was projected to increase, respectively, by 42% and 55%, in contrast to developed countries, where meat consumption was projected to increase by 9% and milk consumption to decrease by 2%. Much of the increased consumption in developing countries would

come from imports and would therefore pose both a threat and an opportunity to domestic producers.

The 'Livestock Revolution' study warned that smallholders might not benefit from rapid growth in international trade. It recommended new measures to defend smallholder interests[1]:

- Removing policy distortions that promote artificial economies of scale, such as credit and tax breaks and other subsidies and trade protection or support to large-scale producers.
- Building institutions to link smallholders to markets, for example by facilitating vertical integration of smallholders, cooperatives and other forms of collective action.
- Creating public goods through the provision of services for animal health and livestock extension, research and education.
- Regulating the environmental and public health costs of livestock production and consumption, such as water pollution and land degradation on the one hand and, on the other, the obesity epidemic and the emergence of new human diseases originating in livestock.

Nin-Pratt *et al.* (2001) analysed the role of China as an importer of livestock and other farm products. They analysed productivity growth in China's pig and poultry sectors and projected China's meat trade to 2010 in a general equilibrium model of the Chinese economy. China's net trade position was projected to be sensitive to posited growth of its GDP and its non-ruminant productivity, implying uncertainty in the policy contexts of other developing countries.

A similar study (Nin-Pratt *et al.*, 2003b) examined the implications of trade liberalization on Vietnam's smallholders, including the consequences for poverty alleviation. While the impact of trade liberalization on Vietnam's livestock production tended to be small, a more open Vietnamese economy would increase competitive pressure on domestic producers.

New non-tariff barriers have emerged in the form of more stringent SPS standards. The implications of such barriers were studied for exports of live animals from the Somali region of Ethiopia to the Middle East, where the exporters faced major high costs of compliance with the standards required by the importers (Nin-Pratt

et al., 2003a). Moreover, a ban on livestock exports from the Horn of Africa imposed by Saudi Arabia in 1998 and 2000 following an outbreak of RVF severely affected trade. The cost to the Somali economy of the ban was estimated to be at least US$21.8 million, with the total reaching up to US$36 million under some scenarios. The estimated loss in regional value added was US$195 million, almost equal to the value added produced in an average year. In the short run, middle- and higher-income households could manage the negative effects of the Saudi import ban by increasing consumption. Poor pastoralists with limited production capacity, however, would lose income because increased consumption of their own production was insufficient to compensate for export losses.

An important concern from the Livestock Revolution was that large producers would displace smallholders as markets opened because they could exploit economies of scale in production and in finance. A study in Bangladesh analysed the effects of policy and scale on the efficiency of dairy and poultry farms (Jabbar *et al.*, 2005). For dairy, they showed that breed, management, feed cost, choice of markets and access to credit for liquidity and to extension contact at times of real need to solve a production constraint were significant variables affecting the profitability and efficiency of dairy farms. Policy interventions – infrastructure, waste management, access to finance and creation of producers' organizations – favouring small farms would increase the overall efficiency of the dairy sector.

Baker and Enahoro (2014), in an overview of six studies, argued that information from a large number of household studies on livestock was not fully utilized by aggregate models, which failed to recognize heterogeneity, dynamics and exogenous forces on livestock systems. Household-level studies are not standardized and rarely identify and characterize key drivers and mechanisms for exploiting heterogeneity in policy analysis. The analysis defined and addressed the dichotomy in approaches to policy analysis for developing countries' livestock sectors and the gap in analytical approaches and identifies aspects of the way forward. Evidence was presented of inconsistencies and practicalities that emphasized the gap, but all studies presented evidence of integrative progress and listed opportunities for accelerating it.

Policy and technical barriers to smallholder dairy development

Dairying was an important theme in the early ILCA policy work because of its potential for expansion in sub-Saharan Africa, its potential benefits to smallholders as a source of economic growth and the growing political problem of rising imports. Early stage studies were conducted in Nigeria, Ethiopia and Kenya.

Research in Nigeria has examined demand, price determinants, policy reforms, and market development. Jabbar and di Domenico (1990, 1993) and Jansen (1992) described dairy consumption and its determinants in northern and southern Nigeria. In both regions of Nigeria, the type of product consumed, and the frequency of consumption differed markedly among ethnic groups and between urban and rural populations. In the south, per-capita income of dairy-consuming households did not differ significantly. Among the consumers, the income elasticity of dairy consumption was higher for rural households in the south-east. In northern Nigeria, dairy product demand was found to be income inelastic, and larger households tended to consume relatively fewer dairy products per household member than smaller households. The strongest conclusion from these studies was that pricing structures and local consumer preferences for traditional products argued for development of traditional production systems using indigenous cattle breeds. Production increase would require provision of breeding and health services and better feeds. Support for better processing, storage and transportation of traditional products would be required to access higher-income urban consumers.

Dairy reform in Ethiopia

The question of dairying potential was particularly important in Ethiopia, where bad policies had limited growth in dairying. A sequence of studies – Mbogoh (1984), von Massow (1989) and Brokken and Senait Seyoum (1992), and later Mbogoh (1992) and Mbogoh and Ochuonyo (1992) – identified policy and technical barriers to dairying in Ethiopia. A later review of dairy development in Ethiopia over 50 years: (i) identified trends in production, consumption, policy and development interventions; (ii) provided

evidence of the potential impact of improved dairy cattle; (iii) examined factors that promote smallholder dairying; and (iv) identified policy and technology issues for public interventions (Ahmed *et al.*, 2003).

Ethiopian dairying has passed through three phases, matching shifts in national economic policies. Since the early 1990s, the transition to a market economy has taken place and the dairy sector has been growing. Milk production during the 1990s expanded at an annual rate of 3.0% compared with 1.6–1.7% during the preceding three decades. Some 60% of the growth in milk production was due to herd growth; only 25% was due to higher productivity per animal.

There were institutional reasons for lower productivity in Ethiopia. Although dairy cooperatives in Ethiopia were not as strong as in Kenya, cooperatives induced increased participation of smallholders in fluid milk markets in the Ethiopian highlands. The survival of the milk groups that supplied inputs and processed and marketed dairy products depended on their continued ability to capture value-added dairy processing and to return those value-added benefits to their members.

Contrasts between Kenyan and Ethiopian dairying were investigated to elucidate the roles of cooperatives in reducing transaction costs. The similarities of the highland agroclimates in Kenya and in Ethiopia imply that dairy development in Ethiopia would benefit from the Kenyan experience, yet Ethiopia's dairy system was for many years less productive than Kenya's. Part of the difference was attributed to informality – in the early 1990s, Ethiopia had not developed a formal dairy system and some 88% of urban milk supply passed through informal markets (Staal, 1995). Another reason was policy taxation – Kenya and Ethiopia both had an international comparative advantage, but Ethiopian supply was restrained by an overvalued currency causing low domestic producer prices. The devaluation of the Ethiopian birr (ETB) in the early 1990s greatly improved the potential of agricultural production for import competition and for export markets.

Staal *et al.* (1997) argued that: (i) the growth in smallholder dairying was limited by high transaction costs for both production and marketing; (ii) transaction costs across producers

in what appeared to be a single market (e.g. fluid milk in Addis Ababa) explained why producers accepted widely different prices for a homogeneous product in the same markets; and (iii) contracts between producer and buyer cooperatives played a central role in reducing transaction costs.

Subsequent work explained the impact of transaction costs and the choice of production techniques on decisions to sell fluid milk to Ethiopian cooperatives (Holloway *et al.*, 2000a,b). Creating local markets to minimize the time required to sell milk increases the number of producers and amounts sold. Institutional investments, such as the formation of milk groups, provided a less costly mechanism for increasing market participation. Although milk groups are a simple institutional innovation, they appear to be a necessary first step in developing more sophisticated cooperatives.

Farmer cooperatives have been identified as catalysts to market participation. Analysis of data from the Ethiopian highlands where farmers organized themselves in a dairy cooperative showed that male household heads and extension visitations affected cross-bred cow adoption positively, while credit use and the number of local-breed cows currently milked affected adoption negatively (Holloway *et al.*, 2000b). Male heads of household, extension visits and the number of local-breed cows affected output positively, while credit use affected output negatively, as did distance to market. This study also suggested that extension is a potentially important catalyst for market expansion. Consequently, several important questions arise concerning the actual impacts of extension on participation, the number of extension-requesting households willing to pay for services if it was privatized, the corresponding demand schedule for extension services and the requisite conditions for the existence of a private market for the service.

One study addressed these transactional issues (Holloway and Ehui, 2001). For each unit increase in extension, the transaction cost was lowered by ETB0.62. Hence, extension was shown as a promising market-entry catalyst. Furthermore, the willingness to pay for one additional extension visit ranged from ETB0.6 to ETB6.7. The study estimated the marginal cost of each extension visit at ETB2.1, based on the annual extension budget of the local administrative

units and the estimated number of extension visits made during the year. The willingness to pay estimates showed that some 39% of participating households would purchase extension services.

Reinforcing the findings of Holloway *et al.* (2000a), other studies found that households with a higher education level, a larger number of cows and a greater non-farm income were positively associated with value of sales of dairy products. This suggests that income from the sale of milk, butter and cheese can be increased through education and training, especially targeting women (Holloway *et al.*, 2000b; Ehui *et al.*, 2003; Lapar and Ehui 2004).

Dairy reform in Kenya

The most productive policy research at ILRI was the long-term engagement in Kenyan dairying. Kenya was an attractive site for policy research in that its dairy sector was highly productive, it had high unrealized potential and major policy barriers to achieving that potential, and it had a base of technical and economic research to inform policy recommendations.

In a study of adoption of improved dairy cattle and related technologies, a methodological innovation was generated by applying GIS-derived variables in econometric analysis. This study by Staal *et al.* (2002) demonstrated the usefulness of integrating GIS-measures into analysis of technology uptake for better differentiating and understanding locational effects. A set of GIS-derived measures of market access and agroclimate were included in a standard household model of technology uptake, applied to smallholder dairy farms in Kenya, using a sample of 3330 geo-referenced farm households. The three technologies examined were keeping dairy cattle, planting specialized fodder and using concentrated dairy feed. Logit estimations were conducted that significantly differentiated the effects of individual household characteristics from those related to location. The predicted values of the locational variables were then used to make spatial predictions of technology potential. Comparisons were made with estimations based only on survey data, which demonstrated that, while overall explanatory power may not improve with GIS-derived variables, the latter yielded more practical interpretations,

which was further demonstrated by predictions of technology uptake changing with a shift in infrastructure policy. Although requiring large geo-referenced data sets and high-resolution GIS layers, the methodology demonstrated the potential to better unravel the multiple effects of location on farmers' decisions on technology and land use.

The above study was done within the framework of ILRI's Smallholder Dairy Project, a joint initiative with the Kenya Agricultural Research Institute (KARI) and the Kenya Ministry of Livestock Development, which began in 1997 to address farming practices, marketing and extension. The policy aim of the Smallholder Dairy Project was to achieve a better policy environment for raw-milk trading to raise producer prices and to improve supply from smallholders. A policy-change strategy was developed, which included generating evidence about raw-milk markets and working with civil-society organizations who were voices in policy advocacy and had connections to public agencies.

Until 1992, the Kenyan Dairy Board (KDB) officially controlled dairy pricing and marketing. During the early 1990s, as input prices paid by producers increased at a higher rate than the KDB-controlled prices of milk, producers began to divert sales to the informal market. Consequently, supply to Kenya Co-operative Creameries (KCC) fell substantially, causing shortages of processed milk in the formal market. To stimulate supply, the Kenyan government announced the liberalization of dairy prices and the lifting of the KCC monopoly on processed milk sales to urban areas. The market response was an increase in raw-milk supply to the KCC and, consequently, in supply of processed milk to retailers. The benefits of policy reform were limited, however, because few dairy traders entered the market owing to the dominance of KCC, which obstructed price liberalization. The raw-milk sales policy, however, did not change.

The path from policy research to policy change in Kenya dairying has been well chronicled (Leksmono *et al.*, 2006; Kaitibie *et al.*, 2010b). A first step was to investigate dairy market liberalization with a policy analysis matrix (Staal and Shapiro, 1994). Following output price liberalization, Kenya continued reducing government support and intervention within the livestock sector, specifically for veterinary

and artificial insemination services. Policy analysis by ILRI measured the changes between 1990 and 1995 in milk marketing and service provision by the dairy farmer cooperative societies, which played a central role in meeting the needs of dairy production (Owango *et al.*, 1998). Most notable were the changes in the unregulated raw-milk market, which helped increase real market prices paid to producers by up to 50%. Large increases were also observed in the provision of veterinary and artificial insemination services by the dairy cooperatives, whose producer base and credit facilities allowed them to compete with independent private traders.

A contentious policy issue following market liberalization was regulation of the informal milk market, a complex network of farmers and groups selling raw milk directly or through venders to consumers or shops. The price liberalization of 1992 allowed other private milk processors to enter the market, causing the near collapse of KCC. The liberalization was also interpreted as allowing the sale of raw milk in urban areas, which was technically illegal, and the raw-milk market quickly expanded through small vendors (Staal and Shapiro, 1994). By 2000, this market was estimated to control 80–90% of the total liquid milk market, even though it was fiercely opposed by the KDB, and officials retained the authority to confiscate illegal vendors' milk and equipment. Research by the Smallholder Dairy Project found that this authority imposed constraints on the markets for milk from smallholders as the price for milk paid by the vendor decreased with the quality of milk bought, even though a larger volume of sales would be expected to impose lower unit transaction costs. This result was thought to be due to the fact that vendors were restricted to handling relatively small quantities (e.g. 30 litres/day) due to risks of confiscation (Staal *et al.*, 2002).

Larger producers opposed the reform. The Kenya Dairy Processors Association launched a high-profile 'Safe Milk' campaign against raw-milk marketing. The Smallholder Dairy Project and its civil-society organization partners responded by publishing some of their results in the local news media. In addition, the civil-society organization partners held a press conference to contest this campaign's anti-raw-milk messages using evidence from the Smallholder Dairy Project showing that unsubstantiated health concerns were likely to lower milk consumption in Kenya, would reduce health benefits to the country's low-income consumers, and would destroy the livelihoods of hundreds of thousands of small producers and vendors.

The KDB and milk processors repeatedly challenged the public statements made by the civil-society organizations but were unable to produce evidence to back up their anti-raw-milk claims, whereas the robust evidence from the Smallholder Dairy Project strongly supported the arguments of the civil-society organizations. Some change in perceptions by the KDB occurred when it visited a group of project-trained milk vendors and saw that the vendors demonstrated good milk-safety practices.

A Dairy Policy Forum was held in May 2004 at the close of the Smallholder Dairy Project, where farmer advocates and senior officials were prominent. At the forum, the minister of livestock committed the government to passing the stalled Kenya Dairy Bill and to take into account the mass of evidence and stakeholder opinion presented. In time, the KDB came to view the training and certification of raw-milk traders as an intermediate step towards formalizing the country's small-scale milk trade rather than as a means to promote raw-milk trading.

An external evaluation used a 'Research and Policy in Development Outcome Assessment' approach to document how the Smallholder Dairy Project research and policy engagement strategy led to the policy change (Leksmono *et al.*, 2006). The study concluded that the Smallholder Dairy Project was the principal driver of the policy changes, notably because of the following:

- Private processors changed their marketing strategy to focus on the value and safety of processed, packaged milk without overtly attacking small-scale milk vendors. Some processors also encouraged small-scale milk vendors to trade in processed products.
- Virtually all subsequent projects in Kenya's dairy subsector have used the research results of the Smallholder Dairy Project, and many have also linked with the project's implementing institutions in other dairy-related activities, both in service-delivery and policy-related areas (Leksmono *et al.*, 2006).

- One point of opposition to reform was health risks from drinking raw milk. Product quality analysis showed that if milk is boiled, a near-universal practice in Kenya, it is almost entirely safe. To further improve hygiene in the informal milk sector, the Smallholder Dairy Project developed a training programme for informal vendors to teach them improved practices for handling milk.

Eventually, the work of the Smallholder Dairy Project achieved an agreement to train and certify small traders of raw milks, with the KDB taking up the training and licensing of traders using guidelines and training materials developed by the Smallholder Dairy Project. There were further revisions of the draft Dairy Industry Act, stalled since 1997, to recognize and formalize the role of small-scale raw-milk traders and to increase the number of groups representing poor farmers.

The change in Kenyan dairy policy to allow greater market participation by small producers had the principal effect of lowering transaction costs, thereby raising prices to producers and lowering prices to consumers. An economic surplus model was used to compute economic benefits of these price shifts, with movements in the milk-supply curve being attributed to the policy changes affecting the informal market. Kaitibie *et al.* (2010b)[2] reported a best estimate of the net benefits of the reform to have an NPV of US$230 million over 1997–2039.

A study following the Kenya dairy reform clarified the reasons for its political support. Informal milk markets created more employment per unit of product than did formal markets. A study by Omore (2004) of employment in milk markets in Kenya, Bangladesh and Ghana found that informal milk markets employed up to five times as many people per 100 litres of milk handled.

The Smallholder Dairy Project in Kenya not only benefited the dairy sector and the wider economy in Kenya, its experiences created positive externalities (international public goods) in the East Africa region and beyond. The partnership and communication strategy in this reform led to the Smallholder Dairy Project receiving the 2004 CGIAR Communications Award. The project's extension materials and market agent training materials and methods were taken up by other projects led by the national agricultural research system, ministry and non-governmental organizations in Kenya and elsewhere in East Africa. The project created greater regional awareness among policy makers in Ethiopia, Tanzania and Uganda of pro-poor policy implications of small-scale milk markets. The Association for Strengthening Agricultural Research in Eastern and Central Africa (ASARECA) and its policy programme, the Eastern and Central Africa Programme for Agricultural Policy Analysis (ECAPAPA), built on the Smallholder Dairy Project and ILRI policy recommendations to seek harmonized pro-poor dairy policies in the region. Through ECAPAPA, dairy policy makers and regulators in Rwanda, Tanzania and Uganda adopted new institutional approaches and appropriate technologies to harmonize standards and improve informal milk markets across the region.

ILRI's results were used to: (i) promulgate common dairy industry standards in East Africa; (ii) advance a regional agreement to promote the movement of certified milk traders across borders; (iii) publish training materials for milk standards, and provide certification of milk traders and accreditation of their trainers; and (iv) train and provide certification of informal milk traders by involving private trainers.

In 2016, ILRI began working with the state government of Assam, India, where the informal market supplied the great majority of local milk. Working closely with Assam's Dairy Development Department, the training and certification approach of the Smallholder Dairy Project was adapted for Assam and was piloted locally, again with a local non-governmental organization as the main training service provider. Studies showed that trained vendors sold safer milk and demonstrated better knowledge of hygiene. This is thought to be the first time in India that public funds have been devoted to improving the informal (or unorganized) milk market (Lindahl *et al.*, 2017).

Comparisons of dairying in South Asia and East Africa

ILRI and FAO's Pro-Poor Livestock Policy Initiative studied dairy development in East Africa and

South Asia to assess the roles of policies and institutions and their impact on the poor (Staal *et al.*, 2008a,b,c). The dairy sector in South Asia followed a different path to that of East Africa. Consumption of dairy products is higher on average in South Asia than in East Africa owing to demand factors. Differences in growth in South Asia are more related to the possibility of expanding supply to match the growing demand for dairy products. Multivariate econometric models incorporating technology and policy factors showed that India and Pakistan were able to link the agricultural transformation originating in the Green Revolution to successfully expand milk production; this is reflected in the contribution of input markets and technology to growth in milk production. In the case of countries with slow growth in milk production, such as Bangladesh and Nepal, development of cereal production and feed markets and a growing demand did not induce a technical change in dairying, as was the case in India and Pakistan. As in East Africa, development of formal milk markets in South Asia is not associated with increased growth rates.

Detailed analysis of the drivers and impacts of dairy sector growth on employment, income and nutrition was done for Ethiopia and Kenya in East Africa and for India and Pakistan in South Asia. Although informal and commercial dairying coexist in both regions, informal production still dominates and is generally competitive. For example, the study conducted an analysis by district across India, which sought to find evidence that the presence and success of cooperatives was associated with greater dairy development. However, there was little evidence towards this, which suggests that India's well-known Operation Flood, which used revenues from donated imported milk powder to fund dairy cooperative development, did not play any significant role in driving dairy development in India, where to this day the dairy cooperative sector retains a relatively small market share. The evidence suggests that relatively efficient informal milk markets played the key role in linking producers to growing consumer demand. In fact, the dairy industry grew more quickly in Pakistan, where cooperatives played almost no role, than in India. Policies that build on traditional production systems, with new focus on employment, food safety and quality, are expected to be pro-poor.

The study found that demand factors explain much of dairy development in East Africa, as shown by the rapid growth of milk production in Kenya, Sudan and Uganda. Development of formal milk markets, input markets, technology and policy do not explain the differences between fast-growing countries and the rest, which may imply that much of the increased production in response to demand came from herd growth rather than from productivity growth.

This finding of lack of significance of input market and technology on output growth was supported by an earlier study by Freeman *et al.* (1998) that analysed the impact of credit on milk output by smallholder dairy producers in Ethiopia and Kenya. It found no consistent relationship between farmers' credit constraints and their borrowing. However, farms that were credit constrained increased output more when given access to credit than farms that were not credit constrained, indicating that the credit constraint did limit the supply response. This finding indicated that demand for credit become important to acquire inputs to increase output for market.

These results suggest that adjusting supply to type and quality of products demanded, expanding demand by reducing consumer prices and reducing transaction costs will contribute to expand the dairy sector in East Africa.

Land rights

Land rights are legally or socially enforceable claims. They can be permanent via ownership or temporary via rental or other fixed-term contracts. The analysis of land rights in animal production is important for two reasons. First, land is the primary factor in both grazing and mixed systems. Second, nearly all modern efforts to expand agricultural production necessarily involve more intensive land use, lowering the amount of land used per unit of output, whether that output is forage, an arable crop such as rice or a permanent crop such as coffee.

ILRI research on land rights has had four themes: (i) early work on pastoral systems, focusing on group ranches and enclosures; (ii) studies on land tenure, resource allocation and productivity beginning in the early 1990s; (iii) collective action for common resource management; and (iv) land rights and fodder trees.

Pastoral systems

Land tenure differs markedly between pastoral and mixed systems. Pastoral/agro-pastoral systems typically use land held in common. Mixed systems depend on private or social land tenure that recognizes certain rights that can be appropriated by individuals or communities.

A common historical view of land rights in African pastoralism was that such rights did not exist or were not enforced. It was argued that this market failure made land use inefficient by weakening incentives to improve it. A common political and development perspective on pastoral land tenure was that it could be ignored as a subject of scientific evaluation; for example, the first major ILCA book was entitled *Evaluation and Mapping of Tropical African Rangelands* but said nothing of land tenure or of changes in traditional forms of land management (ILCA, 1975) as possible remedies on overgrazing. Pratt and Gwynne (1977) mentioned pastoral tenure in East Africa as a barrier to be dismantled on the path to stopping overgrazing, to sedentarizing pastoralists and ultimately to a generalized extension of ranching. The historical work of Gallais, who had meticulously characterized the land administration of the Peulh herders of central Mali in the 1950s (Gallais, 1967) and later proposed a modern legal codification of that system (Gallais and Boudet, 1980), had little effect[3].

Land rights of common property rangelands was, on the other hand, of immediate interest to ILCA researchers. Sandford's magisterial book, *Management of Pastoral Development in the Third World*, which is still the most often cited work in the history of ILCA/ILRAD/ILRI, presented a scheme for allocating land 'among uses and among users' (Sandford, 1983, pp. 135–136).

Early research published by ILCA on Somalia and Sudan found spontaneous range enclosures – the assertion of private property rights in grazing and the defence of those rights by fencing (Behnke, 1986). Such spontaneous enclosures were influenced by density-dependent factors – commercial animal husbandry, commercial fodder markets and 'heavy stocking of pastures' – and by density-independent factors – drought, water development and official land-tenure policies. Behnke found that spontaneous enclosures responded to increasing profits from farming, falling range productivity outside the enclosures and falling costs of enclosures.

The Maasailand study (Solomon Bekure *et al.*, 1991) conducted in Kenya was exceptional in that it made detailed policy recommendations about the land rights of pastoralists.

The Borana study (summarized by Coppock, 1994) in southern Ethiopia found that the Borana system was moving from traditional pastoralism to a semi-sedentary system with more reliance on crops and private grazing. This study highlighted the need for a strengthening of traditional authority in resource management. It further concluded that the agroecological diversity of the Borana rangelands called for selective policies that supported crop–livestock integration and extensive livestock production as necessary rather than a 'one policy fits all' approach to the entire area.

In the early 1990s, ILRI sponsored two literature reviews on land tenure and property rights. The reviews of 18 studies on land tenure in Africa (Swallow, 1994; Swallow and Bromley, 1995) asked the following questions:

- How do property institutions affect the use and management of resources?
- How do property institutions create or deny opportunities for the adoption of new technologies and expansion of agricultural production?
- How does the structure of government affect property institutions?
- How do changes in economic and technical conditions affect resource use and property institutions?

The review by Swallow and Bromley (1994) indicated that groups of livestock owners could manage common property rangelands without formal organizations or institutions if the group was relatively small, if entry into the group was costly and if the members of the group did not discount the future heavily. Thus, a local rangeland management regime could only be effective if its institutions were governed locally. It was argued that it was more effective for governments to enforce boundaries among groups than to seek to establish the internal group conditions for efficient resource management (McCarthy *et al.*, 1999).

