

Banana Breeding

Progress and Challenges



Edited by
Michael Pillay and Abdou Tenkouano



CRC Press
Taylor & Francis Group

Banana Breeding

Banana Breeding

Progress and Challenges

Edited by
Michael Pillay
Abdou Tenkouano



CRC Press

Taylor & Francis Group

Boca Raton London New York

CRC Press is an imprint of the
Taylor & Francis Group, an **informa** business

The picture of male flowers and seeds are courtesy of Mauricio Guzman, Corbana, Costa Rica. The female flowers are courtesy of Moses Nyine, Iita, Uganda.

CRC Press
Taylor & Francis Group
6000 Broken Sound Parkway NW, Suite 300
Boca Raton, FL 33487-2742

© 2011 by Taylor and Francis Group, LLC
CRC Press is an imprint of Taylor & Francis Group, an Informa business

No claim to original U.S. Government works

Printed in the United States of America on acid-free paper
10 9 8 7 6 5 4 3 2 1

International Standard Book Number-13: 978-1-4398-0018-8 (Ebook-PDF)

This book contains information obtained from authentic and highly regarded sources. Reasonable efforts have been made to publish reliable data and information, but the author and publisher cannot assume responsibility for the validity of all materials or the consequences of their use. The authors and publishers have attempted to trace the copyright holders of all material reproduced in this publication and apologize to copyright holders if permission to publish in this form has not been obtained. If any copyright material has not been acknowledged please write and let us know so we may rectify in any future reprint.

Except as permitted under U.S. Copyright Law, no part of this book may be reprinted, reproduced, transmitted, or utilized in any form by any electronic, mechanical, or other means, now known or hereafter invented, including photocopying, microfilming, and recording, or in any information storage or retrieval system, without written permission from the publishers.

For permission to photocopy or use material electronically from this work, please access www.copyright.com (<http://www.copyright.com/>) or contact the Copyright Clearance Center, Inc. (CCC), 222 Rosewood Drive, Danvers, MA 01923, 978-750-8400. CCC is a not-for-profit organization that provides licenses and registration for a variety of users. For organizations that have been granted a photocopy license by the CCC, a separate system of payment has been arranged.

Trademark Notice: Product or corporate names may be trademarks or registered trademarks, and are used only for identification and explanation without intent to infringe.

Visit the Taylor & Francis Web site at
<http://www.taylorandfrancis.com>

and the CRC Press Web site at
<http://www.crcpress.com>

This book is dedicated to our families, who enrich our lives, and to our late colleagues Dirk Vuylsteke, Paul Speijer, John Hartman (IITA), and Phil Rowe (FHIA) for their contributions to banana breeding.

Contents

Foreword	ix
<i>Manjit S. Kang</i>	
Introduction.....	xi
<i>Ivan W. Buddenhagen</i>	
Preface.....	xiii
Editors	xvii
Contributors	xix
Chapter 1 General Plant Morphology of <i>Musa</i>	1
<i>Deborah Karamura, Eldad Karamura, and Guy Blomme</i>	
Chapter 2 Evolution and Genetic Relationships in Banana and Plantains.....	21
<i>Uma Subbaraya, Marimuthu S. Saraswathi, and Michael Pillay</i>	
Chapter 3 Genetic Resources for Banana Improvement.....	41
<i>Markku Häkkinen and Richard Wallace</i>	
Chapter 4 Genomes, Cytogenetics, and Flow Cytometry of <i>Musa</i>	53
<i>Michael Pillay and Abdou Tenkouano</i>	
Chapter 5 Genetics of Important Traits in <i>Musa</i>	71
<i>Eli Khayat and Rodomiro Ortiz</i>	
Chapter 6 Major Diseases of Banana.....	85
<i>Guy Blomme, Simon Eden-Green, Mohammed Mustaffa, Bartholemew Nwauzoma, and Raman Thangavelu</i>	
Chapter 7 Integrated Pest Management of Banana.....	121
<i>Thomas Dubois and Daniel L. Coyne</i>	
Chapter 8 Reproductive Biology	145
<i>Jeanie Anne Fortescue and David William Turner</i>	
Chapter 9 Breeding Techniques.....	181
<i>Abdou Tenkouano, Michael Pillay, and Rodomiro Ortiz</i>	