A collaborative project titled 'Property rights, risk, and livestock development' implemented by ILRI, IFPRI and the Göttingen Research Institute

for Rural Development during 1996–1999 sought to support reforms of property institutions and land policies in the semi-arid areas of sub-Saharan Africa. The specific objectives were: (i) a better understanding of how environmental risk affects the use and management of resources under alternative property rights regimes; (ii) identifying circumstances under which land use and property rights change; and (iii) identifying how policy and other external interventions can assist communities to achieve desirable pathways and mitigate negative impacts of undesirable pathways (ILRI, 2000).

Part of the ILRI/IPFRI/Göttingen study focused on the Borana rangelands in semi-arid southern Ethiopia (Kamara, 2001), where ILCA's historic 1994 study of the pastoral system in the Borana area was characterized by extensive livestock production and was a valuable source of young stock for power and for export (Coppock, 1994; see Chapter 15, this volume). Development in Borana was limited by aridity, causing low plant biomass productivity, and by periodic droughts, causing herd deaths.

The Kamara (2001) study focused on the effects of environmental risk, market variables and population pressure on land use and property rights. The results largely conformed to the principal hypotheses about institutional change. Community cooperation in resource management was determined by demography, wealth, off-farm income and social capital. Rainfall variability affected stock densities only in areas of high rainfall variability. Market variables did not determine stock densities or community level cooperation but did affect land allocation to crops. Changes in property rights were explained by a ban on wildfires, the creation of peasant associations, sedentarization programmes and development interventions (Kamara, 2001). A related study in the same area had examined the evolution of land rights (Kamara, 2000). Kamara found substantial privatization of land, related to the change in national policies after the fall of the Derg in 1991 and, chiefly, as function of rapid growth in population density and cultivation.

Land tenure, resource allocation and productivity

An armed revolution overthrew the Ethiopian monarchy in 1974 and a military regime (the Derg) took power. Under the monarchy, most of the land had been held by the aristocracy and the church. The Derg nationalized all land and redistributed it to farmers on a per-capita basis using local norms, giving them usufruct with no right to sell, rent or transfer. There was provision for periodic redistribution when new families were formed or when some families abandoned farming. The period of the Derg was one of suspended animation as far as ILCA research on land issues was concerned.

Property institutions changed slowly after the overthrow of the Derg in 1991. The new government began to tolerate decollectivization, labour mobility and informal renting within extended families. Changes in land use and the resurfacing of rural factor markets following decollectivization provided evidence that emerging factor markets brought better land use. There were observed changes in adoption of soil conservation, tree planting, crop rotation and fallow practices, and increased use of organic and inorganic fertilizers associated with the new land policy. Selling, hiring, renting, and trade of land, labour and draught animals also grew (Omiti *et al.*, 1999, 2000).

The study of land rights in Ethiopia after the collapse of the Derg was an important part of ILRI's policy research in the 1990s. One study identified factors influencing the evolution of land-tenure institutions to determine the effect of land tenure on investment, productivity and efficiency in crop–livestock systems and to assess the impact of tenure on household access to feed. For instance, the issue of land access by private commercial investors and land tenure and farming practices in the highlands of Ethiopia was presented in one paper (Gavian and Amare Teklu, 1996) and a second paper presented evidence on the nature of access to land by farmers in one region of the Ethiopian highlands (Gavian and Ehui, 1999).

Two studies dealt with the efficiency of land tenure contracts (Gavian and Ehui, 1999; Ahmed *et al.*, 2002). The first indicated that, although the informally contracted lands were farmed 10–16% less efficiently, the hypothesis that land tenure is a constraint to agricultural productivity was rejected. The second found higher technical efficiency between owner-cultivated or rented plots and sharecropped, or borrowed plots. This difference was attributed to

restrictions imposed on the tenant in the share-cropping and borrowing contracts, which sometimes involved labour and animal power supply by the tenant. A mild policy recommendation was to 'facilitate more efficient transactions'

Benin and Pender (2001) found that crop yields in the Amhara region were significantly higher, particularly in villages where the last major land redistribution took place in 1997–1998. The authors also found that plots on which households felt more secure (i.e. expecting to operate the plot for the next 5 years) were associated with higher crop yield, suggesting that security of tenure may be associated with other yield-enhancing management practices. Together, these results suggest that improving tenure security can bring about substantial increments in crop productivity.

Examining the evolution since 1991 in land rental markets of the highlands of northern Ethiopia, Benin *et al.* (2005) showed that changes in the production environment and natural resource endowments, changes in human capital, access to credit, commercialization of cereal production and tenure security are the major forces contributing to the changes in land rental arrangements. Reduction in production risk, through increased availability of moisture or reduced degradation of soil, has reduced the need for risk-pooling arrangements associated with sharecropping in favour of fixed-rent leases. Furthermore, increasing commercialization of cereals caused an increase in land rentals, while an increase in credit supply caused an increase in fixed-rent leases. The same work showed that alternative land rentals had a positive impact on cereal yields, suggesting that tenure innovations after the eviction of the Derg had evolved to reduce production inefficiencies. The most widely cited paper on land tenure and investment in Ethiopia (Deininger and Jin, 2006) found that tenure security could enhance agricultural productivity and that public policy to improve tenure security would therefore be justified.

Related evidence from semi-arid Niger gave evidence on 'traditional land tenure [as] an impediment to allocative efficiency' on millet farms (Gavian and Fafchamps, 1996). Gavian and Fafchamps found that land security was important for input allocation decisions, such as the use of labour and manure, but that the degree of tenure insecurity in western Niger would not justify a major change in the tenure system.

Collective action for common resource management

A subset of the land tenure–productivity problem is that of collective action in common resource management. A long-term area of study by ILCA and later by ILRI was traditional agriculture in highland central Ethiopia which was long constrained by lack of modern inputs, a variable environment and a severe risk of soil erosion. Collective watershed management had been proposed as a model to manage modern inputs while controlling soil erosion. The policy question was whether collective watershed management, as a form of tenure, could achieve these policy objectives.

A public-goods problem of watershed development in Ginchi, Oromia, was presented in a game-theoretical model to study the logic of voluntary contributions to an indivisible public good: namely, a central drainage channel to solve a waterlogging problem that constrained early planting of a high yielding wheat variety (Gaspart *et al.*, 1998). The most striking result of this study was that there is indeed a clear positive relationship between the magnitude of personal stakes and the effort spent on building the drainage channel. In other words, in the equilibrium selection process, a social norm of the kind 'from each according to his expected gains' seems to have been at work to favour coordination of individual efforts. Out of 33 members of the community who contributed to drain construction, five had additional leadership roles. Even though, taken singly, the leadership factor was the most statistically significant independent variable, taken together it was self-interested considerations that played the major role.

A bioeconomic model was developed to evaluate watershed management in central Ethiopia. The baseline in the model showed that, without technological or policy intervention, income and nutrition could not be sustainably improved in the watershed without serious soil losses (Okumu *et al.*, 2004). Although cash incomes could rise by more than 40% over a 12-year period, average soil losses could be as high as 31 t/ha. With the adoption of a package of new land-management technologies, however,

the model projected, on average a 10% increase in cash incomes and a 28% decline in aggregate erosion. The policy implications were: (i) the need for more secure tenure to promote new technology; (ii) a shift from subsistence livestock management to commercial; and (iii) a site-specific approach to land management within the watershed (Okumu *et al.*, 2004).

A study in Tigray region, in northern Ethiopia, investigated the determinants of collective action and its effectiveness in managing community woodlots (Berhanu Gebremedhin *et al.*, 2003, 2004). The studies suggest that collective actions may be more beneficial and more effective when managed at the village level rather than at a county (*wereda*) level. Collective actions were more productive when external interventions were demand driven rather than imposed. Population density and market access affected the probability of successful interventions. Collective actions are more successful in intermediate-population-density communities with poorer market access. At higher population densities and with better market access, private approaches were more effective.

Berhanu Gebremedhin and Swinton (2003) examined the relationships among public and private conservation investments. Public conservation campaigns on private land reduced adoption of stone terraces and soil bunds. Whereas capacity factors largely influenced the adoption decision, expected returns carried more influence for the intensity of stone terrace adoption (measured as metres of terrace per hectare). More stone terracing was built where fertile but erosion-prone silty soils in higher rainfall areas offered valuable yield benefits. The intensity of terracing was also greater in remote villages where limited off-farm employment opportunities reduced construction costs. These results highlighted the importance of appropriate public interventions. Direct public involvement in constructing soil conservation structures on private lands appeared to undermine incentives for private conservation. When done on public lands, however, public conservation activities can encourage private soil conservation. Secure land tenure rights clearly reinforced private incentives to make long-term investments in soil conservation.

A related issue was how tenure security influenced investment in land. A study in Tigray region revealed different causal factors for soil conservation adoption versus intensity of use (Berhanu Gebremedhin and Swinton, 2001). Farmers' reasons for adopting soil conservation measures varied sharply between stone terraces and soil bunds. Long-term investments in stone terraces were associated with more secure land tenure, more labour availability, proximity to the household and learning opportunities via local food-for-work projects. By contrast, short-term investments in soil bunds were strongly linked to insecure land tenure and the absence of local food-for-work projects.

In Ethiopia, particularly in the Amhara region, one source of tenure insecurity was land redistribution, which had been ongoing since 1974 to equalize land holdings and quality across households. However, its short- and long-term effects may have mixed impacts on farmer land management and productivity. Expectations of future land redistribution may undermine farmers' incentives to invest in land improvements and soil fertility, as the farmers' ability to reap the benefits of such investments is undermined. Redistribution might, however, improve access to land of households that have relative surpluses of other important factors of production, such as labour, oxen or cash to purchase inputs, particularly in the context of prohibited land sales and restricted lease markets that exist in Ethiopia. Thus, land redistribution may increase the intensity of land management and use of purchased inputs, which may in turn increase productivity.

A research project in the Amhara region of Ethiopia looked at land degradation and identified options (Pender *et al.*, 2001). That project classified geographical units into various development domains defined by combining production potential or ecology, population pressure (high versus low) and market access (high versus low). It has been found that there are significant differences in the extent of degradation and its causes across the various development domains. Therefore, there are no one-size-fits-all solutions to the problems across the domains. Technology and institutional options suitable for different domains to increase productivity and reduce degradation need to be introduced.

A review article by Williams (1998) covered common property issues in semi-arid West Africa, specifically the problems created by

population growth, land pressure on water and grazing, the lack of participation in governance by resource users, and the role of the state in resolving non-market conflicts.

Land tenure and fodder trees

The International Institute for Tropical Agriculture (IITA) had for many years studied alley farming, a system in which leguminous trees were planted between rows of food crops, such as maize or cassava. Nitrogen fixed by the trees could be returned to the soil as mulch for uptake by crops, or the leaves could be cut and fed to livestock. Long-term collaboration among IITA, ILCA/ILRI and national programmes in West Africa investigated agronomic and economic aspects of leguminous tree farming.

Given the long-term character of tree investments, adequate land tenure was thought to be needed to provide incentives to plant and maintain trees. One study included results from a sample of 248 farms in southern Nigeria between 1984 and 1991. While that study did not collect tenure data, it did show that high turnover in plot ownership had no effect on tree farming (Lawry *et al.*, 1994, p. 3).

A wider study in humid West and Central Africa tested the land tenure argument. This work characterized land and tree tenure practices and their implications for tree management in Cameroon, Nigeria and Togo. The review found that 66%, 50% and 56% of the land, respectively, in Cameroon, Nigeria, and Togo was under tenure that provided long-term security and was, therefore, favourable for adoption of alley farming (Lawry and Stienbarger, 1991, p. 62). Tenure had a significant role in the adoption, continuation and discontinuation of alley farming. Because a significant proportion of the land in the three countries was under a favourable tenure system, it was concluded that land tenure was not a major constraint to the adoption of alley farming, if other favourable factors were present (Lawry and Stienbarger, 1991; Lawry *et al.*, 1994). In a study of southwest Cameroon, Adesina *et al.* (2000) found no statistically significant effect of land tenure security on the probability of adopting alley farming. An aggressive policy of tenure reform would therefore not be generally necessary to promote alley farming in the West and Central African land markets studied, though Adesina *et al.* (2000) showed that relieving the specific land tenure constraints faced by women farmers would be necessary to raise their share of benefits from alley farming or from other fallow substitutes.

Livestock and poverty

Poverty was not a theme of ILCA/ILRAD/ILRI research before the mid-1990s and the words 'poor' or 'poverty' as keywords in published work rarely appear before 2000. There was some analysis of wealth disparities in Maasailand in the 1980s by King *et al.* (1984) and Grandin (1988) but no systematic or even sporadic effort to relate ILRI's work to poverty in Africa, or anywhere else, before 2000.

ILRI adopted the theme of livestock as a 'pathway out of poverty' for its 2002–2010 strategy (ILRI, 2002). Two landmark studies – Perry *et al.* (2002) and Thornton *et al.* (2002) – examined welfare among livestock keepers and paths by which they might escape poverty. Subsequent work identified three paths along which research might assist by: (i) securing the assets of the poor; (ii) improving the productivity of assets; and (iii) encouraging market participation by the poor.

Thornton *et al.* (2002) produced the first set of maps to locate poor livestock keepers by country, region and production system. They estimated that out of nearly 1 billion poor people living in the developing world, about 550 million depended on livestock for their livelihoods, most of them located in sub-Saharan Africa and South Asia. Some 366 million and 103 million livestock-dependent poor people live, respectively, in rain-fed and irrigated mixed systems, another 30 million in rangelands, and the remaining 50 million or so in highlands and other areas.

Subsequent microeconomic studies assessed poverty dynamics and its relation to livestock. Kristjanson *et al.* (2004) followed over 1700 households in 20 communities in western Kenya. The communities differed in population density, farm size, agricultural potential, poverty rate and human immunodeficiency virus

prevalence. As they emerged from poverty, households typically first acquired food, then clothes, shelter, primary education and small animals, including chickens, sheep and goats. The results showed movement by households into and out of poverty over the 25-year period. Of the households that had escaped poverty, 73% mentioned diversifying income into cash crops and/or selling food crops when a household member obtained an off-farm job, 57% mentioned cash crop production and 42% mentioned that they diversified their on-farm incomes through livestock, ranging from poultry to dairy. On-farm diversification of income sources away from a sole reliance on crops through investment in chickens, sheep, goats and/or cattle helped many of the households in the study to escape poverty. Poor health, health-related expenses and funerals were the principal reasons cited by households for having fallen into poverty. The slaughter of livestock to meet emergency needs was mentioned by 63% of households as a reason for falling into poverty.

Kristjanson *et al.* (2007) replicated the community approach in some 3800 households in two regions of highland Peru, based on 10-year and 25-year recall. The reasons for movements into or out of poverty were identified at community and household levels, as was the role of livestock in the different paths. Diversification of income through livestock and intensification of livestock activities through improved breeds helped many households escape poverty, but these results varied across households.

Ouma *et al.* (2003), in a study in Kenya, used data from a survey of cattle-keeping households in intensive, semi-intensive and extensive systems. This work assessed the contribution of non-market benefits of cattle to the competitiveness and survival of smallholder enterprises. Some 50–70% of the benefits from smallholder cattle are non-cash and smallholder cattle production systems are relatively competitive and efficient in the utilization of household production factors when non-market benefits are taken into consideration. This is especially so for extensive systems, which are non-market-oriented. The study concluded by emphasizing the importance of the non-market roles of cattle in evaluations of smallholder cattle production systems, as this will have a bearing on any policy-related interventions whose target are households that

are wholly or partially dependent on the livestock economy.

Little *et al.* (2008) examined poverty among Kenya pastoralists. They argued that external observers tended to 'homogenize' the concept of 'pastoralist' by failing to acknowledge the diverse livelihoods, wealth and income in pastoral areas. The study concludes that what is not needed is another development label (stereotype) that equates pastoralism with poverty, thereby empowering outside interests to transform rather than strengthen pastoral livelihoods.

Radeny *et al.* (2007) showed that education among Tanzanian pastoralists influenced livelihood choices and improved the viability of pastoralism by diversifying it with crop production.

Food security and nutrition

A fundamental policy question under the heading of 'livestock and poverty' is how the benefits of technical change accrue to the rich and the poor and between women and men. The question is especially relevant when technical change involves a cash good such as milk or meat, commodities not consumed in large quantities by most poor households, raising the possibility that producing cash goods can worsen the nutrition of the poor (Pinstrup-Andersen, 2000). Studies in Ethiopia on which ILRI collaborated tended to reject that adverse possibility.

A study was started in 1997 in collaboration with national institutions near Holetta in the highlands of Ethiopia. The work involved an on-farm trial of cross-bred dairy cows and animal draught power to assess the nutritional impacts of market-oriented dairying. A first analysis evaluated the nutritional and health status of women and children in households with and without cross-bred cows (Shapiro *et al.*, 2000; Ahmed *et al.*, 2000). Malnutrition, as measured in pre-school children by stunting, wasting and underweight, and as measured by body mass index in adult women, was lower in households with cross-bred cows than in those with local cows. Calorie, protein and nutrient intake were significantly higher in the cross-bred cow group.

The analysis further assessed the effects of milk and income on decision making (Haider

et al., 2000). Women in households with cross-bred cows contributed over 80% of household expenditure on food. A second extension of the study revealed that steady increases in income from dairy in Ethiopia translated directly into increases in expenditure on purchased food, non-food and farm inputs (Ahmed *et al.*, 2000, 2003).

Tangka *et al.* (2002) analysed the food security and supply effects of smallholder dairying in peri-urban Ethiopia. Econometric analysis of panel data was used to evaluate the effects of dairying on food consumption, calorie intake and marketed surplus in a treatment group of households in contrast to a control group without the dairy technology. There were substantive and statistically significant improvements in food security and marketed surplus with improved cattle. These impacts were reflected mainly through the effects of income and wealth, measured by animal value and land area. Household income had a positive and significant effect on food consumption. Regression estimates show that elasticity of expenditure on food with respect to income, animal value and cropland area at the mean levels was respectively 0.29, 0.18 and 0.26. The largest share (63%) of the difference in calorie intake between the cross-bred and local-breed cattle households was attributed to differences in the explanatory variables, while the estimated parameter differences between the two groups accounted for 37% of the difference. The value of animal assets had a positive and statistically significant impact on calorie intake in both the combined and cross-bred cattle regressions. The increase in animal values for the cross-bred cattle households was estimated to increase their caloric intake by 12.7% relative to the local-breed cattle households. The value of food marketed by the cross-bred cattle group was 82% higher than that in the local-breed cattle group. A total of 76% of the increase in the value of marketed surplus food for the cross-bred cattle over the local-breed cattle groups was accounted for by the difference in household characteristics, while only 24% of the increase could be attributed to differences in the estimated parameters. Households in market-oriented dairying increased their income and animal values significantly compared with households in traditional dairying.

Nutritional status of children under 5 years of age is often a good indicator of community health and nutrition. Anthropometrical indicators – stunting (height for age), underweight (weight for age) and wasting (weight for height) – are generally used as means of assessing prevalence of malnutrition among pre-school children or children under 5 years. A study in highland Ethiopia tested the hypothesis that access to animal-source foods affected nutrition in pre-school children (Okike *et al.*, 2005). A child's nutritional and health status are jointly determined by dietary intake, maternal wellbeing and the state of the physical environment as it influenced agricultural production and health status. Presence of dairy cows in the household significantly contributed to the health of children. The findings implied the need for multi- or transdisciplinary approaches to research and development incorporating heath, nutrition, sanitation, and farming practices for improving the health and nutrition of rural households.

A study in Selale District, in the Ethiopian highlands, examined the relationship between smallholder dairying, time allocation by gender and income receipts by gender (Lenjiso *et al.*, 2016). In market participant households, income from milk was higher because of higher output and marketed surplus, but control of income shifted from women to men compared with non-participant households. Policy lessons from this work were inconclusive.

IBLI in the arid rangelands of Kenya and Ethiopia

An IBLI project developed a market tool for risk management by pastoralists in arid and semi-arid Kenya. Following the inception of household surveys in Marsabit, Kenya, in 2009 and the launch of the IBLI's insurance product in January 2010 (Jensen *et al.*, 2015), the IBLI model has combined biological, economic and institutional research involving scientists, herders, private firms and regulators to: (i) protect pastoralists from livestock losses by assessing forage availability during the rainy season(s), as an index of production risk among a sample of 924 herding households in Marsabit county of arid northern Kenya; (ii) measure household demography, income and wealth in that sample over a survey period of 5 years; (iii) define and sell

insurance policies against covariate risks caused by drought; (iv) measure an index of vegetation to define a trigger for insurance payments, using remote sensing data; (v) analyse the consumption and investment behaviour of pastoralists of varying herd sizes to estimate the impact of insurance on sales, income, consumption and herd viability; (vi) identify effective institutional and extension models for the uptake of the product; and (vii) work with herders and private brokers to monitor demand for index insurance, to continue adaptive testing of the insurance instruments and to analyse the development impacts of IBLI (a recent summary of IBLI is given by Fava and Jensen, 2020).

Impact

There was widespread adoption of index insurance in Marsabit, although many herders did not renew their policies after seasons of low payouts (Jensen *et al.*, 2015, p. 3). Insurance had three broad impacts in Kenya, First, insurance, whether payments were triggered or not, had a positive impact in maintaining consumption and in preserving livestock wealth (Janzen and Carter, 2019), through IBLI's generation of roughly US$10 million in pay-outs to Kenya herders. During the drought of 2011, households in Marsabit county with IBLI coverage had higher incomes and milk production; (Jensen *et al.*, 2015), were 27–36% less likely to skip meals and were 22–36% less likely to make distress sales of livestock (Janzen and Carter, 2019). Jensen *et al.* (2017) found, over 3 years of IBLI coverage, that average veterinary expenditures doubled and livestock sales in non-drought years increased by an average of 46% of the mean.

Impact on the wider policy environment in Kenya is a second category in which the programme had a strong effect measure through the expansion of IBLI by the government of Kenya as the Kenya Livestock Insurance Project (KLIP). KLIP now provides subsidized insurance to 18,000 pastoral households, representing over 80,000 beneficiaries, across eight counties of northern Kenya, and plans to serve 100,000 households across 16 counties by 2021. The 2016/17 drought was among the worst in Kenya in the past 20 years, and KLIP paid out $7 million to pastoralists. One indicator of the policy impact of IBLI was that the insurance product had a favourable benefit:cost ratio compared with other social protection programmes in Kenya (Janzen and Carter, 2019).

IBLI expanded into southern Ethiopia in 2012 and has since generated pay-outs to herders of approximately US$370,000 (Matsuda *et al.*, 2019). A major finding from the studies of IBLI in Ethiopia is that index insurance is a complement, not a substitute, to traditional risk-sharing mechanisms (Takahashi *et al.*, 2019). Since 2019, an IBLI product has been integrated into the Africa Risk Capacity (ARC) to offer index insurance to national partners targeting pastoral regions. To date, more than 86,000 policies have been sold with the ARC micro-insurance scheme and more than 25,000 pastoralists are protected through the macro-level programmes.

Policy lessons

Successful policy is impossible without a base of data collection and analysis

Index insurance for livestock leaves substantial idiosyncratic risks (Jensen *et al.*, 2016), with roughly 60–75% of risk uncovered. These idiosyncratic risks have to be managed by traditional risk-sharing mechanisms or by associated public policies such as social funds.

The arid and semi-arid counties of Kenya are poor enough and risky enough that commercial livestock insurance will need public financial support for some time.

Market agents – insurance brokers, regulators, and extension and research collaborators – had insufficient capacity at the onset of IBLI. The commercial and regulatory capacities of Kenya have grown since the inception of IBLI, but international research support will be needed for some time to maintain a flow of information and analysis on programme operations and outcomes.

Livestock sector analyses and master plans as part of development policies

ILRI has pioneered the use of system dynamics models in agri-food and livestock value chains. One application was in Rich *et al.* (2009) who assessed the viability of a two-stage export certification system in Ethiopia using quarantine

stations and feedlots to ensure disease-free and higher-quality beef for export to Middle Eastern markets. The model found that the costs of complying with SPS regulations did not constrain competitiveness but that high feed costs would do so. Later models at ILRI evaluated sheep and goat marketing in Mozambique (Hamza *et al.*, 2014), reforms to improve competitiveness in the beef sector in Botswana (Dizyee *et al.*, 2017) and assessments of animal disease and food safety (Grace *et al.*, 2017; Rich *et al.*, 2018).

Lie *et al.* (2017, 2018) used spatial techniques in a model of the dairy value chain in Nicaragua to quantify the market effects of feed quality.

A growing area of ILRI policy support has been the development of 'livestock master plans'. Such plans set priorities within livestock development strategies to generate public and private investments. The government of Ethiopia has developed a Growth and Transformation Plan II 2015–2020, which prioritizes agriculture and livestock investments to reduce poverty, to raise national income, to increase exports and to improve food and nutritional security. The Growth and Transformation Plan includes a livestock master plan, based on an analytical tool known as the Livestock Sector Investment Policy Toolkit (www.au-ibar.org/2012-10-01-13-08-42/news/171-au-ibar/451-the-alive-livestock-sector-investment-policy-toolkit-lispt; accessed 9 March 2020).

The Ethiopia livestock master plan (Shapiro *et al.*, 2015) was based on a 15-year sectoral model of potential outcomes of livestock investments in terms of increased production and value added for technology and service investments under associated policy scenarios. The modelling incorporated the red meat and dairy value chains subject to constraints in animal health, feeds and genetics. The livestock master plan, as derived from the sector model, comprises a 5-year investment roadmap and assessments of potential medium-term impacts of combined technology and policy interventions, and informed the Ethiopian government's Growth and Transformation Plan II livestock targets for 2015–2020.

Since 2016, the plan has served as the basis for new funding and projects for the country's livestock sector. This includes livestock investments of US$132 million by the World Bank (http://projects.worldbank.org/P159382?lang=en; accessed 8 March 2020), new donor project financing of US$75 million and new private-sector investments of US$200 million. The higher livestock productivity and income levels resulting from the plan's investment interventions are projected to lift more than 2.3 million of Ethiopia's 11 million livestock-keeping households out of poverty.

The Future

The goal of ILCA/ILRAD/ILRI policy research was to increase smallholder returns by: (i) improving the productivity of technologies through technical, economic and financial analysis; (ii) identifying policy barriers that lower farm prices, raise input costs or increase the financial, information and risk costs of new methods; and (iii) building institutions to raise productivity, create assets and reduce the external costs of animal agriculture.

We are unable to estimate most of the development benefits of policy research at ILRI and partners, for several reasons. One is that many policy studies made little or no effort to calculate impact research on the policy process or on outcomes of policy changes. This pattern began with early ILCA work, such as Addis Anteneh (1983, 1984, 1985, 1991) and the dairy policy studies of Brokken and Senait Seyoum (1992), continuing with McCarthy *et al.* (1999) and the contemporary livestock and poverty (Thornton *et al.*, 2002), animal health (Perry *et al.*, 2002), and climate change investigations (Thornton and Herrero, 2010). One recent innovation is the preparation of 'livestock master plans' (e.g. Shapiro *et al.*, 2015, for Ethiopia, which developed benefit–cost results for specific policy measures). The book of Herrero *et al.* (2014) on African livestock futures proposed specific policy measures, but there has been no effort to cost those recommendations and to see if they have been implemented.

A second reason is broader – the international system has neglected the assessment of policy research with the exception of IPFRI's work. The reasons for this failure include the time lag between research output and policy changes, the difficulty of attributing policy changes to

research products, and the futile and counter-productive demands by donors for simple answers to complex questions in unrealistically short periods, which leads to hasty and inconclusive studies. Exceptions to these generalizations were ILRI's research on the Kenyan dairy policy, which had significant economic and capacity development benefits (Kaitibie *et al.*, 2010a; Leksmono *et al.*, 2006), development of the East Coast fever vaccine (see Chapter 6, this volume) and the public–private partnerships in Latin America that led to the planting of large areas of the forage grass *Brachiaria* spp.

There is an important contrast between the extended data collection and analysis done as part of the ICRISAT village-level studies (Walker and Ryan, 1990) in semi-arid central India and the work at ILRI and other centres. The ICRISAT village-level studies had the greatest scientific impact of economics and policy work across the international agricultural research institutions because the work was sustained for many years and was specifically linked to technology generation. Future field investigations of livestock systems should renew the ICRISAT village-level studies model over a sufficiently long period in African and in other developing country situations.

Acknowledgements

Notes

[1] These were the same classes of measures recommended by Schiff and Valdés (1992) in a global review of agricultural incentives.
[2] There are several versions of the Kaitibie *et al.* (2010b) paper. The version published in a major policy journal had only 37 citations to May, 2020.
[3] Gallais was a member of the 1981 Quinquennial Review of ILCA (CGIAR/TAC, 1982). His deep knowledge of Sahelian pastoralism and land tenure is only faintly apparent in the findings of that Review.

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18 The Impact of ILRI Research on Gender

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Executive Summary

This chapter discusses the evolution of gender research at the International Livestock Research Institute (ILRI) and its predecessors[1], and in the context of CGIAR. It then reviews the impact of ILRI's gender research in a number of areas including development, science, capacity and policy.

Discrimination against women in access to skills, assets, employment, education and healthcare is costly in foregone output and in heightened inequality. Research at international agricultural research centres, although often ad hoc, has long sought to identify technical and policy measures to eliminate or reduce bias against women in agriculture. Specifically, research at ILRI has focused on gendered access to assets, such as livestock and land, and to technology needed to raise livestock and crop production. As livestock often provide a significant share of women's employment and income, and are often an asset they have control over, identifying gender-based biases through research can be a powerful tool to improve the condition of women and improve the sector as a whole. Gender research in livestock also enhances the effectiveness of interventions by increasing the relevance of livestock technologies and institutions to local communities by addressing needs, preferences, constraints and challenges of all farmers. Recent work also looks at how livestock can empower women by revealing social relationships and power dynamics in decision making that affect livestock interventions and how it is possible to build upon livestock as an asset for empowerment.

Research spending and Altmetrics on gender questions

The accounting of ILRI and its predecessors is insufficient to estimate the gender share of research and development spending at the three institutions. During the CGIAR Research Programme (CRP) on Livestock and Fish (2011–2017), this changed with the mandate of the CRP to spend 10% of its budget on gender. At the same time, there has been an increase in direct funding to projects on gender[2], but it is premature to estimate the impact of this funding.

ILRI's presence in the gender literature, as indicated by Altmetric (www.altmetric.com/; accessed 10 March 2020), is limited. The ILRI institutional database on the keyword 'gender' within Altmetrics has 1.0% of the Altmetrics global database; the rate is even lower for the keyword 'women'. The only major papers (over 100 citations) with specific notice of the work and output of women are the systems studies for Maasailand (Solomon Bekure *et al.*, 1991) and Borana (Coppock, 1994). There has been a recent increase in gender-specific articles produced by ILRI staff and partners, such as Galiè *et al.* (2019a) on the Women's Empowerment in Livestock Index (WELI), which had a download index of 1.9k by April 2019.

Scientific impact

Research on gender at ILCA began in the 1970s in the principal systems studies conducted by ILCA, notably those in Kaduna in Nigeria, Borana in Ethiopia, Maasailand in Kenya, and Niono and Macina in Mali. The main gender-related impacts of the systems studies were: (i) to identify gender bias in ownership of livestock, land and other assets; (ii) to identify gender bias in access to technology and advisory services; and (iii) to give methodological guidance on avoiding gender bias in the design and conduct of field investigations.

Recent scientific impacts of gender work at ILRI have included: (i) institutionalizing a strategic approach to avoid bias in experimental design and conduct; (ii) refining field methods to show potential gains from greater gender equity in the generation and application of field results; (iii) a paradigm shift among technical scientists to understand that women, as well as men, are members of their client groups and have their own demands and needs in terms of animal health services, feeds and forages, environment and genetics, as well as facing different constraints and challenges related to livestock; and (iv) developing indicators and an understanding of women's empowerment through livestock.

Development impacts

The following development impacts were identified:

- Defining beneficiary populations for technical changes in livestock investments, including

in dairy, in vaccination campaigns and in plant-breeding programmes.

- Adapting advisory services to the potentially different needs and constraints of female and male farmers in crop and livestock production.
- Strengthening personal and institutional capacities to enable ILRI, other CGIAR centres and several partners to do gender analysis in both pastoral and mixed farming systems.
- More efficient identification of target groups for campaigns to improve food safety.
- Identifying livestock assets as a means of women's empowerment.

Evolution of Gender Research at ILRI and its Predecessors

1970s–1980s

When ILCA opened in 1974, its aim was 'to integrate sociological, economic, and biological research and development related to livestock in Africa' (Waters-Bayer and Bayer, 2014). Despite its development objectives, ILCA did not systematically include gender in its early work. A review of gender-related impacts of CGIAR research criticized the methods and results of international agricultural research on gender issues more than a decade after most of the international agricultural research centres had been established (Jiggins, 1986).

ILCA social scientists working in field conditions (see Chapter 15, this volume) recognized the important roles of women in agriculture and sought to understand these roles within complex farming systems. What became the early, innovative, gender research focused on intra-household decision making, indigenous knowledge, farming systems, the roles of women and even the power and privilege aspects of extractive research (Waters-Bayer, 1985).

The ILCA Subhumid Zone Programme at Kaduna, Nigeria, was a pioneering effort in ILRI's evolution (von Kaufmann *et al.*, 1986). It studied the production systems of settled and seasonally transhumant agro-pastoralists to find ways of increasing crop and livestock production. Milk sellers were exclusively women in the rural markets in central Nigeria, as had been described

in the drier areas of Nigeria and Niger (Dupire, 1960, 2018; Stenning, 1994; Hopen, 2018).

Waters-Bayer (1985), in the Kaduna study, looked at resource control and decision making in Fulani households, specifically at Fulani women's processing and marketing of milk products, and highlighted the ways in which these agro-pastoral women understood market forces and recognized the social and local political functions of their work. The research also explored the limits of Fulani women's knowledge of connections between the local, national and international economies. The study argued in favour of the participatory research to build on rural people's knowledge to enable them to understand and cope better with external influences on their activities and help them 'better defend their own interests against the macroplanning State'(Waters-Bayer, 1985).

In an effort to bring gender more to the forefront, in 1984, ILCA hosted a workshop on women in agriculture in West Africa, sponsored by the Ford Foundation. The conference covered a wide range of topics related to women in development and included an often-cited paper by Okali and Sumberg (1985), which focused on ownership patterns between women and men in small-ruminant production systems and the intra-household processes therein.

By the late 1980s, there had been a shift in ILCA's focus, and it began to emphasize more discipline-based research in animal health, nutrition and genetics, and stressed 'precise' measurement. This approach conflicted with ILCA's previous innovations in livestock systems research and development and its investments in social scientists. This new approach led to the removal of ILCA's social scientists, apart from economists (Romney and Minjauw, 2006; Waters-Bayer and Bayer, 2014), implying that some of the innovation and momentum on gender disappeared.

1990s–early 2000s: the merger and clash of cultures

The merger in 1995 of ILCA and the International Laboratory for Research on Animal Diseases (ILRAD)[3] into ILRI altered livestock systems research. ILRAD had little tradition of field-based research, apart from epidemiology, and

the influence of ILCA's systems work weakened after the merger. ILRI's nascent institutional culture tended to see the social sciences, which had been significant in the systems studies, as 'soft sciences'[4] and this included gender research at ILRI.

ILRI's work in the 1990s on smallholder livestock development later did open opportunities for gender work. CGIAR's Systemwide Livestock Programme was one such initiative, drawing attention to the importance of investing in mixed crop–livestock systems and indigenous livestock breeds and in community-based management of animal genetic resources (ILRI, 2014).

Again, in 1996, ILRI realigned its agenda to emphasize the importance of considering people as part of the livestock systems, which included women. The gender perspective of ILRI's research at the time focused on the roles of, and constraints to, productivity faced by women as agricultural producers. Specific studies of smallholder dairying on the Kenya Coast indicated that women operators were more productive than men, even where men owned cows where the woman operator received the bulk of the additional earnings. The Kenya Coast research also looked at the importance of targeting extension to women as well as to men to make technical advice more effective. Other research in Kenya focused on the importance of understanding women's and men's roles on trypanosomiasis; this yielded a recognition of the importance of understanding gender-differentiated willingness to adopt disease-control strategies (Echessah *et al.*, 1997). Research in Ethiopia involving the Ethiopian Institute of Agricultural Research (EIAR), the Ethiopian Health and Nutrition Research Institute (EHNRI) and ILRI looked at the impact of cross-bred cattle on men's and women's decision making around dairying income (Nicholson *et al.*, 1999).

In 1999, a study of 54 households in a semi-arid subregion of western Niger highlighted shifts in livestock ownership related to long-term economic and environmental changes (Turner, 1999). Turner found significant shifts away from cattle owned by men and towards sheep and goats owned by women over the period 1984–1994. To some extent, these shifts have gone unnoticed in the gender literature, yet they confirm the point, often made in the same literature, that separate survey and analytical approaches are needed to capture the importance of women's economic activities and the potential gains that can be realized by reducing bias against women in access to inputs and services.

2005–2010: institutionalizing a gender research agenda

In 2005, ILRI undertook a gender audit, which reviewed its understanding of gender analysis in research, its gender equity in the organization and its mainstreaming of a gender-based approach. The audit found a good-faith effort to improve gender equity and diversity in the workplace among staff and that management backed this effort. It noted that this effort had helped create a supportive environment for mainstreaming gender analysis in the ILRI's research programmes, as an understanding of gender in the workplace is known to facilitate the integration of gender in research.

In terms of gender analysis in research, the audit found that there was no policy on gender analysis in setting research priorities. It was noted that gender analysis in ILRI was discussed more than practised and that ILRI's strategy did not mention gender issues. The gender audit also found that, although there was an understanding of the importance of gender to this point, there had been little training of scientific staff, managers and students in gender analysis or integration. The institution had not yet instituted a unit or focal point to systematize gender in its programme, although some staff were considered to have expertise in gender analysis (Roothaert *et al.*, 2006). The audit therefore concluded that, while there was good understanding of what gender analysis is in the research capacity of ILRI staff, undertaking such analysis was limited (Roothaert *et al.*, 2006).

As a result of the audit, ILRI formed a task force in 2006 to develop a research agenda on women and livestock issues, but it was only in 2008 that the task force began to have meaningful dialogue with experts and partners (Njuki *et al.*, 2011). This was initiated through a global e-consultation, the Global Challenge Dialogue on Women and Livestock (Gonsalves, 2013). The consultation brought together major livestock players and proposed: (i) the production of a landmark document providing evidence of the feminization of the livestock sector throughout

the world; (ii) a plan for revitalizing a global women's and livestock alliance; (iii) a review of strategies used by research and development organizations to reach women; and (iv) plans for scaling out those strategies that have been successful in reaching women with livestock interventions (ILRI, 2012).

While gender analysis was not systematically integrated in ILRI's research, several projects included gender outcomes. Most projects were development oriented and included women as beneficiaries of the technologies without analysing the actual needs of the women involved. For example, the broad-bed maker tool in some mixed farming systems of the Ethiopian highlands (Rutherford, 2008), the Improving Productivity of Market Success (IPMS) of Ethiopian Farmers project (2008–2013) and the East Africa Dairy Development (EADD) were efforts to introduce interventions that included women as beneficiaries.

The EADD Phase 1 project in Kenya, Rwanda and Uganda (2008–2013) set out to double the dairy income of 179,000 smallholder families in 10 years. Its entry point was women as beneficiaries of training and as producers. In 2009, EADD set out to address this gap by developing a gender strategy, hiring a gender and youth coordinator in 2010, developing gender disaggregated data templates and a gender work plan and performance targets, and outlining strategies to include women in project activities. Although a development project, it did open up a new understanding of gender and the need to focus specifically on women (Baltenweck and Mutinda, 2013).

In 2009, ILRI established a new theme on 'Poverty, Gender and Impact'. This demonstrated a shift in its commitment to ensuring gender-responsive research by focusing on two components: (i) investigations where the research agenda has been set by scientists, such as forages or genetics, and gender considerations are integrated to study the subject more effectively; and (ii) strategic research where the subject is gender.

Important in the 2000s was ILRI's work developing a conceptual framework on livestock as a pathway out of poverty that had, at its core, the importance of assets, markets and other institutions (Kristjanson *et al.*, 2004). ILRI used this framework in a seminal literature review to discuss women and livestock as a pathway out of poverty for women (Kristjanson *et al.*, 2010).

The authors hypothesized that livestock pathways out of poverty: (i) secure current and future assets; (ii) sustain and improve the productivity of agricultural systems in which livestock are important; and (iii) facilitate greater participation of the poor in livestock-related markets. Each of these brought a new attention to gender in its own right and to the importance of livestock as an asset for women.

2010 onward: from an ILRI gender strategy to CRP and beyond

In 2010, ILRI developed a common set of gender, livestock and livelihood indicators to help the centre measure the impacts that projects and other livestock interventions, such as markets and biotechnology, had on poverty, gender and equity (Njuki *et al.*, 2011). These indicators were developed for household-level surveys with the potential for adaptation for community-level focus group discussions.

Another turning point for institutionalizing gender approaches at ILRI came when the Institute produced its 'Strategy and plan of action to mainstream gender in ILRI' (ILRI, 2012). The strategy recognized ILRI's need to guide and design the consolidation of ILRI's expertise and gender resources, to engage stakeholders, and to ensure that men and women participate in and benefit from ILRI's research. It also emphasized the need for commitment from ILRI's board, management and staff and from its many other partners. ILRI's gender strategy represented a true shift over time from research that looked at women as components in farming systems research to a full gender and agricultural research theme including production, processing, markets, value chains and strategic gender research.

In 2014, ILRI introduced a new theme – Enabling Innovation – which focused on adaptive capacity and increased attention to gender. This continued the research of the Innovations Work Unit established in 2007, which, in part, also generated information and learning to empower women in livestock innovation (Waters-Bayer and Bayer, 2014). The Innovation Works Unit recognized women's key roles in livestock production, nutrition and health, noting that most resource-poor livestock keepers are women, and campaigning to keep gender issues at the

forefront of livestock research and development. This included a greater emphasis on the impact of technologies and policies on women and a greater awareness of gender issues overall.

A later shift in ILRI's gender research followed the development of the CRPs in 2010 and 2011. With the CRP on Livestock and Fish (2012–2016), ILRI recognized the need to consolidate the centre's gender expertise and resources to ensure that men and women participated in and benefited from CRP work. Gender was one of the programme's six themes along with animal health, genetics, feeds and forages, sustainable interventions and value-chain development (Galiè and Kantor, 2016; CGIAR, 2013).

The CRP on Livestock and Fish focused on gender relations and dynamics, access to and control of productive resources, and gender-transformative approaches. The CRP explored local meanings of livestock ownership across three CRP value-chain countries (Tanzania, Ethiopia and Nicaragua) (Galiè, 2015). The CRP developed an article reviewing tools developed in livestock and fish value chains (Farnworth *et al.*, 2015) and a policy brief looking at gender relationships and farmers' capacity to mitigate climate change (Gumucio and Rueda, 2015). To enhance the capacity of scientists to integrate gender in their work, the CRP on Livestock and Fish engaged the Royal Tropical Institute in the Netherlands, which, together with the ILRI gender scientists, coached them; this work led to the publication of findings from 14 gender-integrated livestock and fish research studies (Pyburn and van Eerdewijk, 2016).

In 2015, ILRI and Emory University in Georgia, USA, identified a mismatch between the limited attention to livestock issues in the WELI, which focused on agriculture in general (including livestock, crops and fish) and the importance of livestock in East Africa. The WELI was subsequently developed to explore how women's empowerment can be supported through livestock and to assess women's empowerment quantitatively, particularly in a case study of Tanzania (Galiè, 2018a).

Currently, ILRI's gender research work is focusing on: (i) animal health, through enhancing gendered capabilities to address threats through a gendered lens and engaging women in health services; (ii) feed and forages, through gender-sensitive forage interventions, gender

dynamics in fodder seed innovation systems, and gender dynamics in forage conservations systems; (iii) genetics, through gender-sensitive community breeding of small ruminants (Marshall *et al.*, 2019); and (iv) the environment, through gender and land tenure for reduced land degradation, increased intensification, labour dynamics, gender norms, and gender and pastoralism (de Haan and Mulema, 2018).

Impacts of Gender Research at ILRI

The impacts of ILRI's gender work can be grouped by influences on: (i) scientific perspectives, methods and levels of analysis; (ii) farming systems and technologies; and (iii) empowerment.

Scientific perspectives, methods and level of analysis

Influence on scientific perspectives

Research by Waters-Bayer (1985) on agro-pastoral Fulani women in Nigeria and by Okali and Sumberg (1985) on women and small-ruminant production in the subhumid areas of southern Nigeria provided some early understanding on the intersection of gender and livestock production. Recently, gender research has gained ground in ILRI's work and moved from an issue relevant for studying other subjects such as breeding and animal health (integrated gender analysis) to a research topic in its own right (strategic gender research) and is thus part and parcel of understanding how rural households, value chains and livestock systems work, with its own research agenda. Similarly, gender equity through livestock is increasingly accepted as a goal of ILRI's work in its own right and a driver of change, rather than a secondary outcome of livestock interventions.

Methods

Mulema *et al.* (2019) undertook research in Ethiopia that demonstrated the significance of several empowerment indicators (e.g. cultural norms and women's inputs into production decisions; autonomy in plot management; membership of farmer groups; ability to speak in public, enhancing their participation in different stages;

access to information and extension services, education and land size) in influencing women's participation in different stages of agricultural research. This work contributed to the literature on women's empowerment in relation to agricultural research and to promoting the integration of proactive, holistic gender perspectives in research strategies.

ILRI has also developed indicators on gender, livestock and livelihoods to measure the impacts of livestock interventions at household and community levels (Njuki *et al.*, 2011). The women's empowerment in livestock-focused agriculture – the IMMANA project (2015–2018) – in Kenya, Uganda and Tanzania developed new metrics for women's empowerment and animal-source food intakes that are sensitive to maternal and child nutrition, and are relevant to different livestock value chains, including pork, dairy cattle and poultry.

The CRP on Livestock and Fish developed a set of tools for social and gender analysis for value chains (Kruijssen *et al.*, 2016). These tools, adapted from existing tools from other organizations, help users to explore gender relationships and the underlying causes of inequities. One helps users undertake a supplementary gender and social analysis when there is already an existing value-chain analysis, while the other helps users undertake a full value-chain analysis including underlying causes of gender inequality.

In 2016, the CRP on Livestock and Fish integrated gender into the Feed Assessment tool (FEAST), a participatory tool focused on feeds and forage and developed by scientists at ILRI, the Centro Internacional de Agricultura Tropical (CIAT) and the International Center for Agricultural Research in the Dry Areas (ICARDA). This supported researchers and practitioners in their research to surface the issues of gender relationships and how they affect livestock farming, particularly feeding practices and innovations (Lukuyu *et al.*, 2016). The resulting app has now been gendered into G-FEAST, which specifically looks at gendered preferences for forages.

Waithanji and Grace (2014) also developed a gender strategy to support mycotoxin control given that, in many regions, women are responsible for producing food for home consumption and may also have roles in feeding and caring for livestock. The strategy is an important tool for researchers working on mycotoxin control as it outlines a Theory of Change and research cycle approach as well as gender-responsive goals, objectives, research questions, activities and outcomes that can inform research and interventions in livestock health. The WELI has been found to be particularly useful for measuring the impact of livestock projects on women's empowerment over time. ILRI, together with Emory University, developed the WELI and piloted it in Tanzania in 2015 (Galiè *et al.*, 2019a). The WELI helps researchers and decision makers better understand which interventions work best for empowering rural women. Such evidence is important to fine-tune interventions and provide better empowering opportunities for rural women. The actual discussions on empowerment between rural women and men also provide value, opening spaces for individuals, communities and households to think about what empowerment means, who has access to more opportunities for empowerment, and how social and gender norms affect the ability of individuals to succeed.

Tavenner *et al.* (2018) analysed resources, decision making and labour dynamics in dairy farm households in western Kenya. This study found statistically significant differences in practices based on gender. The most divergent responses between men and women were decision making around the morning and evening milk sales. The authors argued that the choice of interviewee affected research findings because survey respondents may have different perceptions or valuation about 'who does what'.

Galiè *et al.* (2019b) discussed some of the difficulties encountered in adopting a mixed-method approach that results in contradictory quantitative and qualitative findings. The article discusses some reasons for this discrepancy including the different definitions, domains and indicators adopted by the two approaches when studying 'food security' 'nutrition security' and 'women's empowerment'. In addition, the qualitative study may have given space to a discussion on 'aspirational' versus 'actual' gender roles in guaranteeing food and nutrition security that quantitative and closed research questions may have not provided.

Gender at the landscape level

Gender work has typically been done at the household level and has studied intra-household

dynamics. To widen the impact of gender research, in 2017, the CRP on Livestock began work on gender at the landscape level through the development of national livestock master plans. New versions of such national master plans will guide investment towards women in the livestock sector (Shapiro *et al.*, 2015 for Ethiopia). There is also a move to integrate gender in modelling work and livestock sector analytics that underpin the national master plans. An ongoing project is developing a methodology to scale gender dynamics from the household and community levels to higher national and regional levels in the context of the feminization of agriculture (Galiè *et al.*, 2019d).

Farming systems and technologies

Institutions

Farnworth and Colverson (2015) found that rural advisory services operate in environments structured by gender relationships. In other words, women often have less-effective participation in community decisions, in value-chain networks and in innovation platforms. Because women are reached less often by advisory services, it is more costly for them to adopt new methods. The study concluded that advisory services should be seen as a facilitation system to tackle underlying gender relationships that constrain access and implementation rather than as a supposedly gender-neutral service.

Omondi *et al.* (2014) found that women were reluctant to participate in dairy hubs in Kenya because of their loss of control of income from milk sales, underscoring the importance of intrahousehold income distribution. The findings implied the need for evidence-based interventions and changes in structures that encourage women's participation, promote more equitable income distribution from dairying and/or compensate women's loss of income, without negative impacts on the stability of gender relationships within the households.

Basu *et al.* (2019) analysed approaches to women's participation adopted by the EADD by looking at how participation actually emerges in specific contexts through gendered negotiations with participatory development policies. The authors discussed how initiatives that include women construct new pathways for women's participation because of the ways that various participatory strategies relate to one another, rather than due to the efficacy of one strategy over another.

Fodder and forages

Work at ILRI and the Kenya Agricultural Research Institute (KARI) on smallholder dairying based on a fodder cut-and-carry system found that an integrated dairy development package had limited acceptance among farmers. A subsequent study looked at women's roles and labour, and found that women were more likely than men to adopt more of the package and demonstrated higher milk yields per lactating cow (11.5 litres/day) than male contact farmers (6.8 litres/day) (Mullins *et al.*, 1996). Although women faced increased workloads as dairy operators, they also perceived improvements in the welfare and long-term development benefits of their households through women's income going to school fees, books, and food purchases (Mullins *et al.*, 1996).

A study on a traditional Maasai forage conservation system (*ololili*) in Tanzania (Galiè, 2018a) found that the system relied heavily on women's labour when it was in use during the dry season, whereas livestock management involved both women and men. Women's and men's groups were found to have similar knowledge of local forage plants but ranked their importance differently. They also showed the same level of interest in intensifying forage growing in the *ololili*. At the same time, gender norms and dynamics were found to strongly affect the ability of women – mostly poor women, and widows in particular – to manage *ololili*. These social constraints in the governance of the *ololili*, if not addressed at the inset of any intensification intervention, were found to be likely to decrease the success of forage technology interventions because they limited the sustainability of the system.