Chapter 10	Mutations and Cultivar Development of Banana	203
	<i>Shri Mohan Jain, Bradley Till, Prasanna Suprasanna, and Nicolas Roux</i>	
Chapter 11	Biotechnology in <i>Musa</i> Improvement	219
	<i>Leena Tripathi</i>	
Chapter 12	Genotype by Environment Interaction and <i>Musa</i> Improvement.....	237
	<i>Rodomiro Ortiz and Abdou Tenkouano</i>	
Chapter 13	Quality Improvement of Cultivated <i>Musa</i>	251
	<i>Edson Perito Amorim, Sebastião de Oliveira e Silva, Vanusia Batista de Oliveira Amorim, and Michael Pillay</i>	
Chapter 14	Postharvest Processed Products from Banana	269
	<i>Cherukatu Kalathil Narayana and Michael Pillay</i>	
Chapter 15	Propagation Methods in <i>Musa</i>	285
	<i>Michael Pillay, Christopher A. Cullis, David Talengera, and Leena Tripathi</i>	
Chapter 16	Hybrid Distribution to Farmers: Adoption and Challenges	305
	<i>Abdou Tenkouano, Michael Pillay, and Ousmane Coulibaly</i>	
Chapter 17	Molecular Breeding of Other Vegetatively Propagated Crops: Lessons for Banana.....	321
	<i>Michael Pillay, Abdou Tenkouano, and Rodomiro Ortiz</i>	
Chapter 18	Future Prospects	351
	<i>Rodomiro Ortiz, Michael Pillay, and Abdou Tenkouano</i>	

Foreword

Food production must be increased year after year to keep pace with population growth. At the current population growth rate of 1.2%, world population is expected to reach 9 to 10 billion by 2050. On the basis of this estimate, food production would need to be doubled in the next 30 years or so and tripled in the next 50 years. We will need to do this without causing ecological damage to our natural resources and the environment.

Although cereals are expected to continue to be the most important calorie providers in the world, crops like bananas will also remain important calorie-providing staples throughout the world, especially in developing tropical countries. Because of the importance of banana in some parts of the world, especially Africa, attention must be focused on it as a staple food.

Several previously published books have included chapters on bananas, but there is no recent book that provides in-depth coverage of all aspects of banana breeding and genetics, including biotechnology. In some recently published books, individual chapters can be found on banana improvement, but all aspects of banana breeding, genetics, biotechnology, genetic resources, and morphology have not received treatment in sufficient detail, especially in light of the fact that major advances have occurred in modern methods of banana breeding and related aspects during the past couple of decades. Thus, there was a need to bring together these advances in a single title. The current book, *Banana Breeding: Progress and Challenges*, edited by Michael Pillay and Abdou Tenkouano, fills this need.

The book is a wide-ranging compilation of chapters by various experts. The book begins with a chapter on the general plant morphology of *Musa*. Subsequently, chapters such as Evolution and Genetic Relationships in Bananas and Plantains, Genetic Resources for Banana Improvement, Genomes, Cytogenetics, and Flow Cytometry of *Musa*, and Genetics of Important Traits in *Musa* are included. Two chapters cover the major diseases and pests of banana. Five chapters cover the central focus of the book, including Reproductive Biology, Breeding Techniques, Mutations and Cultivar Development of Banana, Biotechnology in *Musa* Improvement, and Genotype by Environment Interaction and *Musa* Improvement. The latter chapter should help provide tools for selecting both narrowly adapted and broadly adapted cultivars. The chapters on quality improvement of cultivated *Musa* and postharvest processed products provide researchers and teachers with information to improve quality aspects of banana and how to reduce postharvest losses, respectively.

Because of its vegetative reproduction, the chapter on propagation methods in *Musa* should prove valuable to small-scale farmers in providing enough planting material. In the chapter Molecular Breeding of Other Vegetatively Propagated Crops: Lessons for Banana, the book draws on the strengths and weaknesses of other vegetatively propagated crops to avoid mistakes and to make achievement of success more certain.

The editors and other authors have vast experience in banana breeding, genetics, biotechnology, molecular-marker technology, tissue culture, and other areas. Thus, all the chapters are authoritative contributions. I must congratulate all of them for generating a first-class publication that should be useful to researchers, teachers, and extension personnel around the world. This book is expected to have a major impact on banana research and teaching. This comprehensive book should serve as a ready reference for all researchers and teachers interested in banana breeding and production.

Manjit S. Kang

Introduction

Finally we have a book centering on banana breeding. It is even entitled *Banana Breeding*. This is a most welcome addition to the classical book by N. W. Simmonds, *The Evolution of the Bananas*, now some 50 years old.