Galiè (2018b) showed how a forage breeding intervention can enhance the empowerment of female farmers. The author demonstrated practical challenges faced by a breeding programme that aims to include gender considerations in its activities and showed how a lack of access to seed because of gender-discriminating

norms and practices at local and national levels can hinder progress towards empowerment. Ultimately, the article challenges assumptions that gender considerations be integrated in breeding programmes to enhance their effectiveness only, by showing the empowering potential of a gender-responsive programme to progress towards gender equality. The article also shows the importance of taking into account the wider context (e.g. socio-cultural, policy and seed systems) in which a breeding programme is implemented, to ensure its benefits reach both female and male farmers.

Animal health and food safety

Galiè (2017) studied smallholder livestock keepers in Tanzania and found that while men and women were both involved in animal health management and had similar knowledge of diseases, women faced more constraints than men in accessing livestock services, disease information and veterinary drugs because of restrictive norms on both their movement and their interactions with unrelated men, because of biases about their reliability in identifying diseases and paying for services, and because they had limited control over the household resources. The study suggested supporting women's groups as a way of enhancing women's control over livestock and revenues, and access to animal health information and income-generating opportunities. The study recommended enhancing the capacity of service providers in gender-responsive approaches and organizing community outreach activities that highlight the benefits of shared intra-household decision making. It recommended that research institutes include gender considerations when identifying priority species and diseases for research on animal medicines and assess which format (e.g. size or temperature sensitivity) increases the accessibility of animal medicines at local level.

Dione *et al.* (2016) explored how gender relationships affect African swine fever control protocols and how current male-centred approaches often disregard women's roles in pig husbandry. Specifically, the research looked at how women and men in Uganda perceive African swine fever and the factors affecting how they respond to it in efforts to encourage farmers to adopt improved husbandry practices and

disease-control measures. The study noted that to control the disease, farmers require information and money for disinfectant as well as the agency to make decisions. It found that women work closely with livestock, often detecting the disease or symptoms. However, men typically make decisions, control household income, and have access to training and veterinary services.

Elsewhere, Kiama *et al.* (2016) conducted a qualitative study with male and female dairy farmers in Kenya on their awareness and perceptions of mycotoxins and how their risk of dietary exposure of mycotoxins is influenced by these. The gender analysis found that those responsible for mitigating risk of exposure are not always those with the knowledge of how to do so. It also pointed to the importance of extension services targeting women as they are the main handlers of food. The study found that farmers had a high level of awareness of the harm of eating mouldy food even though risk categories, awareness of mycotoxicosis and carcinogenic effects were generally low. Typically, women were more careful than men not to feed cattle spoilt maize and they were key decision makers in dairy cow diets and disposal of mouldy foods. Furthermore, while farmers agreed that hygienic handling was the most important method to enhance meat and milk safety, it was women who took more care in ensuring that this happened, while men were more likely to treat sick animals.

Kimani *et al.* (2012) investigated the gender and social determinants of the risk of exposure of *Cryptosporidium* spp. from urban dairying in Dagoretti, Nairobi. The study found that gender, age and household roles are all determinants in exposure to *Cryptosporidium* spp. For example, farm labourers and people aged 50–65 years had the most contact with cattle, while women had greater contact with raw milk and children had relatively higher consumption of raw milk. Women had more contact than men with cattle faeces. Age also played a factor, as older women had more contact than older men. Socioeconomics was a partial factor, with those living in poverty consuming less milk than others, although their exposure to cattle was not affected. There was no significant gender difference in knowledge of cryptosporidiosis symptoms or other zoonotic diseases in the dairying sector; however, the level of education was a determining

factor in awareness, with those with higher levels of education more aware of the disease and factors affecting its transmission.

Jumba *et al.* (2016) illustrated that vaccines against East Coast fever, a major tick-borne disease of cattle and buffalo, can increase overall household productivity while making it more unequal. This resulted from an increase in women's labour on livestock at the same time as their husbands controlled income from increased livestock sales. As a consequence, women were sometimes reluctant to buy vaccines.

Working on contagious bovine pleuropneumonia (CBPP) in Kenya, Muindi *et al.* (2015) noted that women and men perceived the effects of, and were affected differently by, CBPP occurrence because of prevailing gender norms. While women perceived cattle mortality to be the greatest effect of CBPP because it caused food shortages and a decline in income from milk sales, men perceived reduced participation in cattle markets to be the greatest effect of CBPP occurrence. The findings pointed to the need to incorporate gender in animal health research to develop appropriate interventions to prevent or mitigate small-ruminant diseases. A related example is given by Wieland *et al.* (2016) in Ethiopia in a Participatory Epidemiology and Gender Project. This project provided insights about the differential veterinary knowledge of women and men in households keeping sheep and goats related to their gender-specific roles and about the need to target interventions, such as deworming, accordingly.

Research on 20 livestock and fish value chains found that the influence of gender on risk exposure and management is essential for improving food safety in informal markets (Grace *et al.*, 2015). Socially constructed gender roles were more important determinants of health risk than biological differences between men and women; variations in risk exposure were mainly due to gender-based differences in occupational exposure.

Genetics

Gender inequalities can affect the orientation and outcomes of programmes to improve livestock genetics. A study by Rijke (2017) focused on the gender capacities of national partners in the African Chicken Genetic Gains project.

It measured gender capacities at organizational and staff levels of national and regional research institutes and assessed them in relation to the institutional and policy environment that enables or disables other capacities. On a scale of 1–5, the study found that core gender capacities are insufficiently to partially developed (2.4–2.9), pointing to the need to substantially improve the gender capacity of these organizations to support genetics research.

Other research by Mora Benard *et al.* (2016) in Nicaragua demonstrated gender disparities in milk production and breeding technologies (artificial insemination). Ramaswamy and Galiè (2018) studied gender trait preferences in poultry in Ethiopia and showed that women valued traits related to behaviour and feathers that breeding programmes usually neglect by focusing on meat yield and taste only. Women's preferred traits affected whether a breed was adopted by a household or not. The same study also showed that men respondents preferred traits related to productivity, health and marketing of chickens with a view to scaling up their poultry keeping to an intensive system for business. Women responders, in contrast, aspired to increase the scale of their poultry keeping within their household level only and therefore valued traits to increase productivity in extensive systems. Women were not interested in upgrading poultry to a business because of the high labour requirements (mostly their responsibility); their lack of land to keep chickens intensively or assets to make financial investments needed for intensification; and their loss of control over the benefits provided by chickens when, with intensification, men took on the marketing of the birds. The authors, therefore, recommend that, to increase adoption, poultry breeding programmes include gendered preferences for both traits and chicken-raising systems.

ILRI participates in the CGIAR Gender and Breeding Initiative, which seeks to build an approach that incorporates gender perspectives from the beginning of a breeding programme through implementation and impact assessment. The initiative is currently working on a toolbox that helps such incorporation. The toolbox will be used to assure the gender relevance of tools in the CGIAR Excellence in Breeding Platform (Liljander *et al.*, 2015), while supporting national agricultural research institutes and

other breeding programmes. As part of this initiative, Galiè *et al.* (2019a) analysed approaches to see what is effective in making a plant-breeding programme gender responsive. The authors argued that a programme needs to: (i) adapt its criteria to select farmers to host and evaluate trials to ensure women (who own smaller parcels of land than men or none at all) are involved; (ii) adapt its process to evaluate trials in ways that women can express their preferences (e.g. by using scoring systems that require little literacy or, for example, by creating a safe space for women to assess the crops and express openly their preferences; in a community with strong purdah practices, this may entail a women-only field trip and domestic space to discuss and score trials); (iii) expand the traits it considered for further breeding to include traits preferred by different groups of women and men; (iv) expand the crops it included in its portfolio (to include crops of interest to women and men); and (v) include both oral and visual information-sharing approaches to reach women who are often more illiterate than men. However, for a gender-responsive breeding programme to result in actual gender-equitable outcomes (e.g. producing seed that benefits both women and men), a coherent and comprehensive package of technological (e.g. improved seed) and institutional (e.g. policy and governance) solutions needs to be developed by multidisciplinary teams.

Environment

The EADD programme in Kenya examined sustainable milk intensification, climate change mitigation and gender dynamics in determinants of participation and in distribution of benefits (Tavenner *et al.*, 2018). Household surveys covered decision making, resources and labour dynamics in cattle-keeping households in Bomet, Nandi, Uasin Gishu and Kericho counties. While women and men reported similarly on some issues, they contested others. The research demonstrated the challenges of interpreting gender dynamics and addressing challenges in the dairy sector methodologically and programmatically.

Gumucio *et al.* (2015) looked at capacity and gender relationships in the context of mitigating climate change. Based on a review of silvopastoral production systems in Costa Rica, Colombia and Nicaragua, the work found that gender relationships affect the capacity of livestock producers to mitigate climate change. The study also demonstrated that women face certain limitations as agents of change compared with men due to gaps in access to, and control over, productive resources. Related work by Gumucio and Rueda (2015), derived from a review of 105 national policy documents in seven Latin American countries, concluded that development and environmental policies often failed to recognize women's roles as producers in the national economy.

Nutrition and food security

Galiè and de Haan (2019) highlighted the relevance of gender in policy pathways for food and nutrition security. Price *et al.* (2018) explored the linkages between women's empowerment and household nutrition in relation to livestock knowledge and looked at perceptions of women's empowerment from the perspective of female farmers in Tanzania. The study found that women perceived an increased ability to provide nutrition for their families if they had more control over livestock, income and agricultural resources. However, women were reluctant to describe the direct links between empowerment in livestock work and household nutrition, in part because they could not imagine that it would be possible to gain significant power over livestock within their societal constraints. Women frequently described opportunities for becoming empowered outside the livestock sector (i.e. in new crop agriculture or business) where gender norms were less entrenched than in livestock because they are less constrained by tradition.

Similarly, Galiè *et al.* (2019b) presented a mixed-methods study that examined the relationship between women's empowerment, household food insecurity, and maternal and child diet in two regions of Tanzania. Indicators across three domains of women's empowerment were scored and matched to a household food insecurity access scale. Qualitative research helped appreciate the gender dynamics affecting the empowerment–food security nexus in a forage conservation system. In cluster-adjusted regression analyses, scores from each domain were significantly associated with women's dietary diversity but not with household food security. All three empowerment domains were positively

associated with food security and nutrition in the qualitative analysis. The authors discussed some of the methodological challenges encountered when combining quantitative and qualitative methods and the implications of the findings.

Other research in rural Kenya examined how 'women's time use and decision-making patterns related to dairy income and consumption are associated with intensification' and found that 'children in high-intensity households received more milk than children in medium-intensity households' and that women in high-intensity households also spent less time on dairy activities than women in medium-intensity households. Although women seemed to be gaining control over evening milk sales, men appeared to be increasingly controlling total dairy income, a trend countered by the increase in reported joint decision making (Njuki *et al.*, 2015). Galiè *et al.* (2019b) confirmed this in their recent article on milk production.

Markets and value chains

Farnworth *et al.* (2015) examined current research to develop analytical frameworks and implementation guidelines to support gender analysis in livestock and fish value chains. Njuki and Sanginga (2013) carried out research on women and livestock and provided empirical evidence from different production systems in Kenya, Tanzania and Mozambique of the importance of livestock as an asset to women and their participation in livestock product markets. They explored intra-household income management and the economic benefits of livestock markets to women, focusing on how markets, products and women's participation in markets influence their livestock income.

From experience in the IPMS project in Ethiopia, Aregu *et al.* (2010) demonstrated that site-specific commodity-based gender analysis is essential for understanding the different roles of women and men in the production of specific commodities, marketing and decision making and their share in the benefits; in identifying potential barriers for women's and men's participation in market-led development initiatives and technology adoption; and in identifying what actions may be required by the project in order to overcome some of these barriers that limit women's participation in these particular commodities

development initiatives. It helped to explore challenges and identify opportunities for promoting gender equality and women's empowerment through increasing women's access to skills, knowledge and assets and by increasing women's participation in market-oriented agricultural production and their control over the benefits.

Recent research on cattle and dairy market participation in Kenya demonstrated the advances in gender research in recent years to include attention to the gendered nature of market participation and privilege over dairy income (Tavenner and Crane, 2018). This research demonstrated the importance of considering the social trade-offs and the gendered costs of dairy commercialization in interventions aimed at redressing gender power imbalances. Elsewhere, recent work on milk trading in peri-urban Nairobi revealed strong gender-based constraints faced by women milk traders that result in milk business being more lucrative for men than for women (Galiè *et al.*, 2019c).

Similarly, market-oriented smallholder development in the dairy sector in Holetta in Ethiopia and Kiambu in Kenya contributed to the question of whether smallholder research results in women were losing control over income in the East African highlands and suggested the need for more robust understanding of the context in which gender roles and relationships exist and the subsequent impact on women's time use, participation in market-related livestock activities and benefits (Tangka *et al.*, 1999). McPeak and Doss (2006) also highlighted the importance of understanding gendered roles and relationships in producing and marketing dairy products through their research on mobile pastoralists in Kenya. They found that women had the right to sell milk, but men were responsible for the whole herd and where they would camp. If women's marketing objectives conflicted with men's herd-management objectives, then men used location to restrict women's access to markets.

A study on pork consumption in Uganda studied the reasons why pork consumption is lower for women than for men at pork joints (Mabwire, 2018). The study focused on two main possible reasons: the attributes of retailer outlets and gendered perceptions associated with pork consumption at joints. The study found hygiene

(of the outlet environment and the waiters and waitresses) to be the main attribute that women consider when eating at joints. It also found that the communities usually negatively label un-accompanied female pork consumers as 'lonely', 'single' or 'prostitutes'.

Empowerment

Empowerment through livestock is a new area of work for ILRI. It has meant a move away from simply ensuring that women can benefit from technologies developed by ILRI to one where the research is on how women can benefit from livestock based on their own needs and aspirations, and how they can potentially be empowered by livestock. Three initial areas of work have been understanding: (i) the concept of livestock ownership as part of empowerment; (ii) the links among food security, nutrition security and empowerment; and (iii) livestock as an asset for empowerment (Galiè and de Haan, 2018). The team has also engaged in developing new conceptualizations of empowerment based on fieldwork with livestock keepers (Galiè and Farnworth, 2019).

As empowerment is often also within a context, it has also meant increased engagement and research of gender-transformative approaches. Gender-transformative approaches aim to deepen social change by addressing some of the norms that constrict a particular group by determining, for example, what behaviour is acceptable for women and men (e.g. of a given ethic group, social status or age) or what resources and opportunities they are entitled to or can claim (Galiè and Kantor, 2016). Gender-transformative approaches are often contrasted to 'accommodative approaches'. Accommodative approaches recognize and respond to the specific needs and realities of men and women based on their existing roles and responsibilities as shaped by existing social and economic structures; they do not question the systemic barriers put up by the social context of people's lives (Cornwall and Edwards, 2010). Using both empowerment as an entry point and gender-transformative approaches is a new area of work for ILRI but an important one in understanding the potential for livestock to improve livelihoods.

Capacity development and partnerships

Working closely with scientists and partners has been the best approach to develop capacity on gender and to leverage that capacity for a larger impact. In 2013, in collaboration with Transition International, ILRI produced a gender capacity assessment tool to evaluate existing skills and gaps in partners' gender capacities and identify measures to address them. In 2015, the tool was implemented in four of the value-chain countries (Ethiopia, Nicaragua, Tanzania and Uganda) in the CRP on Livestock and Fish (ILRI, 2017). The ILRI gender team has engaged in addressing some of the identified gaps during capacity development workshops and through the use of a training manual. The team has also undertaken capacity development at national levels through, for example, close collaboration with the Ethiopia Institute of Agriculture Research (EIAR) and with the Food and Agriculture Organization of the United Nations (FAO) to develop an approach to building capacity at policy levels.

Under the CRP on Livestock and Fish, the gender team was embedded under different flagships to provide coaching to individual scientists and technicians. Doing so resulted in a cadre of researchers who had a more in-depth understanding of gender in their subject area and in the development of a book on how to integrate gender within different areas of livestock development (Pyburn and van Eerdewijk, 2016). It also resulted in the investment of a gender strategy for the African Chicken Genetic Gains project and the placement of a gender expert in the project to provide support in Ethiopia, Tanzania and Nigeria (Rijke, 2017).

Working together, EIAR, ILRI and ICARDA, together with the Ethiopian Agricultural Transformation Agency, began to integrate gender in agricultural programmes by sharing the gender capacity assessment methodology and tools developed by the CRP on Livestock and Fish (ILRI/ICARDA, 2017). The results and experiences from gender capacity assessment of the small-ruminant value-chain partners were also distributed through the Agricultural Transformation Agency to stimulate interest in and appreciation of the methodology and tools.

Policy impacts

A regional dairy development project was implemented in Kenya, Tanzania and Uganda by Heifer International with ILRI and other partners. One project objective was to increase women's participation in producers' organizations and in the dairy value chain (Pyburn and van Eerdewijk, 2016; Basu *et al.*, 2019). The project included two studies, one to assess women's roles in the dairy value chain beyond production, and the second to analyse the inclusion of women and youth in producer organizations. Both studies illustrated that in all three countries, participation of women was higher at the production links of the value chains and weaker at higher links. Participation of women in leadership positions in producer organizations, cooperatives and credit agencies was insignificant.

A study of a sheep value chain in Ethiopia identified gender-specific constraints for participation in the value chain (Wieland *et al.*, 2016). The results showed that men and women both faced constraints in terms of capital – social, financial, human, natural, political, cultural and physical – but women faced more severe constraints than men. Projects to support pro-poor value chains would therefore need to devise mechanisms to release women's capital constraints.

Another study in Tanzania showed that women and men had similar knowledge of animal disease management and its possible impact on food security (Galiè *et al.*, 2017). However, women faced more constraints than men in gaining access to veterinary services, information on diseases and animal drugs. The implications are that veterinary and extension services should give proper attention to different service constraints faced by men and women.

Quisumbing *et al.* (2013) assessed the impact of dairy value-chain interventions on gender issues, including ownership of assets, asset control and decision making, and time allocation. The study results indicated that value-chain interventions increased joint household assets of men and women. Value-chain interventions did not alter production decision making, although they did have an impact on intra-household decisions. The value-chain interventions also increased the time allocated to dairying, most of which was provided by women.

Improving data and statistics for policy

Of note is the contribution to science impacts of the development of the WELI, which helps quantify empowerment in a way whereby scientists can measure its changes over time. The WELI provides a common framework for determining the effectiveness of various interventions and can support decision makers and policy makers in measuring progress against the investments they make and can strengthen the integration of empowerment in development policies and programmes.

The Rural Household Multi-Indicator Survey (RHoMIS) framework produces standardized, coherent, cost-effective, quantitative, decision-relevant information to support efficient and impactful development programming for planning and monitoring investments in sustainable intensification across a range of rural contexts. RHoMIS captures information on farm productivity and practices, nutrition, food security, gender equity, climate and poverty (van Wijk *et al.*, 2016). The core set of data feeds into a global discussion on the success of sustainable intensification. RHoMIS includes a gender equity indicator, 'Gendered income over assets and foodstuffs' (van Wijk and Hammond, 2018), and since its inception in 2015, RHoMIS has been applied in 22 countries.

The Future

Based on ongoing work, the future of research on gender and livestock covers two different but equally important agendas (for further elaboration, see chapter on 'Conclusion: The Future of Research at ILRI', this volume):

- Improving the productivity and efficiency of the livestock sector by increasing the opportunities for women and men to engage in the livestock sector.
- Strengthening (economic) empowerment of women through livestock.

Research to inform and support this will be undertaken under the following themes:

- Conceptual framing of gender and livestock.
- Increasing options to engage equitably in the livestock sector and identifying

gender-specific interventions in ILRI's research for development.

- (Economic) empowerment through livestock and livestock as a business for women.
- Gendered empowerment and nutrition.
- Gender in livestock policy and at the landscape scale. This includes investment plans in the livestock sector (in Ethiopia and Namibia) that focus on gender at a broad scale rather

than the household scale. From the perspective of modelling, the RHoMIS and GENNOVATE (a global comparative research initiative that addresses the question of how gender norms and agency influence men, women, and youth to adopt innovation in agriculture: https://gender.cgiar.org/themes/gennovate/; accessed 14 April 2020) initiatives provide potential for impact.

Notes

[1] ILRI refers to the International Livestock Centre for Africa (ILCA, 1974–1994) and the International Laboratory for Research on Animal Diseases (ILRAD, 1973–1994) unless specified otherwise. ILCA and ILRAD were merged to form ILRI in 1995.

[2] In terms of gender in the workplace at ILRI and the institution's inclusion of women among its scientists, the share of female scientists rose from an average of 22% in 1980–1986 to 32% in 2006–2011 (the most recent period before the arrival of the CRPs.).

[3] ILRAD's work on gender was limited to some aspects of its field epidemiology studies in East Africa after 1986.

[4] One experienced ILRI ecologist was said to have referred to gender as the 'really hard science'.

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Annex 1: Gender Research in CGIAR

CGIAR's efforts to address gender in international agricultural research began in the 1970s and have evolved across time and institutions. A recent evaluation of gender in CGIAR identified three phases of gender mainstreaming: a first phase in the 1990s, a second from the 1990s to 2011, and a third after 2010 (CGIAR/IEA, 2017). The recent CGIAR 2010–2015 Strategy and Results Framework provided the foundation for the first round of CRP proposals and identified gender inequality as a critical area directly affecting CGIAR's likelihood of success in achieving its four system-level outcomes of reducing rural poverty, increasing food security, improving nutrition and health, and the sustainable management of natural resources. This was a crucial step in acknowledging the importance of gender equity to the effectiveness of CGIAR research. The Consortium developed and adopted its first explicit Consortium Level Gender Strategy in 2011 and implemented this in 2012 alongside the first-generation CRPs, covering both gender mainstreaming in research and at the CGIAR workplace (CGIAR/IEA, 2017). Gender Research Coordinators were appointed in each CRP to lead the gender strategies, supported by a Senior Gender Adviser at the Consortium, and the wider Gender Network has provided the capacity to advance the process (CGIAR/IEA, 2017).

Several CGIAR programmes have focused on gender and have had wide influence across the centres. These include: (i) the Intra-household Research Programme (1992–2003), led by IFPRI; (ii) the CGIAR Gender Programme (1991–1999), led by CIAT, focusing in part on gender staffing as well as on gender analysis in research; (iii) the Participatory Research and Gender Analysis Programme (1997–2011), which was a systemwide programme until 2010 when it became a CIAT programme; and (iv) the Gender and Diversity Programme (1999–2012) hosted by the International Centre for Research on Agroforestry (ICRAF) (CGIAR/IEA, 2017). The Participatory Research and Gender Analysis Programme essentially moved gender analysis out of the Gender and Diversity Programme (Gurung and Menter, 2002) and focused on gender research primarily on crop and natural resource management research.

ILRI and its predecessors played an active part in the Consortium, although the focus and intensity of gender research changed over time. Gender efforts began with researcher-led intra-household approaches to farming systems research in the 1970s and 1980s. Reinvigorated efforts on gender in the 1990s were in part due to the influence of CGIAR's Gender and Diversity Programme and of the Systemwide Programme on Participatory Approaches and Gender Analysis. In the early 2000s, gender found growing attention, with a focus on poverty reduction and renewed interest in social sciences. The hiring of a Programme Leader in the latter part of the 2000s for a theme that included gender (Livelihoods, Gender and Institutions) and a new Gender Strategy helped institutionalize gender in ILRI. These efforts strengthened under the inter-centre research collaboration on the CRP on Livestock and Fish, followed by the more recent CRP on Livestock and were supported by gender strategies to guide more strategic research as well as gender-mainstreamed research and capacity strengthening.

ILCA had played an important role in early CGIAR research by highlighting women's roles in farming systems research. Notably, ILCA's research drew attention to the importance of women in pastoral livelihoods in East and West Africa and, importantly, contributed to the discourse on participatory versus extractive knowledge systems.

Conclusion: The Future of Research at ILRI

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Contents

Introduction

This book has presented the achievements and development impacts of livestock research conducted by the International Livestock Research Institute (ILRI), its predecessors the International Livestock Centre for Africa (ILCA) and the International Laboratory for Research on Animal Diseases (ILRAD), and selected partners over a 45-year period. These achievements and impacts are summarized in the Introduction to this volume and in the Executive Summaries of each chapter. This final chapter looks at the future – what should ILRI do in the next 10 years? – by considering the challenges facing livestock research and livestock development and suggesting priorities for work in those areas.

The chapter considers future priorities for ILRI by reviewing the following:

- The contributions livestock make to human welfare.
- Global projections of animal product consumption, production and resource use.

- The research context for livestock in terms of global Sustainable Development Goals.
- Research challenges in the principal domains covered in this book – animal health and genetics, including livestock and human health; primary production, focusing on animal feed and forages; livestock systems, including policy and economics, climate change, and gender.
- The potential research contribution to the Sustainable Development Goals.
- Future operational issues for ILRI and partners.

The Contributions of Livestock

Livestock and food and nutrition security

An estimated 820 million of the world's people are food insecure. Some 2 billion are undernourished because they do not consume enough protein, vitamins and minerals to lead healthy lives; of these people, perhaps 1.5 billion may

suffer from micronutrient deficiencies. The majority of food-insecure and malnourished people live in the tropics, which is ILRI's principal mandate zone (FAO/IFAD/WFP, 2018).

The welfare effects of food and nutrition insecurity are significant. Some African and Asian nations may be losing as much as 10% of their annual gross domestic product (GDP) to undernutrition (World Bank, 2019). A leading example of these effects is childhood stunting, manifesting as low height for age and often causing delayed cognitive development and durable harm to individual welfare. The Food and Agriculture Organization of the United Nations (FAO) has estimated that about 150 million children are stunted in low- and middle-income countries (FAO/IFAD/WFP, 2018).

Nutritional benefits of animal-source foods (ASFs)

ASFs – milk, meat, offal and eggs – provide scarce nutrients in much of the world. These foods produce approximately 26% of the protein (often of higher biological value than plant protein) and 13% of the calories consumed globally. They also provide essential micronutrients, including calcium, iron, phosphorus and zinc, as well as vitamins A, B12 and D. Many of these micronutrients tend to be more bioavailable in ASFs than in other foods. Some micronutrients, such as vitamin B12, are found naturally only in ASFs. For many groups, it is physiologically impossible to maintain bodily health without consumption of ASFs. The international scientific community agrees that the first 1000 days of life are critical for child development; many nutritionists assert that the nutritional requirements of this period cannot be achieved without ASFs in the diet (Adu-Afarwuah *et al.*, 2017; Grace *et al.*, 2018). Part of the global effort to improve the food and nutritional status of millions of people will be increasing their consumption of ASFs from their existing low levels of such consumption.

Overconsumption of ASFs

One cost of overconsuming milk, meat and eggs, as well as other foods, is that it can contribute to increased health risks, including obesity. Now considered the world's number one health problem, obesity kills three times more people than undernutrition; approximately 1 billion adults are now overweight and a further 600 million are obese (HLPE, 2016, p. 15). It has been contended for some time that high levels of meat consumption in particular may increase risks of heart disease, diabetes and certain cancers. However, recently the evidence for this has been questioned (Leroy and Cofnas, 2019). Part of the global research agenda will be to reduce overconsumption of ASFs in high- and middle-income countries where it has adverse health effects.

Livestock and prosperity

The demand for livestock foods is increasing as both the global population and household incomes increase. With growth of the world population projected to increase from 7.8 billion in March 2020 to 9.7 billion by 2050, and with growing incomes and urbanization, demand for ASF is projected to continue to increase; the highest growth in total and per capita consumption of ASFs is expected to occur in low- and middle-income countries.

Some 750 million people in the world live in extreme poverty (World Bank, 2019). Many poor people keep livestock as their only productive asset and as one of their few sources of income. The world livestock sector provides employment to 1.3 billion people (about one in six people on the planet at the end of 2019) and some form of livelihood to 1 billion poor people. Meeting the growing demand for ASF can therefore be a source of economic growth (incomes and employment) of the poor.

Ten times more women own livestock than own land, and a majority of poor livestock producers are women (HLPE, 2016). Empirical work, to which ILRI has contributed, suggests that increasing women's control over assets, including livestock, improves welfare, food security, household nutrition, education and health (see Chapter 18, this volume). Research to improve livestock productivity is therefore likely to improve women's welfare in direct ways.

Livestock and natural resources

Livestock can both benefit and harm natural resources. On the positive side, livestock convert large amounts of biomass and waste material, for which there is no alternative use, into valuable products. Some 26% of global ice-free land,

much of which cannot be used for crops, is used for grazing animals. Globally, livestock is estimated to use 3.73 billion ha of land: 3.38 billion ha for grazing and 0.35 billion ha for feed production (HLPE, 2016, p. 35). In addition to using land that is not suitable for crops, animals are beneficial to mixed crop-and-livestock farming by providing manure for soils and power for cultivation and by consuming crop residues. Research to intensify animal production using resources that are not usable for direct consumption by people can therefore produce substantial benefits.

On the negative side, livestock are an important user of natural resources (land, water and soil nutrients) that have competing uses. Some 33% of cropland is used for cultivating feed crops, which can compete with food crops in many regions. Some 15% of agricultural water use is linked to livestock production. Animal production can also be a cause of deforestation and biodiversity destruction (HLPE, 2016). The local resource effects of livestock, including damage to soils and water, can also be adverse. Research to mitigate the resource costs of animal production should therefore be an explicit global priority, with attention to the differing intensities of ASF and protein crops, such as soybeans and grain legumes, in terms of water footprint and marginal land use.

Livestock and climate change

The life cycle of livestock production and consumption contributes an estimated 14.5% of global greenhouse gas (GHG) emissions. After the first global estimates of livestock-generated GHGs were published (Steinfeld *et al.*, 2006), much has been done to measure animal contributions to climate change and to explore mitigation options (Gerber *et al.*, 2013). It is now accepted that significant potential exists for cutting emissions from tropical livestock through efficiency gains at the level of the individual animal, as has been done in temperate areas. Wider adoption of best production and marketing practices and technologies in feed, health, husbandry and manure management – as well as greater use of technologies such as biogas generators, renewable energy, and energy-saving methods – could help the global livestock sector reduce its outputs of GHGs by as much as 30% (HLPE, 2016). GHG mitigation technologies may come at a cost to animal welfare and other environmental variables, however, and practices that have beneficial rather than detrimental co-effects should be favoured.

Climate change will force tropical farmers to adapt and this is particularly true of animal agriculture, where stresses from heat, varying growing periods, and pests and disease are expected to become more severe. Climate adaptation (see Chapter 16, this volume) has recently been an important part of ILRI's global research portfolio and should become more important in the next 20 years.

The Research Context: Demand and Supply of Livestock Products

Demand

Demand for ASF has grown rapidly in low- and middle-income countries, driven by rising household incomes and population growth (Delgado *et al.*, 1999; Rosegrant *et al.*, 2009; Alexandratos and Bruinsma, 2012). FAO (2011, p. viii) notes that the 'vast majority of growth in [demand from 2000 to 2030] is caused by increasing per capita consumption rates rather than by increasing population levels'; this income effect will continue to dominate through to 2050. Projections of consumption show continued demand growth in all regions, as illustrated in Fig. F.1 for meat and Fig. F. 3 for milk with a general slowing of demand growth for all regions except South Asia and sub-Saharan Africa until 2050. Growth rates for meat and milk commodities are projected to remain higher in developing than in developed countries, notably in South Asia and in sub-Saharan Africa, suggesting that the derived demand for research on those goods will remain strong for decades.

Supply

Livestock populations have grown rapidly across developing countries, notably in China and other East Asian nations, and most rapidly in poultry. Estimates for the period 1971–2007 (Fig. F.2) showed consistent trends: (i) meat production in developed countries grew more slowly than in developing countries; and (ii) monogastrics grew more rapidly than ruminants in all country groupings.

Projections for the periods 2007–2030 and 2007–2050 (Fig. F.2) indicated that: (i) meat
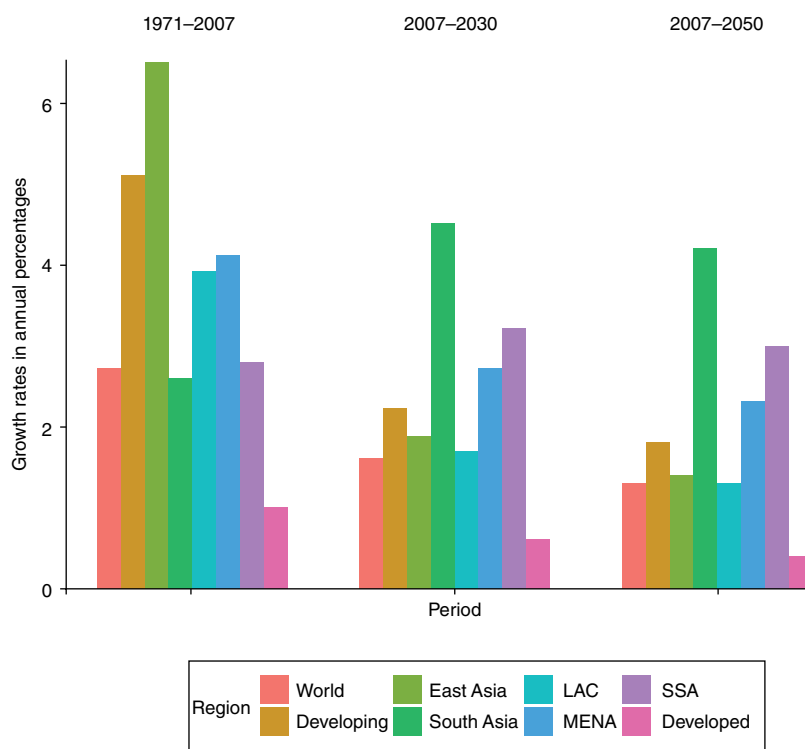
Fig. F.1. Aggregate meat consumption growth rates by period and region, 1971–2007, 2007–2030 and 2007–2050. Rates for 1971–2007 are estimated from historical data; rates for 2007–2030 and 2007–2050 are projected from a world agricultural model. LAC, Latin America and the Caribbean; MENA, Middle East and North Africa; SSA, Sub-Saharan Africa. (Data from Alexandratos and Bruinsma, 2012.)

production growth rates for all species are expected to decline until 2030 and to remain roughly constant from 2030 through 2050; (ii) numbers for developing countries are projected to grow more rapidly than those of developed countries (Fig. F.4); (iii) growth rates for poultry exceed those for the other species in all regions to 2050 (Alexandratos and Bruinsma, 2012, Table 4.19); (iv) the high annual rate of growth in pig production from 1971 to 2007 will fall to barely 1.0% between 2030 and 2050; and (v) the high historical rate of growth in poultry production is also expected to fall from 2030 to 2050.

At the rates of growth applied here, by 2050 it is projected that developing countries will produce about 70% of the world's meat (ruminant and monogastric) and about 63% of the world's milk, which are substantial gains over the estimated 2007 values (58% for meat and 46% for milk). This trend towards an increasing share of production and consumption in low- and middle-income countries holds for all livestock commodities – poultry, beef, milk, mutton, pork and eggs. While the livestock number growth rates of sub-Saharan Africa will rise somewhat more rapidly than those of other regions (Fig. F.4), the share of sub-Saharan Africa in world livestock numbers is projected to rise only from 3% to 5%. This pattern of growth to 2050, although slower than observed in the past 50 years, will offer important production and trade opportunities for African and Asian producers.

Animal supply growth has two components: (i) numbers of animals; and (ii) productivity per animal, such as carcass weight or milk yield. In the earlier period of 1961–2007 (Fig. F.5), growth of numbers was roughly three times as high in developing countries as in developed. Growth rates of animal numbers in both groups of countries are projected to fall from 2007 to 2050 although the rate in developing countries will remain about twice as high as that in developed countries. The lower projected growth of animal numbers to 2050 will be general across continents
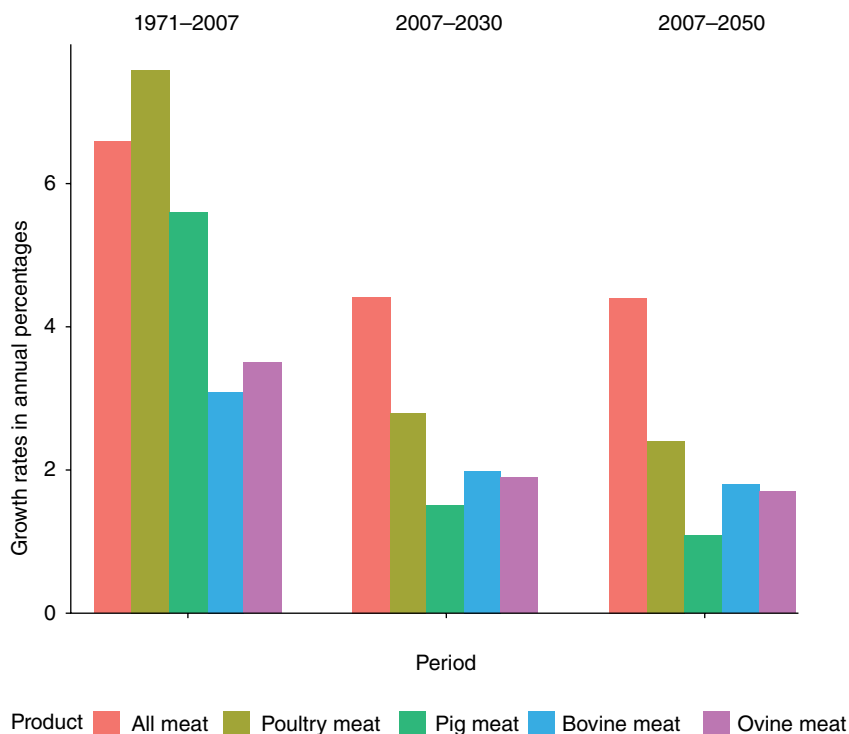
Fig. F.2. Aggregate meat production growth rates by period and product, 1971–2007 to 2050. Rates for 1971–2007 are estimated from historical data; rates for 2007–2030 and 2007–2050 are projected from a world agricultural model. LAC, Latin America and the Caribbean; MENA, Middle East and North Africa; SSA, Sub-Saharan Africa. (Data from Alexandratos and Bruinsma, 2012.)

and species, although growth in aggregate animal numbers in sub-Saharan Africa will continue to be strong through 2050.

Productivity growth per animal, as measured by rates of carcass weight growth, rose dramatically in developing countries for pigs and poultry in the period 1962–2006 (Fig. F.6). Estimated aggregate rates of carcass weight growth across species and regions averaged more than 6% in that earlier period. Productivity growth rates are projected to fall over the period 2006–2050.

The projected patterns of growth in animal numbers and carcass weight will adjust the importance of the two factors in output growth over time. As shown in Figs F.6 and F.7, growth of animal numbers explained more of production growth in the historical period of 1962–2006 than did growth of animal weights. In the projection period of 2006–2050, the share of growth in animal weights is projected to become more important for cattle and poultry. Sub-Saharan

Africa will dominate global productivity growth in all species save poultry in the period ending in 2050. Vigorous projected productivity growth in sub-Saharan Africa will depend on development and application of new methods and on reduction of intermediation costs through investment in infrastructure.

An important question for ILRI's research is how supply of ASF in its mandate areas can meet growing demand in economically, socially and environmentally sustainable ways while improving competitiveness from those mandate areas. Supply for ILRI's principal mandate region of sub-Saharan Africa has three components: through imports, industrial production or smallholder production.

Imports

Imports now meet much of the demand for ASF in sub-Saharan Africa. Sub-Saharan Africa's
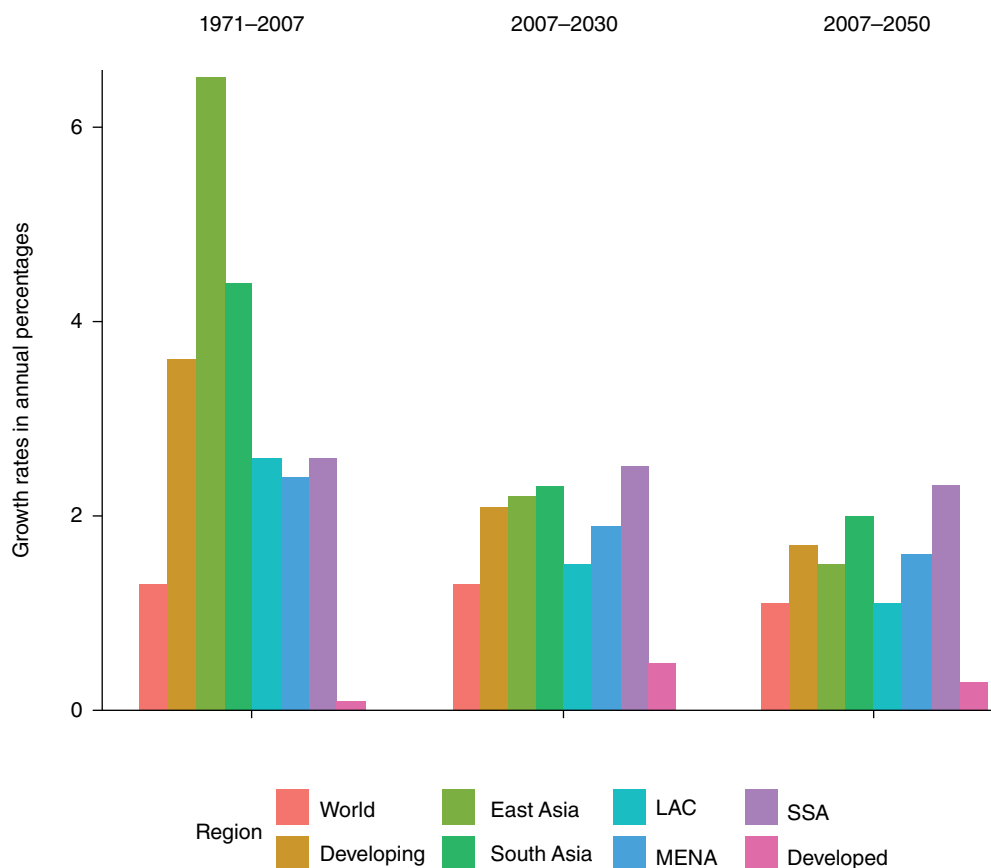
Fig. F.3. Aggregate milk consumption growth rates by period and region, 1971–2007 to 2050. Rates for 1971–2007 are estimated from historical data; rates for 2007–2030 and 2007–2050 are projected from a world agricultural model. LAC, Latin America and the Caribbean; MENA, Middle East and North Africa; SSA, sub-Saharan Africa. (Data from Alexandratos and Bruinsma, 2012.)

average 2008–2014 annual food import bill was about US$46.1 billion, representing about 3.2% of regional GDP. Milk, meat and eggs accounted for 14% of food imports, or 0.4% of regional GDP. Projections using the International Model for Policy Analysis of Agricultural Commodities and Trade (IMPACT) (http://impact-model.ifpri.org/; accessed 11 March 2020) showed that the food import bill could reach US$147 billion annually by 2030 (US$142 billion in 2015 terms), or around 2.9% of projected GDP, with milk, meat and eggs accounting for US$36 billion, or 0.7% of GDP (i.e. the relative share of net imports of milk, meat and eggs as a share of GDP would more than double from 2016 to 2030). While ASF imports are likely to grow in sub-Saharan Africa, they are not projected to pose a significantly larger burden on the region's capacity to finance

food imports, given projected exports. Sub-Saharan Africa has some potential for additional exports of meat and milk, but any increase will require reducing yield gaps with competing regions.

Industrial livestock production

A second component is industrial livestock production, which has been essential in Latin America and East Asia. The potential for industrial supply in Africa is high but confronts barriers of feed transformation efficiency, infrastructure and regulation of externalities. Where concentrate feeds for monogastrics are accessible at competitive prices, industrial systems have grown; where feed costs are high relative to product prices, industrial systems will grow more
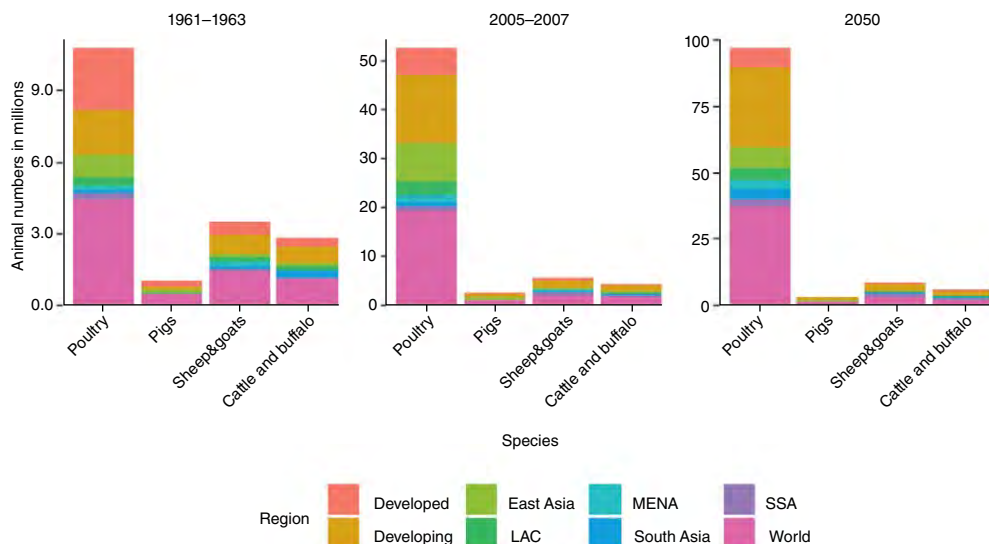
1961–1963 and 2005–2007 numbers estimated from historical data; 2050 numbers projected from world agricultural model.
LAC, Latin A,erica and the Caribbean;MENA, Middle East and North Africa; SSA, sub-Saharan Africa. +
(Data from Alexandratos and Bruinsma, 2012).

Fig. F.4. Animal numbers by period, region and species, 1961–1963, 2005–2007 and 2050. Numbers for 1961–1963 and 2005–2007 are estimated from historical data; numbers for 2050 are projected from a world agricultural model. LAC, Latin America and the Caribbean; MENA, Middle East and North Africa; SSA, sub-Saharan Africa. (Data from Alexandratos and Bruinsma, 2012.)

slowly than extensive ruminant systems. Consequently, ruminant subsystems, apart from dairying, will probably remain extensive into the foreseeable future because their feed-conversion ratios are much higher than those of monogastrics. Another factor maintaining extensive animal production is labour costs, where low wages favour smallholder agriculture over larger enterprises. Wages in Africa are likely to remain low for some time compared with Latin America and East Asia, based on projections of per capita economic growth rates. Furthermore, industrial livestock production systems can have high environmental costs owing to waste disposal, water nutrient loading and antimicrobial resistance. The projected costs of production factors – feed costs, infrastructure and environmental externalities – suggest that smallholders will continue to dominate ruminant production in sub-Saharan Africa, and that larger units will gradually dominate monogastrics.

Supply from small- and medium-sized producers

A third element is expanding supply from small- and medium-sized producers in Africa and in parts of Asia. Although imports of ASF are growing in developing countries, over 85% of the total consumption of ASF is now met by local supply, much of it from smallholders. With respect to sub-Saharan Africa, United Nations projections are that the rural population share in Africa will remain high for decades, providing a labour base for the smallholder sector to dominate agriculture; this is unlike much of Asia where the rural population has peaked, and farm sizes have already increased substantially due to consolidation. Africa's evolving demography and land:labour ratios therefore imply both falling farm sizes (Masters *et al.*, 2013) and a long-term opportunity for smallholder agriculture.
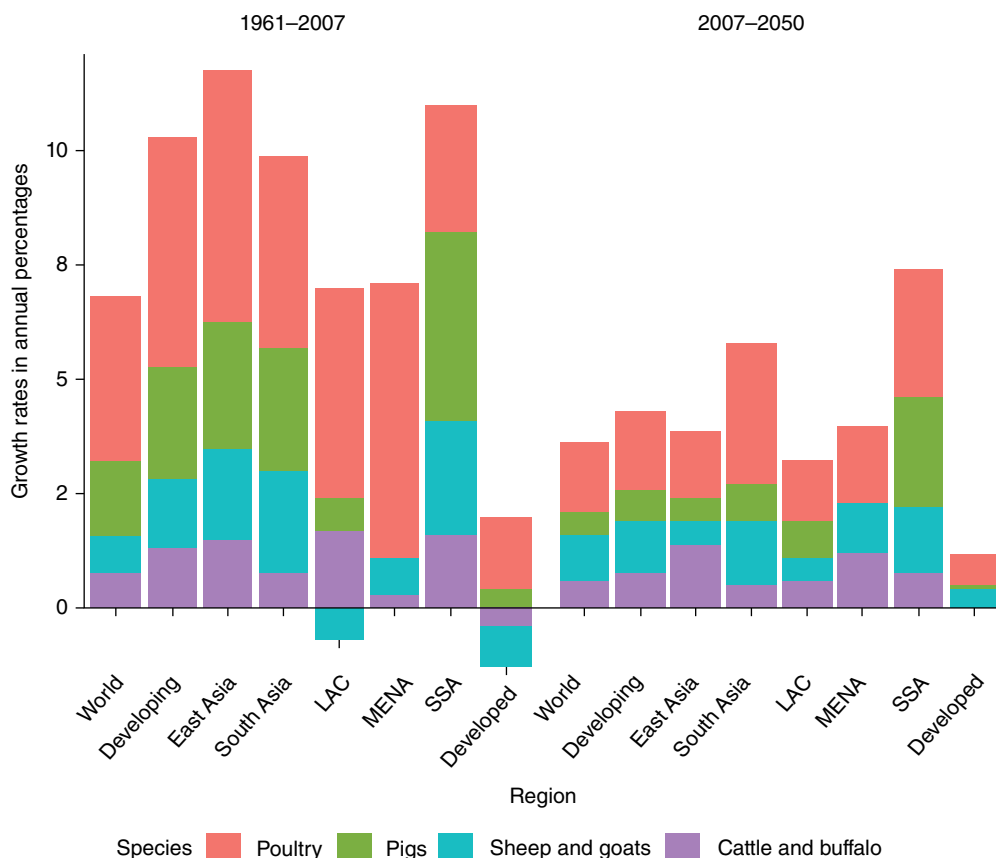
Fig. F.5. Growth rates of animal numbers by period, region and species, 1961–2007 to 2007–2050. Rates for 1961–2007 are estimated from historical data; numbers for 2007–2050 are projected from a world agricultural model. LAC, Latin America and the Caribbean; MENA, Middle East and North Africa; SSA, sub-Saharan Africa. (Data from Alexandratos and Bruinsma, 2012.)

Meeting growing ASF demand in sub-Saharan Africa and achieving the region's ASF export potential implies several research objectives for ILRI. The first is to develop genetic, health and feeding improvements to lower production costs in ruminants for small and medium farmers; Chapters 1–9 (this volume) show the important progress in animal health and genetics made at ILRI to date. The second is to develop genetic and health improvements in monogastrics for all enterprise scales, given the likely continued global trend towards larger production units in monogastrics. The third is to identify policy and infrastructure barriers to agricultural production

generally, given the growing integration of crop and livestock production at all scales. A fourth objective is to reduce the environmental costs of livestock production, processing and marketing.