This book is a wide-ranging compilation of chapters by various authors covering plant morphology, origin, genetic resources, reproductive biology, diseases, pests, quality improvement, propagation, and distribution to farmers, as well as the central focus chapters covering breeding, genetics, and biotechnology. There is even a chapter comparing breeding with three other major clonal tropical crops.

When one considers that banana breeding based on modern science is now some 90 years old and yet farmers are still mainly growing the diverse clones selected by villagers thousands of years ago from their natural environment, one must ask why. How could so many diverse and excellent clones have arisen by purely natural events of pollination, seed set, seed germination, and then selection?

The answers are complex, but things must have been very different then. Indeed, in an excellent chapter by Fortescue and Turner on reproductive biology, it is made very clear that low seed set and germination today are major detriments to breeding progress and that little research has been applied to understand the physiological/biochemical reasons for ovule abortion/low seed set. When early man first found and brought into cultivation parthenocarpic plants, they were probably quite fertile. As plants were moved about, encountering genetically diverse bananas, seed set was probably abundant. With time, seed set was negatively selected and, hence, has led to present-day sterility. Some parthenocarpic clones are still quite fertile, but exploration and evaluation for this character has been neglected. Even our understanding of parthenocarpy itself and its inheritance go back to work now 50 years old.

But the breeding programs themselves have waxed and waned as support varied and objectives changed. There are six existing breeding programs outside the center of origin of *Musa*, and only two minor efforts in India and none at all in the Southeast Asia center of diversity, where wild bananas still exist and clones are still being domesticated. Research on coevolved pathosystems is neglected, and no feedback from the natural systems into breeding exists.

Many chapters in this book reveal the enormity of molecular research applied to bananas and the attempts to apply molecular techniques to banana breeding itself. Molecular-assisted selection is still in its infancy and much dynamism continues in the molecular field.

Breeding techniques and breeding philosophies are expertly detailed in a chapter by Tenkouano et al. It is clear that much has been learned to direct the future of breeding. Excellent bibliographies in many chapters provide a valuable documentation of the diverse and enormous scattered research activity on bananas of the last 50 years.

Breeding bananas started with the simple objective of a Fusarium wilt-resistant 'Gros Michel.' Breeding objectives changed and proliferated as new programs started and local farmers' needs were addressed. Objectives are now very diverse and complex, and they differ in different regions. Much has been learned of banana evolution through molecular science. Yet breeders still use only a very limited pool of parents compared with the great natural diversity existing. It is clear that much research is still needed to assess and to reduce reproductive barriers.

A perusal of these chapters with the literature and an examination of the experience on which they are based reveal a wealth of knowledge and views not readily available elsewhere. It is an excellent new resource on bananas and banana breeding.

Ivan W. Buddenhagen

Preface

This book comprises a collection of chapters written by experts in banana research. Banana is one of the most important agricultural crops, providing food, income, and employment for millions of people, especially in the tropics. The crop is threatened by various diseases and pests that are being compounded by environmental change. Breeding resistant cultivars appears to be the only sustainable solution. The crop has been largely neglected and there are a few isolated breeding programs in the world. The last major book covering a diverse range of topics in bananas and plantains was written over 10 years ago. Since then, a large body of new information on banana has emerged, and this is reflected in the number of publications in various research areas. We believe that there is a need for updated information in banana breeding and new responses to old challenges facing the crop. The purpose of this book is to portray our personal perspectives on the challenges facing the crop. To enable us to cover a wider range of topics, we have enlisted the ideas of leading experts, including agronomists, biologists, biotechnologists, breeders, crop improvement and integrated pest management (IPM) specialists, plant pathologists, and taxonomists. In this book our aim is to concentrate the current information and provide an accessible source of information to those interested in banana research, especially the development of new disease- and pest-resistant cultivars. This book provides basic as well as advanced information for those interested in learning more about banana as well for those pursuing further research in the crop.

Chapter 1, written by Deborah Karamura, Eldad Karamura, and Guy Blomme, individuals with vast experience in bananas and plantains, provides a detailed botanical description of the plant. In addition to describing the aerial shoot corm and root systems, they also address the role of morphology in classifying banana and the confounding effects of mutations and genotype \times environment (G \times E) interactions. They emphasize the importance of distinguishing cultivars, even those produced by breeding programs, with regards to breeders' rights and the fact that traders and buyers can select the cultivar of their choice.