Livestock and resource use

Labour

Employment is a major policy problem in Africa, particularly among the young, where the 15–24-year age cohort represents 19% of the population (United Nations Economic Commission
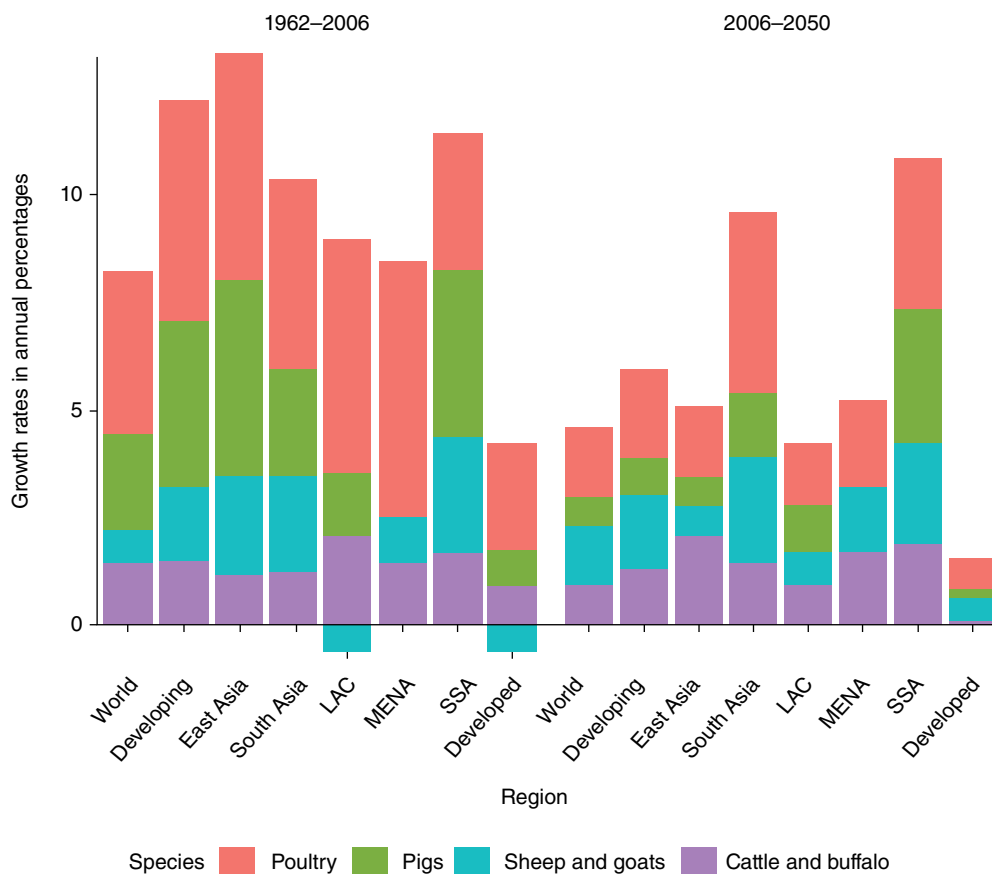
Fig. F.6. Growth rates of animal carcass weights by period, region and species, 1962–2006 to 2006–2050. Rates for 1962–2006 are estimated from historical data; rates for 2006–2050 are projected from a world agricultural model. LAC, Latin America and the Caribbean; MENA, Middle East and North Africa; SSA, Sub-Saharan Africa. (Data from Alexandratos and Bruinsma, 2012.)

for Africa, 2016, pp. 17–18). Labour-intensive agricultural production, including livestock, has substantial rural job creation potential in Africa where demand for new employment is high for demographic reasons. To the extent that growth of livestock production occurs in more labour-intensive segments – dairy, pigs and poultry – as is projected to be the case in sub-Saharan Africa, then animal agriculture, including processing and marketing, will promote labour use.

Land

Livestock use land directly, as pasture, and indirectly, by consuming grain and crop residues. The historical phase of pastureland expansion in Africa, the Middle East, South Asia and East Asia

is largely complete, and hence additional land for pasture in these regions is unavailable. New pasture is available for livestock in Latin America and Central Africa but mainly from forest land conversion, which has unbearable costs in GHG emissions and would therefore not be sustainable.

The historical phase of cropland expansion is nearly complete. Alexandratos and Bruinsma (2012, Tables 4.8 and 4.9 and Fig. 4.3) projected slow global growth in arable land and in its rainfed and irrigated components for 2007–2050. Arable areas of all types will contract in developed nations, expand slowly in sub-Saharan Africa and in Latin America and the Caribbean, and remain roughly constant in the Middle East and North Africa and in South Asia and East
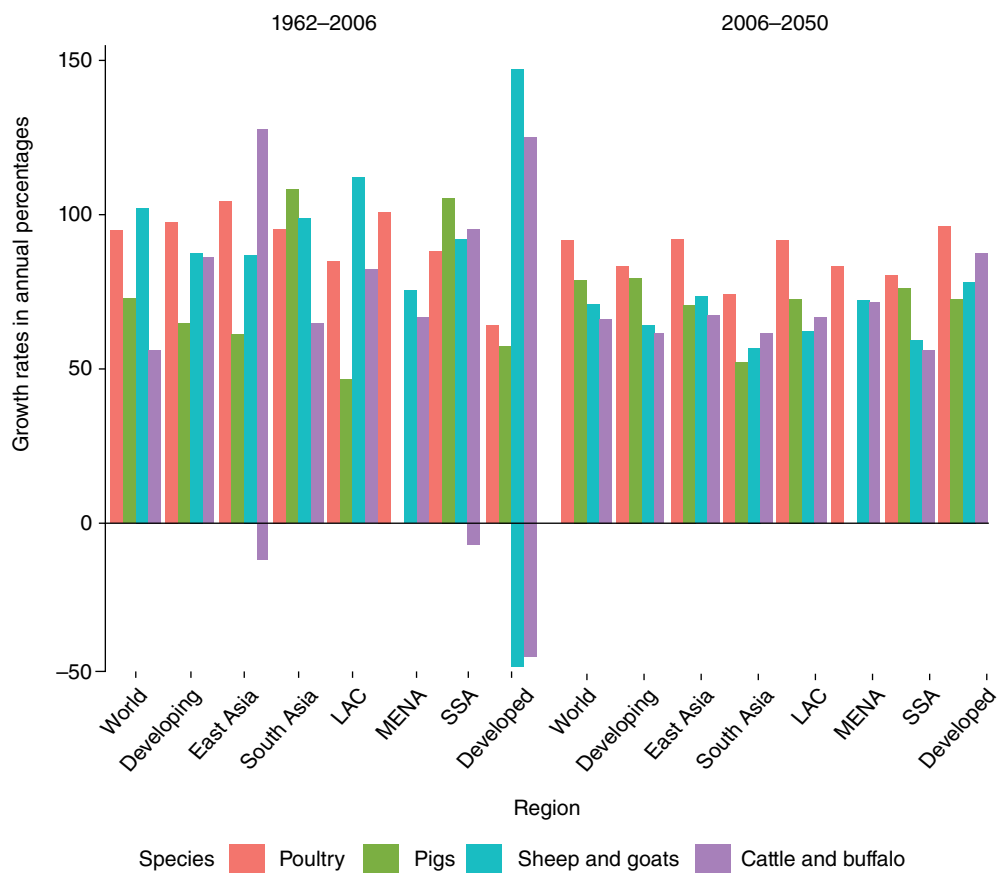
Fig. F.7. Shares of growth rates in animal numbers by period, region and species, 1962–2006 and 2006–2050. Rates for 1962–2006 are estimated from historical data; rates for 2006–2050 are projected from a world agricultural model. LAC, Latin America and the Caribbean; MENA, Middle East and North Africa; SSA, Sub-Saharan Africa. (Data from Alexandratos and Bruinsma, 2012.)

Asia. Arable land per capita will become particularly scarce in developing countries, falling from an estimated 0.19 ha per person in 2017 to a projected 0.14 in 2050. The quantity of cropland for livestock use will therefore contract globally in per capita terms, implying that more intensive use of that land will be necessary. Such increasing land scarcity will, of course, drive an increase in cropping intensity in all regions, but this growth will be limited by rising water scarcity and environmental constraints to irrigation.

One argument in favour of livestock production for food is that it uses resources, such as pastures and crop residues, that do not compete with direct human use. While it is true that most of the dry feed consumed by livestock is now inedible by humans, this is projected to change over time. Long-term projections of grain disappearance imply a shift in developing countries to more feed-grain use (Alexandratos and Bruinsma, 2012, Fig. 3.5) and to less use of pastures and crop residues. Therefore, while ruminants will remain important converters of inedible biomass into high-quality protein for human consumption, the share of edible biomass (i.e. grain and soy) fed to animals will increase in developing nations, where agricultural land is scarcest. Research on intensification of animal production – in essence, research to raise feed:product conversion ratios – will correspondingly become more important.

Environmental costs

The principal global environmental costs of live-stock are GHGs and zoonoses. Assessments across the production cycle of animals indicate that some 14.5% of global GHG emissions are attributable to livestock (see Chapter 16, this volume). The developing world contributes 75% of global GHG emissions from ruminants and 56% of emissions from monogastrics (Herrero *et al.*, 2013). The shares attributed to the developing world will rise if productivity per animal in the tropics does not rise, as it has done in the developed world (Capper *et al.*, 2009, for dairy; Capper, 2011, for beef). Research on the global environmental costs of animal production will become increasingly important given expected human and animal population growth; land competition among animals, crops and trees; and the projected long-term growth in the global carbon burden.

Zoonoses are diseases that are transmissible between humans and animals through direct contact or from food, water or the environment (see Chapters 8 and 9, this volume). Perhaps 60% of all human infectious diseases and as many as 75% of emerging human infectious diseases are zoonotic. Zoonoses sicken several billion people each year and kill millions, mostly in low- and middle-income countries; one estimate is that emerging zoonoses cost around US$7 billion a year (World Bank, 2012). Global syntheses of the impacts of zoonotic diseases, led by ILRI, estimated that in least-developed countries, 20% of human sickness and death was due to zoonoses or diseases that had recently jumped species from animals to people (Grace *et al.*, 2012). The risks of zoonoses in the tropics or originating in the tropics, including those with pandemic potential, will rise as human and animal populations expand. Expanded research on the animal aspects and the epidemiology of zoonoses will become increasingly important for ILRI and its collaborators. The 2020 coronavirus pandemic has made this work even more urgent at ILRI, which has long experience with zoonoses.

Livestock and Global Development Goals

The research and development challenges of today are more complex than when ILCA and ILRAD were created, in part because of new expectations from the world community. The original CGIAR mandate was to produce more food through generating technologies as international and regional public goods. That mandate subsequently expanded to include poverty reduction, embodied in ILRI's theme in the early 2000s of 'Pathways out of Poverty'. The 'new expectations' include participation in achieving the global Sustainable Development Goals. Figure F.8 indicates the potential contribution of livestock research and development to the 17 Sustainable Development Goals (www.un.org/sustainabledevelopment/sustainable-development-goals/; accessed 11 March 2020). The priorities of ILRI would be organized around livestock's role in meeting global goals in five domains: (i) food and nutrition security; (ii) human health; (iii) climate change; (iv) livestock and natural resources; and (v) prosperity and growth with equity.

Priorities for ILRI's Research in the Next 10 Years

Livestock and food and nutrition security

Global evidence suggests that higher agricultural productivity and food availability do not necessarily improve food and nutrition security. Randolph *et al.* (2007) reviewed the three potential pathways along which livestock can strengthen food and nutrition security.

- One is the own production to own consumption availability pathway, in which household consumption of ASF increases through own production, as shown empirically by Hoddinott *et al.* (2015) in rural Ethiopia. While greater own production of ASF should lead to greater consumption, existing studies give mixed results about this pathway, and the reasons for the differences are not clear.
- A second is the income/wealth access pathway in which incremental animal production results in new sales, new income and new food purchases. Research on the access pathway is the study of livestock value chains, which provide employment

Fig. F.8. Contributions of livestock to the 17 Sustainable Development Goals (SDGs).

17 Partnership for the goals
- Stateholders of the livestock sector have come together to form the Global Agenda for Sustainable Livestock and recognize the UN SDGs in their strategy

16 Peace, justice and strong institutions
- Numerous conflicts in areas where access to land creates tensions between communities (e.g. pastoralists)
- Livestock can also be a threat to biosecurity

15 Life on land
- The major part of land is used for livestock
- Livestock contribute to biodiversity losses through impacts on habitats, LUC, water, land-use change, soil pollution, grassland species, etc.
- They also contribute to preserve biodiversity and domestic animals are part of biodiversity

14 Life below water
- Livestock use large amounts of fishmeal, which leads to overexploitation of marine resources and losses of biodiversity
- Eutrophication and hypoxic water conditions

13 Climate action
- Poor livestock keepers are among the most vulnerable to climate change.
- Livestock are responsible for a significant share of GHG emissions but have large mitigation potential, including through soil carbon sequestration in grasslands

12 Responsible consumption and production
- Wastes and losses along livestock supply chains are high
- Rebalancing diets and the share of animal products can contribute to sustainability and health

11 Sustainable cities and communities
- Hundreds of million of people in cities keep livestock
- Benefits for food security, nutrition, jobs creation
- Potential threat to health and sanitation
- Supports rural–urban linkages

10 Reduced inequalities
- Livestock are a source of income, create employment opportunities and provide market participation to poor rural households

1 No poverty
- Many rural poor rely on livestock
- Livestock provide three major pathways out of poverty: (1) securing assets, (2) improving productivity and (3) increasing market participation

2 Zero hunger
- Food (energy and high value protein)
- Traction and fertilizer for crop production
- Income

3 Good health and well being
- Essential micronutrients, especially for children, women and the elderly
- Majority of animal diseases could cause human pandemics
- Use of antimicrobial expected to rise in livestock
- Diseases limit livestock productivity

4 Quality education
- A healty diet is key to learning capacities (e.g. school milk programs)
- Livestock provides income, which supports education

5 Gender equality
- Majority poor livestock keepers are women, especially with small ruminants and poultry
- Women have less access to resources (land and capital)

6 Clean water and sanitation
- Livestock use large amount of water
- They are source of water pollution (e.g. nitrates)
- Water contaminated by livestock causes hygene problems
- Livestock can contribute to protect water quality

7 Affordable and clean energy
- Livestock are an energy sink and source
- Recycling animal manure (e.g. biogas) provides an alternative to fossil fuels or wood

8 Decent work and economic growth
- 40% of agricultural GDP is provided by livestock
- The sector is growing at a fast rate
- High rate of child labour and occupational hazards

9 Industry, innovation and infrastructure
- Many depend on livestock, including from jobs provided in the value chain (feed, processing, retailing)
- Small scale livestock keepers lack market access and inclusion
- Livestock products are mainly consumed locally and marketed informally

and income to allow the purchase of nutritious foods.

- A third pathway follows incremental local sales of livestock products, which increase the availability of ASF for households that are not rural or that do not keep animals. This is the dominant path in developed countries and will become more important with growth and urbanization in developing countries.

A major gap in knowledge is the extent to which these pathways are important in different contexts. Until we have this understanding it will be difficult to design interventions and policies to optimize the contribution of livestock to nutritional security in different settings. Therefore, ILRI will work to understand the drivers of food choice through the different pathways. We will investigate, for example, what drives decisions on consumption of ASF within producer and consumer households; where and under what circumstances the different pathways operate, including when livestock production within the household increases; and what incentives are needed to modify/increase consumption. ILRI will develop new methods for estimating the intake of ASF and the minimal levels required for vulnerable groups.

A related research domain is the mitigation of the adverse consumption effects of ASF. Research to mitigate negative effects of ASF consumption will focus on food-borne disease, zoonotic diseases under the umbrella of OneHealth, and equitable consumption of ASF globally.

Livestock health

ILRI's lifetime programme has seen major changes in the tropical animal health sciences. ILRI and its predecessors, ILRAD and ILCA, have made major scientific achievements in animal genetics (Chapter 1, this volume), the control and management of trypanosomiasis (Chapters 2 and 3, this volume), the elucidation of problems in immunology and immunoparasitology in cattle (Chapter 4, this volume), the control and management of East Coast fever (ECF; Chapters 5 and 6, this volume) and vector biology (Chapter 10, this volume, on ticks), while launching novel

investigations of food safety, transboundary diseases and zoonoses (Chapters 7–9, this volume).

We can identify four evolving trends in livestock health that will influence ILRI research priorities in the coming decade (Perry *et al.*, 2018).

The first trend is new problems. Emerging and other zoonotic diseases are likely to have large consequences for human health and livelihoods. Illnesses from ASF, such as contaminated milk, meat and eggs, can cause significant morbidity and mortality. The growth of antimicrobial resistance, which is arguably a result of misuse of antimicrobials in people and in animals, can make some human infections hard or even impossible to treat (see Chapters 7–9, this volume). ILRI has consequently expanded research in these areas, as described in the section on 'Livestock and human health' below.

Second, technological advances have revolutionized our ability to detect, diagnose, cure and prevent animal diseases. Some of these technologies are health specific (e.g. lateral flow diagnostics), while others are novel applications to health problems (e.g. disease reporting via advanced mobile-phone applications). ILRI and its Biosciences eastern and central Africa (BecA) Hub operate platforms for disease detection, and ILRI is studying cutting-edge technologies such as metagenomics (the study of genetic material recovered directly from environmental samples) and phenomics (the study of phenotypes), while exploring other platforms to deliver animal health services and to control antimicrobial resistance in pathogens.

Third, a warmer, wetter world will very likely be a sicker world. Vector- and food-borne diseases are highly climate sensitive, and their distributions may alter dramatically if climate change causes major ecosystem disruptions. One likely outcome of climate change is the further extension of disease vectors and tropical diseases into temperate climates, which may spur greater investment in tropical animal disease research.

Lastly, animal health constraints are increasingly addressed through a systemic, 'holistic' lens rather than through a 'single disease perspective'. This multi-disease, multidisciplinary approach has necessitated stronger partnerships among ILRI health, gender, environmental and economic scientists. This systemic approach includes the ethical treatment of animals.

We expect these trends – greater understanding of the relationships among livestock, human health and livelihoods; innovations from research; interactions among climate change, crops, land use and animals; and a new systemic approach to animal health management – to orient ILRI priorities. In light of these trends, ILRI's future livestock health research will focus on: (i) a 'herd health' approach; (ii) transboundary animal diseases; and (iii) developing vaccines and diagnostics for specific diseases.

Herd health

The reasons for poor herd health in the tropics include inadequate husbandry, lack of inputs, poor knowledge of disease prevention and management, and environmental disease pressure created by tropical conditions. Herd health research at ILRI will work to understand the impacts of diseases (both infectious and non-infectious) in small- and medium-sized farms and herding households, and to develop and test interventions to prevent and control disease.

Whereas early ILRI (ILRAD/ILCA) research focused on diagnosis and control of specific diseases (especially ECF and African animal trypanosomiasis), the institute has broadened its approach to investigate co-infections in animals and syndromes such as perinatal deaths rather than investigating individual diseases such as brucellosis or toxoplasmosis.

ILRI's attention is now expanding to include intervention delivery. Many vaccines and other animal health treatments remain on the shelf because insufficient attention has been paid to providing access to them for poor farmers. For example, cheap, effective, thermostable vaccines exist for Newcastle disease virus, often the worst killer of village poultry, yet uptake of the vaccine in village systems has been limited and dependent on transient animal health projects. In future, we will increasingly prioritize animal health challenges in different systems and contexts and develop and test appropriate packages of herd health interventions for different contexts. We will look at how these can be tailored for specific livestock keepers (e.g. the differential access to vaccines by men and women and the differential benefits they derive) and how these can be delivered by public and private agents.

Transboundary animal diseases

Many animal diseases are best understood and managed at ecosystem or regional rather than local levels. Among such afflictions are transboundary animal diseases (see Chapter 7, this volume), which are both transmissible and highly contagious. They can easily spread and quickly become epidemic where control, management or exclusion require costly cooperation among countries. Transboundary diseases have been the main preoccupation of veterinary health services in low- and middle-income countries, and while emphasis on herd health has rightly grown, transboundary diseases remain important constraints to livestock production. ILRI's work on transboundary diseases will involve global collaboration for their progressive control. ILRI will support trade that benefits poor producers by developing and testing new innovations for better control of these diseases.

Diagnostics and vaccines

Vaccines and diagnostics are as important to animal health as they are to human health and have been central to ILRI research since the 1970s. Diagnostic tools play a critical role in understanding infection and epidemiology, monitoring disease, discovering pathogens and developing control strategies. In tropical countries, there is a need for more specific, sensitive and field-adapted tests for livestock diseases. Some low-technology applications have potential for controlling livestock diseases, such as implementing biosecurity protocols, although ILRI research has shown how difficult this is in smallholder systems. In general, reliable diagnostics and effective vaccines represent the most sustainable and cost-effective solutions to preventing specific diseases, especially in under-resourced agricultural systems. Although vaccines are available for many infectious diseases, many are unsuitable for use in developing countries due to high cost or unreliable supply. In such cases, policy

and market changes could increase the use of livestock vaccines and other products to improve herd health. In some cases, vaccines used in the developed world exhibit limited efficacy against pathogen variants present in tropical climates. Current knowledge allows veterinary companies to rapidly respond to some livestock disease emergencies, such as Schmallenberg virus and bluetongue virus. Good manufacturing and vaccine-production facilities are needed in developing countries to meet such needs and to supply vaccines in suitable formats for use in diverse situations, such as thermostable vaccine formulations for regions where use of a cold chain is problematical.

Combining new tools in vaccinology in 'difficult-to-make' vaccines can ultimately benefit the most people. These tools can be used: (i) to monitor and map immune responses to infection and immunization; (ii) to identify candidate vaccine antigens; and (iii) to redesign vaccine antigens and immunization methods to increase their efficacy.

Deep sequencing and gene-expression profiles are leading to maps that describe networks of innate and acquired immune responses in disease and health. Mapping antigen epitopes has given rise to algorithms that can predict antigenic determinants. Peptide–major histocompatibility complex tetramer technology to track and characterize antigen-specific T-lymphocytes is now available for veterinary research. Synthetic antibody libraries and tools to engineer antibodies with desired properties are revealing their value for both therapeutic vaccines and diagnostic purposes. Crystal structures of antigens are providing clues on how they can be manipulated to serve as superior antigens. The realm of adjuvant research is offering guidelines on their use to skew immune responses towards desired responses. Collectively, these approaches will find greater utility in characterizing immune responses to infection or to vaccination and in defining *in vitro* correlates with immunity, significantly reducing the time needed to attack neglected diseases.

ILRI will continue to work on research to develop novel vaccines or methods for the control of African swine fever, contagious bovine pleuropneumonia, contagious caprine pleuropneumonia and ECF. Other diseases of interest will include foot-and-mouth disease, malignant catarrhal fever, peste des petits ruminants, Rift Valley fever, and tick-borne haemoparasitic pathogens and their tick vectors.

Animal welfare

ILRI constantly seeks to improve the welfare of animals under its direct and indirect care and has done much to improve animal health, which, by necessity, improves animal welfare. However, ILRI has done little as yet on other aspects of animal welfare. Animal welfare is an economic as well as an ethical issue because it involves other aspects of livestock development, such as animal housing, processing and management. ILRI is exploring win–win interventions that improve animal welfare as well as productivity and efficiency.

Livestock genetics

ILRI's genetics programme has applied a dual strategy of characterizing population diversity per se for the purpose of understanding the relationships and origins of different ecotypes, while parallel studies have addressed individual genes or traits of interest (reviewed in Chapter 1, this volume). The intersection to date between the population and individual approaches has been in the use of population studies to detect regions or alleles under selection in order to validate candidates derived from trait-specific studies such as trypanotolerance (see Chapters 1 and 2, this volume).

The population and individual approaches will be joined more closely as sequencing and informatics technology advance. For example, the African Dairy Genetic Gains (ADGG) programme and its predecessors initially used single-nucleotide polymorphism analysis to determine breed composition of individual cattle and to generate genomic relationships, where pedigree records did not exist. These relationships were then used with phenotypic and pedigree data to derive genomic breeding value predictions. Valuable though such predictions are, they tell us little about genome function. As ADGG data accumulates it will generate insights into regions of the genome controlling important functional genetic variation, which coupled with other studies could allow

functional genetic variants to be identified and used in future. This approach has started to approximate the livestock landscape genomics studies envisioned in the 1990s. We are now beginning to integrate geographic, phenotypic and genetic characteristics to allow detection signals for heat tolerance, for example, and to link these signals to genomic make-up. These data will soon be complemented by targeted investigations at ILRI's Kapiti Research Station and the Addis Ababa poultry facility, which offer controlled environments for the calibration of field observations.

This wealth of information will be transformational. We look forward to a new and much more integrated approach in which genetic hypotheses are raised from populations, tested in the laboratory and returned for validation in the population. Such an approach allows modelling of the possible impact of a given genetic intervention, which in turn allows prioritization of such interventions. This integrated approach is built into a livestock genetics strategy, which envisages three phases: (i) targeting, (ii) gene discovery, and (iii) delivery.

The targeting phase exploits information about the sensitivity of populations to a particular environmental pressure to predict the potential values of adaptations. For example, studying the impact of thermal stress on milk production allows us to consider the diversity and heritability of response in existing populations, to consider the introduction of new variants, including by genome editing, and to model the effects on productivity, interactions with the value chain, and environmental impact. Similarly, modelling the impact of trypanosomiasis allows quantification of the consequences of introducing trypanotolerant or resistant cattle, or the prediction of climate-change effects.

The gene-discovery phase follows in a close cycle between field and laboratory data to understand the genetic basis of a targeted trait. Information from other species and related traits can be used to identify fruitful variants. This is a process that relies on bioinformatics and comparative sequence data to explore pathways as well as on traditional mapping studies and laboratory work used in earlier studies to map regions of the genome associated with trypanotolerance. Such studies might identify variants already in the population at sufficient frequency to be exploited by means of marker-assisted selection, rare variants or variants absent from the target population, in which case genome editing becomes a possible mechanism for delivery, or genes or variants absent from the target species, in which case more substantial genetic modification becomes a likely tool. There are examples of all three types of variant already under study today.

In all the genetic studies, it will be necessary to consider the possibility of unexpected pleiotropies (when one gene influences two or more seemingly unrelated phenotypic traits). An unambiguous win–win from a particular genetic intervention that nature and thousands of generations of livestock keepers have not discovered might seem unlikely and we might expect to see downsides from attempts at 'improvement'. However, the simple fact that current performance is primarily limited by feed, water, disease and management suggests that we have an opportunity for very significant, absolute improvement in performance through improved genetics combined with a modified environment in the form of better husbandry.

The final and most difficult phase is delivery. This requires exploration of links with farmers, artificial insemination providers, commercial breeders and many other value-chain agents. Our approach to this has been to use mobile technologies to collect the raw information needed, for example to plan improved breeding systems. In return, we offer management information, training and links to input providers and markets to the farmer. There is thus a short-period cycle of information between farmers and researchers within the delivery component, while the same data form part of a long-term cycle involving the targeting and gene-discovery phases of the model.

ILRI's livestock genetics programme thus looks to a future that builds on wide genetics and genomics expertise and on unique field experience while using modern informatics to create an integrated view of performance. It also seeks to understand the broader social and economic context for which we are 'designing' livestock and to ensure the sustainable and equitable transformation of animal agriculture in the 21st century.

Livestock feed and forages

Lack of quality feed has constrained livestock productivity in the mixed and pastoral systems

of the tropics (see Chapters 11–14, this volume). The feed constraint will tighten with evolving climate change and with greater land scarcity. Increased demand for cropland will further reduce grazing areas and leave remaining grazing lands at risk of degradation. The growing scarcity of grazing will require an additional research effort on crop residues and on planted forages.

Crop residues will provide the main feed in mixed systems (see Chapters 11, 13, and 14, this volume), given the constraints to grazing resources. Research over the past two decades has shown that genotypic variation in fodder traits can be captured to improve feed quality without loss of grain yield and quality (see Chapter 14, this volume). With perhaps 50 billion t of cellulosic biomass annually produced globally, the opportunities for leveraging investment in second-generation biofuel technologies could be a turning point in converting lower-feed-quality biomass into higher-value feeds. ILRI is exploring with partners the business models that would allow these technologies, which break the lignocellulose bonds in plant cell walls to release their sugars, to be exploited.

Planted forages are an important source of livestock feed after crop residues, despite historical disappointments with planted forages in the tropics (see Chapters 12 and 13, this volume, and the meta-analysis of White *et al.*, 2013). The challenge will be to meet new feed demands on a narrower land base without damaging the land resource or destroying biodiversity, and while seeking to overcome past failures with planted forages in tropical and subtropical environments. A focus of new research will be to understand the biotic and abiotic reasons for slow adoption of planted forages on small farms in the semi-arid and subhumid tropics.

There will be two broad areas of feed work: (i) improvement of feed systems and (ii) improvements of feed materials.

Improvement of feed systems includes enhanced targeting of simple technologies, commercialization of forage seeds, better postharvest processing, and application of new feeding methods under local conditions. Considerable effort has been invested in promoting livestock feed interventions using blanket approaches, which failed to recognize the various agroeco-

logical and socio-economic conditions across developing countries (Sumberg, 2002). ILRI will lead this effort by characterizing feeding systems to enable prioritization of options based on an understanding of local and regional constraints.

Feed and forage research will include the following:

- Work using new genetic tools on plant productivity.
- The Feed Assessment Tool (FEAST; https://www.ilri.org/feast; accessed 11 March 2020), which can be used to estimate feeding constraints and options to relieve them (see Chapter 13, this volume).
- Defining feed options based on expert knowledge, national survey and census data, and global comparators.
- Mainstreaming near-infrared spectroscopy analysis as a default platform for feed analysis as an extension of historical work on the feed value of multi-purpose crops (see Chapter 14, this volume).
- Optimized feed strategies and sourcing.
- Reduced cost of feed and improved feed value-chain function.

Plant improvement of feed and forages

New tools in molecular genetics and genomic technologies, together with high-throughput phenotyping capabilities, offer rapid, accurate and cost-effective methods to quantify traits, allowing the capture of genetic diversity in plants that can be used for feed. These advances have been widely applied to crop improvement and offer the opportunity for new approaches to enhance the quality and performance traits of concentrate feeds, planted forages and crop residues.

Opportunities to capture the genetic diversity of crops have been revolutionized by advances in genomics and automated phenotyping. ILRI research will use these and other advances to enhance relevant traits in planted forages and crop residues. These advances offer new approaches to enhance the performance traits of both feeds and forages at a relatively low cost, including targeting improved agronomic performance by tapping the genetic variation in ILRI's forage gene bank and partner collections (see Chapter 12, this volume).

There is inadequate information on genetic diversity, genetic maps and genome sequences for feed crops. ILRI will therefore seek to develop a platform of genomic and other biological technologies integrated into a forage improvement programme, including, as set out for animal genetics above, genomic selection and genome editing. The work will generate superior cultivars of planted forages to be disseminated by public and private partners. Enhanced multidimensional crops will be made available with the same wide collaboration.

Reduced cost of feed and more efficient feed value chains

Feed is the largest single cost in most livestock enterprises. Work to reduce costs will include the development of approaches for rapid economic appraisal of feeds. We will also develop a data collection and analysis framework to calculate the cost:benefit ratios for individual feed technologies already identified by the FEAST tool, and we will pilot-test candidate technologies to ground-truth cost–benefit analyses (see Chapter 13, this volume).

Lack of good-quality seed constrains forage development. ILRI will address this by building on recent research in Ethiopia that piloted development approaches to seed supply. This will involve developing local capacity in seed and forage production, as well as testing new approaches for the promotion, sales, and marketing of forage seeds (especially in small quantities for smallholders) and clarifying the roles of the public and private sectors. ILRI will also support seed certification and seed-quality programmes for the forage sector in target countries.

A further area of work will focus on feed quality analysis/certification. Farmers are often reluctant to buy feed supplements and complete feeds for ruminants because of uncertain quality and distorted feed quality-price relationships. This work will be used to promote livestock feed options based on their costs and benefits. Finally, we envision feed producers branding products with quality marks based on certification support originating in ILRI.

The prioritization of feeding options will build on developments of FEAST and the Tropical Forages Tool (TFT). FEAST and TFT are already in widespread use (see Chapter 13, this volume), so the future emphasis will be on assessing their efficacy in feeding strategies. A further strand of research will assess wide-scale feed supply and demand to investigate options for improved feed sourcing and to support national decision making for improved feed supply. One such tool is FEEDBASE, which constructs feed supply-and-demand scenarios from secondary data sets of cropping patterns, land-use patterns, and livestock census. Initially established in India, FEEDBASE has now been developed for Ethiopia, based on more than 60 districts in the country, and there are plans for tests in Malawi, Mali, and Vietnam.

Optimized feed strategies and sourcing

Feed demand-and-supply scenarios provide an important tool to support rational decisions around investments in livestock and feed and fodder value chains at local levels as well as policy decisions at higher levels. These scenarios can: (i) identify hotspots of feed surplus and deficit areas; (ii) identify priorities for investment in feed resources, considering projected national targets; and (iii) quantify feed-dependent yield gaps in livestock productivity. Work will involve locating and matching suitable secondary data sets to estimate feed availability from data sets on cropping (crop residues, by-products and grains), land use (pasture, common property, forests, and planted forages) and location of agro-industries to calculate feed supply. Feed demand will be estimated using data sets on livestock populations and distributions combined with calculations of animal maintenance, production, and reproduction. Work will also involve ground-truthing scenarios using project findings and direct surveys and inventories of feed resources and demand. We will develop interactive web, tablet, and phone-based feed demand-and-supply tools for use by different stakeholders. We also envision livestock line departments, non-governmental organizations, and private companies using ILRI's feed supply-and-demand scenarios to inform national and subnational decision making around livestock feed development.

Livestock and human health

Work on livestock and human health fits within a framework of OneHealth, defined as

multidisciplinary collaboration to attain optimal health for people, animals and the environment. Under the umbrella of OneHealth, ILRI's research on the links between livestock and human health will proceed under four rubrics: (i) food-borne disease; (ii) emerging zoonoses; (iii) neglected zoonoses; and (iv) antimicrobial resistance associated with farming.

Food-borne diseases

Food-borne disease was a minor topic in ILRI's early years but in recent years has risen rapidly in the global health agenda (see Chapter 9, this volume). A recent global assessment of the health burden of food-borne disease found that it was comparable to that of the 'big three diseases' – human immunodeficiency virus/acquired immune deficiency syndrome (HIV/AIDS), malaria, and tuberculosis (Havelaar *et al.*, 2015). Food consumers are increasingly concerned about food-borne disease: in several countries it ranks as their single highest concern (Grace, 2015). Current evidence indicates that ASF is responsible for most food-borne disease (Hoffmann *et al.*, 2015) and that the economic burden of food-borne disease is high, but national data are lacking. While most communicable diseases are declining, it appears that food-borne diseases may worsen as a result of agri-food system transformation in low- and middle-income countries, making food-borne diseases increasingly important and relevant to development.

A first step is to generate data on food-safety priorities, based on the human health risks of food-borne diseases and their economic burdens. ILRI research has helped to disclose an underinvestment in food-borne disease research. In Africa alone, around US$2.4 billion is invested in the 'big three' (malaria, tuberculosis, and HIV/AIDS) each year compared with around US$40 million in food safety, an imbalance that is not likely to change soon.

Risk management follows risk assessment. A recent assessment carried out by the Global Food Safety Partnership (GFSP) in collaboration with ILRI concluded that many previous food-safety investments were poorly aligned with public-health priorities. Their work estimated that in sub-Saharan Africa between 2010 and 2017, approximately 80% of all food-safety projects were focused on three areas – national food-safety control systems, aflatoxins and pesticide residues – yet the public-health benefits of these investments were hard to determine (Alonso, 2019).

ILRI has been a leader (see Chapter 9, this volume) in generating evidence for new food-safety priorities. We believe the following will become more important:

- Understanding the presence, prevalence, and risk factors associated with food-borne disease.
- Identifying food-safety risks in informal markets, where most of the poor trade and where the heaviest burden of food-borne disease is felt.
- Quantifying the health and economic burdens of food-borne disease.
- Exploring relationships among food safety, gender, and nutrition.
- Discovering, developing, and testing technologies to mitigate hazards, or improving their detection and removal.
- Testing the 'triple approach' to food safety – regulation, capacity, and incentives for behaviour change.

Emerging zoonoses

Diseases that jump from other species to humans, known as zoonoses, are a relatively new area for ILRI (Grace *et al.*, 2012). Some 75% of new human infectious illnesses are classed as zoonoses. Domestic animals are involved in some zoonoses with the highest pandemic potential. As the spread of COVID-19 is showing, human pandemics are one of the highest ranked global catastrophes in terms of probability and impact and yet are among the most predictable and preventable catastrophes. Livestock pandemics can also result in widespread human misery and animal suffering, especially in communities dependent on livestock.

We will continue to work on high-priority zoonotic diseases with a livestock interface and pandemic potential, including highly pathogenic avian influenza, Rift Valley fever, Middle East respiratory syndrome, and animal aspects of Ebola. We will further develop tools for mapping and targeting the risk of zoonotic disease, modelling

zoonotic pandemics, forecasting short-term disease risks, developing and testing surveillance systems, crafting decision-support methods, and advising on vaccination strategies. We will also assess the impacts and costs of pandemics and the benefits of their prevention.

Neglected zoonoses

While emerging diseases often receive the most attention, neglected zoonoses continue to exact a high toll on poor consumers and poor livestock-keeping communities. Among the 'unlucky 13' zoonoses responsible for millions of deaths and billions of illnesses each year are brucellosis, cysticercosis, and tuberculosis (Grace *et al.*, 2012). Most neglected zoonoses are highly amenable to progressive control: we plan to support this through the development of tools for assessing, managing, and evaluating control of neglected zoonoses. Cysticercosis, caused by the pig tapeworm, *Taenia solium*, has been identified as a priority neglected zoonosis because of its high burden and high potential for control and will be an immediate focus for ILRI, which has already contributed to a roadmap for its progressive eradication, led by the World Health Organization.

Antimicrobial resistance

Antimicrobial resistance is a special case of an emerging disease (Grace, 2015). Recent years have seen rapidly growing numbers of failures of previously effective drugs to treat human infectious diseases. The use of antimicrobials in agriculture may have contributed significantly to these failures of medical treatment, suggesting that a OneHealth approach to managing the rise in antimicrobial resistance in pathogens is appropriate. ILRI is developing tools for mapping, measuring and mitigating antimicrobial use globally. This includes work to develop vaccines and other alternative means of controlling livestock disease. The goal of ILRI's antimicrobial resistance research is to develop, test, and evaluate interventions to mitigate antimicrobial resistance risks in livestock value chains. ILRI will increasingly support judicious policies on antimicrobial resistance and national action plans and capacity-development programmes. This work will be operationalized through the CGIAR Antimicrobial Resistance Hub, launched at ILRI in Nairobi in 2019, to influence the development agenda on antimicrobial resistance issues.

Livestock and climate change

For nearly 20 years, ILRI has contributed to the scientific understanding of livestock and climate change (see Chapter 16, this volume) in three areas – livestock-based climate-change mitigation, adaptation, and policy. The main findings of this work were as follows:

- Climate-change mitigation requires greater focus on results in tropical conditions and must rely less on direct transfer of models from Organisation for Economic Co-operation and Development (OECD) situations, implying more empirical study of environment–animal–climate interactions.
- Adaptation of livestock production to climate change requires a broader view of its impacts. This demands a greater effort on the tropical problems of heat stress and animal performance, livestock reproduction under heat stress, and livestock and forage pests and diseases that do not exist in temperate climates or which will expand more aggressively in the tropics.
- Climate-change policy recommendations from agricultural research require a much closer integration of supply-and-demand modelling and a much more realistic use of feasible policies and their likely outcomes.

Mitigation

Global research has established the climate change mitigation potential of technical changes in animal production systems. The best understood systems are dairying and beef, which account for nearly 70% of GHG emissions (Gerber *et al.*, 2013, p. 18) from livestock supply chains. Gerber *et al.* (2011) studied intensive dairying in a temperate climate and estimated mitigation gains from technical changes in feed, genetics, and health. This work found that the potential to reduce GHG emission intensity, defined as GHG emissions per unit of product, in tropical systems is large due to the current low productivity

per animal, but the scientific potential to reduce emissions from beef cattle in the tropics is not well established (see Chapter 16, this volume).

The future of climate-change mitigation research at ILRI is: (i) to estimate potential mitigation gains in less-well-studied systems, such as extensive beef raised on tropical pastures and intensive meat production on tropical mixed crop-livestock systems so that we are not reliant on estimates from temperate regions; (ii) to identify the sources of these gains through improved feed, genetics, health, and management; (iii) to refine estimates of the probability of mitigating GHG emissions by, for example, improving tropical feed-use efficiency; (iv) to identify profitability and social constraints, including policies and gender norms, to potential application of technical gains; and (v) to extend field tests under tropical conditions of actual emission levels and possible reductions.

Adaptation

Climate-change adaptation requires a broader view beyond technical change, including changes in behaviour, institutions, and cultures. Priority areas for adaptation are the following:

- Understanding the genetics of climate adaptation in domestic livestock.
- Improving technical and institutional support for rangelands to promote their sustainable management.
- Improving capacity for surveillance of climate-sensitive diseases, coupled with new diagnostics for testing for these diseases.
- Testing and disseminating perennial forage species adapted to hotter and more variable climates.
- Developing decision-support tools to target agricultural adaptations and to monitor their impacts on production, adaptive capacity and the environment.
- Developing measures of adaptation success. Adaptation cannot be observed directly because it is a synthetic indicator constructed from sets of variables. An approach is needed that combines household enterprise, assets, and poverty measures as functions of governance and policy factors at community and national levels.

Policy modelling

While there is extensive process and agent modelling of climate problems in tropical livestock systems, the literature comparing supply-and-demand policies for climate-change mitigation is limited. Future modelling must involve closer integration of supply-and-demand models, as was done by Weindl *et al.* (2017). The dependence of arid rangelands on livestock demands an extended data collection, research, and policy modelling effort that recognizes that technical options are limited (Herrero *et al.*, 2016). Policies to enable responses to climate change need to consider future uncertainties and system transformations that could affect development goals, such as economic growth, food security, and livelihood maintenance.

While there has been extensive modelling of the interactions among livestock systems and climate, the scope for mitigating livestock's contributions to climate change remains unclear in terms of productivity and income distribution. We will model and quantify climate-change impacts such as on pre- and post-production losses, infectious/vector-borne livestock diseases and animal health costs, costs of loss of productivity (with potential gains in productivity in some areas), the economic disease burden, and implications for public policy and investment. One modelling focus will be on the economic costs of climate change and another will be on policies and investments for mitigation.

Livestock and natural resources

Tropical livestock research recognizes the interactions among agriculture and natural resources in the main production systems. ILRI historically focused on extensive dryland systems (see Chapters 11 and 15, this volume) and intensive mixed systems (see Chapter 15, this volume).

Rangelands research has been reinvigorated by renewed global interest in drylands and pastoral livelihoods. The economic potential of pastoral (and agro-pastoral) production systems depends on research that stimulates rangeland productivity. The key challenges facing productive rangelands remain competition over resources, heightened by increasing conflicts, overuse of

rangeland resources as land fragmentation continues, and the failure of past governance approaches. At the moment, the outlook for rangelands is worrying – as their productivity declines, so does their capacity to sustain pastoral livelihoods.

Various community-based approaches have been tested in rangelands. Evidence of what makes participatory and community-based rangeland management successful is accumulating, but researchers have not yet systematically consolidated this evidence (see Chapter 11, this volume). Evidence is emerging that simple interventions by communities to establish (or re-establish) seasonal grazing patterns can have a quick and significant effect on rangeland condition. To assess the feasibility of rangeland management, however, we need more trials of interventions such as planned seasonal grazing, rangeland rehabilitation, and management of bush encroachment. Cost–benefit analysis of rangeland management must be joined to impact assessments of their economic, social, and biophysical impacts.

Scaling local successes beyond pilot sites often proves challenging, given the costs of resource access, the site specificity of many areas, and the need for flexibility. Validation and dissemination of evidence for appropriate models of governance and technology in diverse communities is thus another priority.

Documentation of the ecosystem services provided by rangelands, including but not limited to carbon sequestration, is sparse. More work to quantify and map these services would allow more careful assessment of investment potential in ecosystem services (IPBES, 2018). Much of ILRI's previous work on ecosystem services focused on wildlife biodiversity. However, carbon sequestration has recently attracted greater interest as an option to offset other GHG emissions. While rangelands offer theoretical potential for carbon sequestration, there is inadequate quantitative evidence about feasible sequestration in arid and semi-arid environments.

For mixed crop-livestock systems, ILRI's environmental agenda will address the impacts of livestock production on soil and water resources. While livestock are often criticized for being heavy water users, eroding soils, and degrading lands, this narrative is based on insufficient data from tropical systems. For example, in the rainfed systems that dominate much of Africa and Asia, the water used to grow fodder crops and for animals to drink is 'green water', which is not diverted from other uses.

ILRI's future mixed crop-livestock system agenda includes the following:

- Measuring livestock's impact on soil, water, and GHG emissions in intensifying mixed systems, which will be the systems that expand most rapidly.
- Testing how livestock can contribute to sustainable water use across landscapes.
- Analysing the contributions of livestock to sustainable agricultural intensification at the landscape level, using a range of data sets, indicators from several different frameworks, and simple trade-off analysis tools.
- Using *ex ante* evaluations of sustainable intensification interventions to pilot interventions, addressing barriers to adoption such as lack of input and output market linkages and lack of incentives to manage soil and water sustainably.

Livestock and prosperity: growth with equity

Markets and consumption patterns are changing dramatically with the growth in demand for livestock products in developing countries. There has been a rise in the share of purchased food in rural consumption – up to 45% in East and southern Africa and up to 70% in Vietnam. Urban centres are no longer the sole food-processing areas, and now more than 50% of food purchased is processed in rural areas in Africa and Asia. As markets transform to meet demand, the 'midstream' of the food-supply chains (e.g. processors, wholesalers, truckers) comprises 40% of the value chain. As incomes increase and tastes change, the types of food demanded are also moving away from traditional staples. In Africa, more than 50% of purchased food is now non-grain, including vegetables and livestock products (Reardon *et al.*, 2019).

This 'quiet revolution' is occurring largely in informal markets, and in the case of livestock is managed by small- to medium-scale agents, many of whom handle live animals, raw products, or locally processed products. Some agents are adding modern, small-scale processing of products such as yogurt, or hygienic packaging

of traditional products, at the same time that larger-scale modern processing, marketing and distribution grow.

These structural changes have important implications for understanding how small and medium producers can participate in the growing livestock markets. Will they be marginalized due to their inability to meet market demands for higher quality or for reliable delivery? What are the market mechanisms and organizations that will allow small to medium agents to participate while meeting increasing demand? What are the policy approaches to allow both women and men to benefit as livestock keepers and as market agents?

The future of smallholders

Despite the fact that smallholders play a large role in livestock supply in many countries, many observers assume that larger-scale production will replace smallholder producers. This assumption is based on the trend towards larger-scale production in developed nations and on the fact that economies of scale are inevitable. The evidence to support these assumptions is mixed. While economies of scale for monogastrics (pigs and poultry) are observable, where low-margin production relies on efficient feeding and on biosecurity best managed by professionals, in contrast, economies of scale are not easily achieved for ruminants, particularly in dairy but also in small ruminants (Delgado *et al.*, 2008). A large part of this reality is due to the fact that for ruminants, smallholders can make use of own-grown fodder and crop residues, communal fodder sources and family labour. These factors are only likely to change when wages rise due to economic growth and so the opportunity costs of labour require its substitution by capital investment, which in part depends on scale to be efficient. The question is thus when and under what circumstances should decision makers and investors prioritize larger production systems over the smallholders who dominate production in much of the tropics.

ILRI will pursue analysis of the conditions in which smallholders remain viable, across different settings and species, particularly in sub-Saharan Africa and South Asia. This work will generate more rigorous findings than the mostly case-study evidence available to date, as compiled

in http://whylivestockmatter.org/ (accessed 11 March 2020). The evidence generated will inform policy making and public investment. The factors behind smallholder success will be used in models of livestock systems to guide public investment plans that decide which livestock systems are prioritized to assist in meeting national and global Sustainable Development Goals.

Market links

Business models for linking smallholders to markets and services have had a mixed record. For example, contract farming has usually failed in ruminant systems such as dairy and small-scale cattle or small-ruminant production due to the ability of producers to rely on spot markets. Contract farming has, however, proven successful in broiler production, where the risk of having a large batch of broilers at market-ready weight with no reliable buyer provides incentive for more formal producer–buyer arrangements. Other approaches use a 'hub' model, particularly in small-scale dairy systems, where a milk-collection centre provides a location for business activities to be consolidated, including provision of veterinary services, genetics, and feeds, potentially with integrated financial services to facilitate savings and credit for producers to access.

New tools in information and communications technology are being explored to provide market information, production, and process monitoring and feedback, or extension information, which can be linked to these organizational models. Such models suffer in the same way that other cooperative approaches often do, from poor management and inadequate or excessive regulation, and many have failed despite significant public or private investment. In addition, such models are most likely to succeed in intensive production systems where there is a lot of economic activity to drive demand for such services. Linking informal to modern markets is often a challenge, for example, due to the need to address food safety and quality. Much less certain are successful models to link producers to output markets and particularly to services in remote and economically less dense settings, such as in dryland and pastoral systems where many livestock are situated. Mobile service providers face high transport costs there, and producers cannot easily assemble to aggregate demand for the same reason.

ILRI's future research on markets will involve the following:

- Analysis of organizational models that can create market and service links for livestock producers, including: (i) the policy, regulatory, and private-sector settings required for success; (ii) the business and capacity-development support required in typical cases; (iii) the manner in which information and communications technologies can facilitate the better functioning of such organizational models; and (iv) how organizational models can benefit value-chain actors, women, youth, and other marginalized groups. Particular attention will be paid to remote and economically marginal settings and to exploring how small-scale mobile services can be linked to information and communication technologies and GIS tools to allow cost-effective flows of products and services.
- Analysis of gender-equitable approaches to ensure that the needs and capabilities of both women and men are taken into account when designing and evaluating organizational models, as well as assessing the impact on women's empowerment and social equity more generally.
- Regarding the specific case of local and indigenous species and products and given consumers' persistent preferences for many of these products in sub-Saharan Africa and much of Asia, an examination will be made of the scale of speciality livestock markets and an assessment made of smallholder opportunities to meet this demand. This work will include the development of business models with backward links to livestock producers and suppliers of genetics and forward links to specialized restaurants and retailers.

Trade in livestock products

Only about 10% of global livestock production is traded internationally. This is partly due to perishability because many livestock products must be transformed to be safely traded and such transformation – requiring drying, canning, freezing, or other processing – adds to costs. In addition, the threat of transmitting and geographically spreading potentially devastating animal diseases has led to the creation of sanitary and phytosanitary (SPS) standards imposing strict limitations on places from which livestock products can be sourced and on their manner of quality control, processing, packaging, and so on. Some countries, such as those where foot-and-mouth disease is endemic, are limited from exporting some bovine or pig products except to similarly infected zones.

In spite of such limitations to international livestock trade, many livestock trade opportunities for low- and middle-income countries are underexploited, particularly where SPS constraints may be less binding among countries with similar disease prevalence. ILRI's future research will consider the following:

- The potential place and role for approaches to overcome SPS barriers such as commodity-based trade and disease-free zones. Commodity-based trade aims to establish narrowly controlled supply chains that allow a specific product to meet SPS regulations across borders. Disease-free zones aim to set up broader systems to control disease. In both cases, the economics of the required investment versus the potential market returns are uncertain and often suspect. ILRI will identify in which cases such investments potentially make sense and where they do not, and inform policy makers and private investors of this.
- National statistics often fail to provide good information on the consumption of specific meat cuts, including beef and poultry cuts and offal, flowing into developing countries. ILRI will examine these nuances, cataloguing approaches with the potential to enhance livelihoods, food security and nutrition via local livestock value chains faced with lower priced but imperfectly substitutable livestock food product imports.
- The national governments of poorer countries are often attracted to the goal of exporting livestock and livestock products to rich countries, particularly with the aim of generating hard currency. Evidence suggests, however, that larger and more attainable markets are often closer to hand – either domestically or among regional neighbours. These markets are, however, often constrained

by poor infrastructure and inconsistent standards and rules at their borders. ILRI will examine the levels of comparative advantage for livestock exports across key developing countries. We will also examine the main constraints to greater regional trade, particularly in Africa, and assess their impacts and the costs and returns of investments required to alleviate these constraints.

- While some work has been done to assess postharvest losses in livestock value chains, which found relatively low levels of loss, almost no work has addressed the much larger (by volume) markets in live animals in low- and middle-income countries. These pose greater problems methodologically and practically. ILRI has begun to develop a suitable methodological approach and will apply it in several countries, particularly where there are long and complex supply chains for live animals, especially ruminants.

Modelling livestock systems and economies

Demand for livestock products in low- and middle-income countries will continue to grow significantly in the coming decades. Managing the external costs of this demand on health and the environment will require better models. Current tools for livestock-sector modelling are disjointed and poorly coordinated, and so fall short of their potential. Both FAO and the International Food Policy Research Institute (IFPRI) have developed global models that address agriculture and the environment, but their suitability for addressing the livestock sector is still limited. IFPRI's IMPACT model and FAO's model, the Global Agriculture Perspectives System (FAO, 2016), both fail to capture the contribution of grazing land, planted forages, crop residues and other feeds to livestock production and do not yet adequately model the herd growth dynamics that are important in livestock production (Msangi *et al.*, 2014). Current analytical tools, while able to conduct supply-and-demand projections, may be inadequate to answer important questions regarding the potential implications for socioeconomic, public health and environmental impacts and for returns on investment. These models

can only partially capture the direct effects of climate change on livestock systems, such as impacts on animal performance at higher temperatures, or not at all, and even when they do, the results are not analysed in an economic-optimization context.

ILRI has collaborated with governments' efforts to develop livestock master plans in Ethiopia, Rwanda, and Tanzania (Shapiro *et al.*, 2015). In Ethiopia, this work has stimulated directly and more recently in the State of Bihar in India or indirectly several hundred million US$ in new investments in the livestock sector, from both the public and private sectors. As new requests for livestock master plans emerge, it has become apparent that a wider range of metrics is desirable from the plan's outputs, which currently focus only on the supply and demand of livestock products and their economic impacts under alternative scenarios. In addition, the current tools do not address substitutability among livestock products and market dynamics. Developing broader system indicators will allow public and private agents to make better decisions on livestock investments.

DATA QUALITY. A joint activity is being initiated to improve and harmonize data, tools and methods of global and regional livestock systems modelling at ILRI, FAO, IFPRI, the Commonwealth Scientific and Industrial Research Organisation (CSIRO), the Centre de coopération international en recherche agronomies pour le développement (CIRAD) and other partner institutes. This is required to exploit the commonalities and complementarities of the multiple efforts to develop tools and databases, which are currently not well harmonized. A key objective is not only to improve the quality of projections by much better incorporations of feed and crop-related interactions but also to improve the metrics for environment, climate change, and other socio-economic and livelihood indicators. Part of this work would look at investment in different types of livestock technologies, including those for disease control, assessing short-versus long-term gains and benefits. There is also the potential to begin to incorporate the long-term implications of the growth in 'cultured (laboratory-grown) meat', once supply-and-demand parameters are better understood.

PUBLIC EXPENDITURE. Data from the OECD indicate that some 4% of official development assistance goes to agricultural development, of which only a small part is invested in livestock development and the majority is invested in crops. This amount is a small fraction of the share of livestock in global agricultural GDP. The reasons for this apparent bias against livestock include the dominant role of crop scientists in agricultural investment decisions, the perception that crops support food security more than livestock do, and public pressure on donors to reduce support to livestock for environmental and health reasons.

ILRI will investigate trends in public investment in livestock research and development work and the reasons for these trends where private research has lagged. More work is needed to determine returns to investment (and the broader welfare impacts) in livestock research and development, including identifying the highest returns to guide resource investments. Part of this work will be to understand the right balance of investments in smallholders and commercial agents. A total economic valuation approach will also be used given the multiple benefits of livestock.

One area for model improvement in the analysis of public expenditure will be in stakeholder engagement. ILRI will develop model extensions: (i) to apply parameters defined by users, such as national policy makers; (ii) to generate results that are easy to communicate; and (iii) to represent the objectives of decision makers while creating a feedback loop between users and developers that enhances continuous model development.

Livestock and gender equity

Ensuring that the benefits of livestock production are broadly shared is the present and future goal of equity research at ILRI. Improving gender equity is important for livestock because research shows that women often do not receive benefits commensurate with the labour and capital they invest in animals (see Chapter 18, this volume). Some of ILRI's portfolio over the next 5 years will concentrate on gender equity, which provides opportunities for women and men alike to benefit from ILRI's interventions.

The history of gender research at ILRI is relatively brief but productive. We have evidence that livestock can be a cornerstone of economic empowerment for women (see Chapter 18, this volume) for several reasons. Livestock are easier for poor women to own or to manage than land. Livestock propagate themselves and can provide regular income through the supply of milk and eggs. A woman can take livestock assets with her in case of divorce or conflict. The development of the Women's Empowerment in Livestock Index (Galiè et al., 2018) was an important step in creating a metric of progress.

Research on gender equity will be undertaken under the following specific themes:

- *Quantifying the links between gender and increased agricultural production.* We need to know whether increasing women's access to resources and innovations leads to greater livestock production and higher efficiency. We need to know if and when this greater access leads to greater female empowerment and if and when it leads to losses of power to men.

- *Identifying gender-specific interventions in research for development.* More study is needed to understand gender roles in different production systems. One example is the urgent need to conduct time and labour studies to understand task, ownership, and decision-making roles within animal production systems. These studies will inform a much-needed empirical underpinning of how households work – individually and collectively – and will allow a better understanding of gendered labour dynamics. With this more detailed knowledge of labour dynamics, we will be able to better ascertain the implications for given interventions and approaches for women as well as for men.

- *Framing gender policy problems specific to agriculture.* One class of gender policy question can be posed as: which animal species and therefore which livestock diseases are most important to women? Regarding any given species, what role do women play in the care and management of that species – and how can that be tapped for better animal health care? In our forage research, how often and when are women responsible for feeding the family livestock? How

do we ensure that we are selecting and pro-
moting animal genetic traits that may be
preferred by women? In our genetics re-
search, what are the genetic traits of a given
breed of animal that are preferred by
women? Why are these traits preferred?
Can we give women greater access to the
traits they prefer? An important and un-
der-researched area is ensuring that our
interventions do not increase the labour
burden within households, particularly for
women, whose labour is already often unre-
warded in monetary terms. For example,
making improvements to animal feeding
may entail more work for women, who may
need to spend more time gathering fodder
and thus have less time to care for their chil-
dren. Routinely including gender aspects in
our work creates potential for higher agri-
cultural productivity.

- *Extending livestock as a business opportun-
  ity.* We need to understand what women
  need to start and be successful at commer-
  cially oriented livestock enterprises. Mov-
  ing from keeping a few backyard chickens
  to raising hundreds of birds in a poultry
  business requires new skills and inputs:
  which are most important and how do we
  ensure that women have ready access to
  these? We also need to better understand
  which women would be interested in mak-
  ing such a transition. We need to know
  under what circumstances a commercial
  activity like this gets taken over by the
  household men.
- *Expanding the nutritional benefits of women's
  empowerment through animal production.*
  Regarding ASF and nutrition, it is ILRI's
  aim not only to help women make the best
  nutritional choices for their families but also
  to help ensure that females have adequate
  access themselves to milk, meat, and eggs,
  especially young girls, pregnant and lactat-
  ing women, older women, and those who
  are ill.

An aspect of equity is youth employment. Popu-
lation growth in Africa is expanding the num-
bers of young people seeking jobs. While labour
force growth presents opportunities, it also rais-
es fears of un(der)employment, migration, and
violence. While the food and agricultural sectors
are wide paths for youth employment, the evi-
dence on youth employment in agriculture and
livestock remains thin. ILRI and partners will
target youth employment creation within the
agricultural sectors of mandate countries as a
response to these demographic opportunities.
Three lines of inquiry will be pursued: (i) devel-
opment and adoption of new livestock practices,
including digitization and mechanization, and
institutions on farms and in value chains; (ii)
promotion of youth employment and entrepre-
neurship in the small-scale livestock sector; and
(iii) strategic research on youth and livestock.

The results of work by ILRI and partners fo-
cusing on gender equity and youth employment
should lead to a series of inclusive business
models that allow women to get competitive
returns on their capital and labour investments
and to benefit fully from these returns. A recent
example of such work is the integration of gen-
der in the development of livestock master
plans of nations and states (see Chapter 18, this
volume).

ILRI Operations in a Competitive Global Environment

Changed funding environment

The work summarized in this volume has con-
firmed the major scientific impacts of research
by ILRI and its partners. We have seen that
greater investment in livestock and livestock sys-
tems research can lead to significant benefits in
food and nutrition security, in economic devel-
opment, and in natural resource management.
Despite good evidence for these benefits, the glo-
bal funding environment relative to the scale of
the research problems has become more chal-
lenging.

The CGIAR funding environment was very
different when ILRI's predecessors – ILRAD and
ILCA – were founded in the early 1970s (Özgediz,
2012). Unrestricted ('core') funding was pro-
vided to centres to do public-goods research on
agricultural productivity to improve food security.

As more centres joined CGIAR in the
1990s, the historical growth in real system
funding began to fall after 1995[1]. Associated
with a decline in the rate of the growth of real

funding was a collapse in the share of core funding, which fell from almost 100% in the 1980s to some 40% in 2002. In response to the decline in total funding emerged new multi-centre funding models, including 'challenge programmes'; these multi-centre programmes managed to attract limited additional funding but at the cost of diverting core funding to external partners in the challenge programmes.

A new financing mechanism began in 2012 in response to the spending decline that began in the 1990s. Instead of core funding going directly to centres, supplemented by project funding, the core funding was converted to programme funding (Windows 1 and 2) through multi-institutional CGIAR research programmes, known as CRPs. Restricted projects (under the so-called Window 3) were aligned to the CGIAR research programmes. After an initial increase, the 'programme funding' declined from about 40% in 2012 to 20% in 2018. Despite unrealistic statements made by some officials of what was then the 'CGIAR Consortium', there has been no widening of the donor base; the Bill & Melinda Gates Foundation is the only new donor to provide significant funding to livestock.

ILRI and collaborators will continue to argue for more investment in tropical livestock, focusing on low- and middle-income countries and on excluded producer groups, but these efforts are unlikely to provide major resources without substantial commitments from new donors. ILRI's funding from 2014 to 2018 averaged about US$75 million in 2015 US$, or perhaps 7–8% of CGIAR system funding from Windows 1, 2, and 3, and it is unlikely that the ILRI total or the ILRI share of the global amount will grow significantly in real terms.

Collaboration with national agricultural research systems (NARS)

Collaboration with the NARS of the developing world has been a foundation of ILRI's work since the institute's founding. While some of these national systems have strengthened considerably since the 1970s, many still have limited scientific capacity relative to their needs. ILRI will increasingly work with the world's stronger NARS to leverage its expertise. This will be achieved through joint programmes and laboratories,

building on ILRI's successful partnership with the Chinese Academy of Agricultural Sciences. ILRI will generally continue to collaborate with national systems as a means of doing research and of developing human and institutional capacity.

Impact at scale

The founding model of the international agricultural research centres was that their research would generate technologies and interventions that were applicable by hundreds of millions of poor farmers in developing countries. These technologies would first be adapted for local use by national partners and ultimately extended to farmers. While this model did achieve much, as testified by the many achievements detailed in this volume, its linear character – from research to adaptation to development – no longer serves the world well, because the challenges of agriculture in the tropics have become more complex.

ILRI's core expertise will continue to be livestock research for development, but there will be two ways in which ILRI departs from its past. The first way is that research programmes and projects are increasingly being conceptualized by 'starting with the end in mind'. This means we start by identifying the development challenge(s) we want to meet – the impact we want to make, where and on whom. Then we work back to what outcomes are required to achieve this, what research outputs are needed to produce those outcomes, and what research activities and resources are needed to produce these outputs. This approach requires ILRI to be more purposeful in identifying which partners can increase impact. Given the increasing role that the private sector will play in development, the new approach includes greater engagement with private agents at all scales.

The second way in which ILRI's business will evolve is to develop mechanisms to engage more effectively with development agencies. In 2017, ILRI established an 'Impact at Scale' programme, which is designed to manage the interaction between research and development. It identifies products and innovations from ILRI and other research organizations that have been piloted and are ready to be deployed at scale,

packages them (with adaptations as required) and then works with development agencies, including classic public extension, NGOs, and private companies. While not engaging directly in field development activities, ILRI will continue to develop the expertise needed to engage effectively with partners that do field development.

This more complex agenda requires a different way of working, including more diverse partnerships and applying different skills and disciplines across the biophysical and social sciences. The 'omics revolution' has created research opportunities that were unimaginable 40 years ago, allowing the creation of new genetic, biophysical, and economic models. ILRI is committed to bringing to bear the best science in tackling these challenges and in partnering with research institutions in both developed and developing countries in pursuit of this.

We are also committed to ensuring that ILRI's research is used effectively to make a real difference to the hundreds of millions of people in developing and emerging economies that depend on livestock – and that our research manages this in ways that are socially equitable as well as environmentally sustainable. We will continue to work closely with our funding and development partners to ensure that our research is supremely relevant and reaches all those who need it most.

Note

[1] Real CGIAR system spending, in 2015 US$, averaged US$271 million during the period 1971–1993, during which it rose at a real annual rate of 7.4%; real spending from 1994 to 2011 averaged US$510 million and rose at an annual rate of 2.9% from 1994 to 2010; real spending averaged US$876 million during the period 2011–2018 and rose at a real annual rate of 1.3%. It should be noted that real spending took a great leap forward from 2010 to 2011, when it rose by slightly more than 20%.

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APPENDIX 1: CIAT and ICARDA Livestock Research

CIAT Livestock Research, 1967–2018[1]

A thorough history of the Centro Internacional de Agricultura Tropical (CIAT) stated that one purpose of '...CIAT's research over the past 50 years has been to establish fundamental knowledge on tropical forages' (Lynam and Byerlee, 2017, p. 81). The search for this knowledge began with CIAT's Beef Program in 1969[2]. The programme's objective was to '... increase cattle productivity in the lowland tropics of Latin America...at elevations below 1000 m' (CIAT, 1973, p. 4). The farm type targeted by CIAT animal research was ranches of varying size, typically with sown pastures, and some small- and medium-scale dairying in Central America[3]. Research themes were ambitious, seeking to: (i) improve the quantity and quality of feed; (ii) control diseases and parasites; and (iii) 'devise production systems that produce good quality beef efficiently and cheaply' (CIAT, 1973, p. 5). Feed work involved collecting and evaluating legumes and grass species, initially in Latin America and later in sub-Saharan Africa and in Asia, with related soil analyses. Work on production systems included field surveys, modelling and economic analysis. Animal breeding and health were initially seen as major themes in the Beef Production Systems Programme but were later left to the national programmes and the private sector in Latin America (CGIAR/TAC, 1977, p. 47). The Beef Production Systems Programme ultimately evolved into a Tropical Pastures Programme in 1979, later becoming the Tropical Forages Programme (CIAT/TFP) and shedding along the way the work on animal health, breeding and reproduction.

The CIAT Tropical Forages Programme had three broad themes after 1980: (i) forage germplasm, in response to the identified need to increase the available species and genotype pools of forages, both grasses and legumes, for screening for adaptation to limiting abiotic (mainly soil) and biotic (pests and diseases) constraints; (ii) on-farm forage development using materials that could thrive on acid soils and resist insects and diseases, notably anthracnose on _Stylosanthes_ spp.; and (iii) natural resource management, involving plant, animal and soil components.

Forage germplasm

Two phases can be distinguished in the development of the CIAT forage gene bank: (i) a first phase with the main focus on assembling and using the forage germplasm collection (1972–1993); and (ii) a second phase that comprised continuing use of germplasm, diversity studies and routine germplasm management and its optimization (1993–2017)[4].

In the early 1970s, CIAT began systematic missions throughout tropical America to collect germplasm of wild species with forage potential. The objective was to create a diverse germplasm pool for cultivar development via selection or, if

natural variability failed to provide the desired traits, via breeding (Lynam and Byerlee, 2017, pp. 81–82). Collecting missions ranged from excursions of short duration, particularly in Colombia, to several weeks-long expeditions. Another germplasm source was opportunistic collections made by CIAT staff and collaborators during field visits. There was a combined target focus on acid-soil regions and plant genera of particular interest. The emphasis was on legumes, in many cases including associated rhizobia, as the Neotropics are the main centre of diversification of the Fabaceae (Leguminosae) family. From 1979 onwards, collection missions expanded to South-east Asia, an important centre of legume diversification (e.g. *Pueraria* and *Desmodium* spp.). Collections extended in the 1980s to Africa, with a focus on grasses, as sub-Saharan Africa is the main centre of Poaceae diversity. Maintenance of the forage collection passed on to the CIAT Genetic Resources Unit (GRU) after its foundation in 1977. The GRU manages seed testing, seed increase, germplasm preservation, safety backups of the collection, maintenance of living collections, seed distribution, etc., all of which are routine and costly germplasm conservation measures.

Achievements in forage germplasm (paraphrased from Lynam and Byerlee, 2017, pp. 85–88) were: (i) the collections conserved in the gene bank with provision of germplasm for selection and breeding programmes; and (ii) forage adoption particularly in tropical America.

The forage gene bank

With a total of approximately 23,000 accessions (about 21,500 legumes and 1500 grasses) from some 75 origin countries, the CIAT collection is the largest tropical forages germplasm collection worldwide. Its particular value lies in its focus on: (i) plants from, and subsequently adapted to, acid, low-fertility soils; and (ii) legumes. However, as far as countries and regions on which germplasm collecting missions concentrated in the past are concerned, there are still important gaps: the collection is probably far from being representative of the geographic diversity of tropical Poaceae and Leguminosae.

Forage adoption

The greatest achievement in tropical forages has been the wide-scale adoption of such materials in Brazil (Schultze-Kraft *et al.*, 2020), for which most of the credit goes to the national program of Brazil, with some more recent input from CIAT. It is estimated that about 120 million ha are planted to forages, of which nearly 100 million are *Urochloa* spp. and approximately 17 million ha are *Megathyrsus maximus* (Jank *et al.*, 2014). Arguably about 50 million ha are planted to one cultivar, *Urochloa brizantha* cv. Marandu, in Brazil alone (Lynam and Byerlee, 2017, p. 87). Particularly impressive is the rapid adoption from an estimated 16 million ha in the mid-1980s to nearly 120 million ha by the early 2010s, indicating the transformative potential of improved forages when respective support structures, including involvement of the seed industry, are in place. Together with parallel improvements in animal breeds and animal health, more productive forages contributed to a fourfold increase in productivity per area and per animal; this is recognized as one of the major successes of global agriculture in the past 30 years (Lynam and Byerlee, 2017, p. 87).

In 2002, a *Urochloa* (syn. *Brachiaria*) *decumbens × brizantha × ruziziensis* cultivar from CIAT's breeding programme was released as the first bred *Urochloa* sp. cultivar worldwide. Uptake based on documented seed sales until the end of 2016 is estimated at 750,000 ha mostly sown in the past decade. Adoption includes more than 40 countries in Latin America and the Caribbean, tropical Africa, tropical Asia, Australia and Oceania, tropical/subtropical North America and southern Europe; most adopters appear to be small- and medium-sized livestock producers[6].

CIAT has released materials from its germplasm base, including 11 grasses and 16 legumes in Mexico and Central America. The CGIAR Standing Panel on Impact Assessment (SPIA) found limited published work that evaluated the adoption and impact of these materials in Mexico and Central America (Jutzi and Rich, 2016, pp. 46–55).

Better documented is the uptake of *Urochloa* grasses in Mexico and Central America where plantings of over 3 million ha were reported up to the early 2000s (Holmann *et al.*, 2004).

Surveys in Colombia's Eastern Plains carried out in 2017 suggested that about one-third (about 3 million ha) of improved pastures is sown using *Urochloa* cultivars selected by Corporación Colombiana de Investigación Agropecuaria (CORPOICA)[7] and CIAT, or bred by CIAT (Labarta *et al.*, 2017). Empresa Brasileira de Pesquisa Agrícola (EMBRAPA), with CIAT contribution, achieved another success with about 1.5 million ha sown to *Andropogon gayanus* up to 2000 (Rivas Ríos, 2002). The national system of Nicaragua, supported by CIAT, promoted the adoption of improved forages such as *Urochloa* spp. and *Canavalia brasiliensis*, benefiting about 2000 smallholders and giving a 28% increase in daily milk yield (Pinillos *et al.*, 2018).

Notable production gains were achieved in the Eastern plains of Colombia as part of the collaboration between CORPOICA and CIAT. These gains were due to the inclusion of *Urochloa* spp. in crop–pasture rotations leading to a twofold gain in carrying capacity over degraded pasture and a tenfold gain over native savannah (Rincón and Ligaretto, 2008).

ICARDA Livestock Research, 1977–2018[8]

Research at the International Centre for Agricultural Research in the Dry Areas (ICARDA), established in 1977, has covered improvement of barley, chickpea, faba bean, grass pea, lentil and wheat, as well as development of water and land management and crop–range–livestock integration. ICARDA livestock research has focused on three areas: (i) introduction of *Medicago sativa* into North African and West Asian farming systems; (ii) conserving and using forage germplasm; and (iii) understanding soil–water–plant–animal livestock interactions in the mixed grazing systems of North Africa and West Asia.

Conserving and using forage germplasm

ICARDA plays a crucial role in conservation and use of global forage genetic resources. It holds more than 155,000 accessions in trust, including 38,955 accessions of temperate forage and range species. ICARDA gene banks hold a highly diversified collection of temperate/Mediterranean forages including globally important and unique collections of members of the genera *Lathyrus*, *Medicago*, *Pisum*, *Trifolium* and *Vicia* representing 16.6% of holdings reported in Genesys. The bulk of the collection is still conserved in the gene bank in Syria, although after 2014, gene bank core activities were relocated to Lebanon and Morocco where new facilities were established and efforts to regenerate and characterize the active and base collections were undertaken.

The ICARDA forage collection is unique in its geographical coverage (originating from 112 countries) and its species coverage (631 taxa including many neglected species). The base collection has a total of 30,008 accessions representing 77% of the active collection. Only 62.5% of the collection is safety duplicated in four gene banks representing mostly the accessions collected by ICARDA. ICARDA also conserves an important *Rhizobium* spp. collection totalling 1483 strains belonging to 73 taxa, most of which are related to forage legumes. In 2008, ICARDA started sending the accessions in its active collection to the Svalbard Global Seed Vault in Norway, and approximately 23,360 accessions have been sent there for long-term conservation.

The ICARDA forage gene bank has distributed over 30 years approximately 205,000 samples for use by ICARDA scientists and external partners. Most have been used to select ecotypes for pasture improvement or as sources of traits for plant-breeding programmes.

Notes

[1] Material on CIAT is derived from Lynam and Byerlee (2017) and from Schultze-Kraft *et al*. (2020, forthcoming).

[2] Lynam and Byerlee (2017) present a history of CIAT from 1967 to 2017.

[3] CIAT's early swine programme closed in 1978 (Lynam and Byerlee, 2017, p. 29).

[4] CIAT germplasm collections and its accessions database are described in Schultze-Kraft *et al*. (2020, forthcoming).

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Index

THE IMPACT OF THE INTERNATIONAL LIVESTOCK RESEARCH INSTITUTE

EDITED BY JOHN MCINTIRE AND DELIA GRACE

Providing the first evidence-based global estimates of the many scientific, economic, policy, and capacity development impacts of livestock research in and for developing countries, this volume is an indispensable guide and reference for veterinarians, animal and forage scientists, and anyone working for the equitable and sustainable development of the world's poorer agricultural economies.

Livestock is one of the fastest growing agricultural sectors, with most growth occurring in developing countries. For more than four and a half decades one global centre has been mandated to conduct research on leveraging the benefits and mitigating the costs of livestock production in poor countries. This book focuses on the achievements, failures and impacts of the International Livestock Research Institute (ILRI) and its predecessors, the International Livestock Centre for Africa (ILCA) and the International Laboratory for Research on Animal Diseases (ILRAD). The scientific and economic impacts of tropical livestock research detailed in this work reveal valuable lessons for reducing world hunger, poverty and environmental degradation.

Describing the impacts of smallholder livestock systems on the global environment, the book also covers animal genetics, production, health and disease control, and livestock-related land management, public policy and economics, all with useful pointers for future livestock-for-development research.

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Front cover image: Detail of a bull figure – a symbolic animal of the Babylonian weather god Adad – in the Ishtar Gate of Babylon in Southern Mesopotamia. ©ILRI/Susan MacMillan