In Chapter 2, Uma Subbaraya, Marimuthu S. Saraswathi, and Michael Pillay draw on their personal experiences to present a comprehensive treatment of the evolution, diversification, and molecular genetic relationships in bananas and plantains. The early recordings of banana in India and indigenous knowledge of the uses of banana is a unique aspect of this chapter. The authors also indicate the various research needs in banana with regards to molecular taxonomy, especially of unique germplasm available in India.

Markku Häkkinen, a highly respected field botanist, and Richard Wallace provide information in Chapter 3 on some of the new banana germplasm that have been recently identified. They report on members of the five sections and their potential usefulness for conventional breeding. They conclude by stating that "The incorporation of genetic traits (disease and pest resistance, drought and cold tolerance, and so forth) from these sections will play an important role in the development of new, improved hybrid bananas for use by future generations."

In Chapter 4, Michael Pillay and Abdou Tenkouano provide a comprehensive treatise of the genomes in *Musa*, the part played by molecular cytogenetics in identifying the genomes, and the role of genomes in *Musa* classification. They formulate from their personal and practical experiences the opinion that conventional and molecular cytogenetics have played and will continue to play a vital role in breeding of banana. Various biochemical markers to identify the different genomes are discussed. The importance of flow cytometry, especially in ploidy identification, is highlighted. Recent information on cytogenetical aspects of fertility is addressed briefly.

The genetics of important traits are discussed in Chapter 5 by Eli Khayat and Rodomiro Ortiz, two individuals with vast experience and knowledge in banana genetics. The chapter presents new

perspectives on the genetics of plant architecture, fruit parthenocarpy, fruit ripening and senescence, nematode resistance, and resistance to black leaf streak disease.

In Chapter 6, Guy Blomme, Simon Eden-Green, Mohammed Mustaffa, Bartholemew Nwauzoma, and Raman Thangavelu use their firsthand field experiences to provide an extensive review of the Sigatoka diseases, Fusarium wilt, Xanthomonas wilt, and viral diseases of banana. This is perhaps the first comprehensive treatise of Xanthomonas wilt of banana.

Thomas Dubois and Daniel Coyne present an excellent overview of integrated pest management of banana in Chapter 7. In addition to the major pests—nematodes and the banana weevil—that generally receive the most attention, they outline a wide range of pests associated with banana cultivation. They define integrated pest management (IPM) and present an important assessment on how IPM principles can be applied to various banana cultivation systems.

Chapter 8 is a comprehensive treatment of the reproductive biology of banana by Jeanie Fortescue and David Turner. The authors' probing writing style and personal experiences make this chapter one of the best treatments written on this topic. The floral biology, breeding systems, pollen and seed production, and reproductive systems are fully discussed. This is excellent reading for researchers wishing to start banana breeding programs.

Chapter 9 by Abdou Tenkouano, Michael Pillay, and Rodomiro Ortiz highlights the experience of these banana breeders with their work in Africa and presents some of their own research findings. A short history of banana breeding is followed by the main reasons for breeding in the crop. The chapter outlines the objectives and difficulties of banana breeding and the progress made in this field. Future breeding goals are elaborated.

Shri Mohan Jain, Bradley Till, Prasanna Suprasanna, and Nicolas Roux, specialists in mutation research, discuss the value of mutations in producing new banana cultivars in Chapter 10. The chapter is ideal for anyone interested in using mutations in banana since it addresses the best methods for inducing mutations, the types of materials to use, and the steps to follow after mutation induction. The value of targeting-induced local lesions in genomes (TILLING) in banana is also introduced.

The value of the many facets of biotechnology in *Musa* improvement is addressed by Leena Tripathi in Chapter 11. The application of tissue culture in *Musa* research is discussed. The role of genomics and transgenic technology for *Musa* genetic improvement is highlighted, with examples of genes that will be useful for developing transgenic banana. The challenges facing researchers in the development of transgenics, especially in less-developed countries, are elaborated.

In Chapter 12, Rodomiro Ortiz and Abdou Tenkouano give an overview of the progress made in research related to GxE interactions in banana. The components of phenotypic stability for some traits are discussed. The chapter reviews how to manage GxE to have efficient selection schemes and multilocation testing before release of improved cultivars. Broad-sense heritability (H^2) and repeatability (R) estimates for growth, bunch, and fruit traits in triploid *Musa* germplasm are provided. The authors discuss new ways of using GxE information, inclusive of market-related information, to develop end-use approaches to breeding and to target new cultivars to areas where they are most likely to add value.

In Chapter 13, Edson P. Amorim, Sebastião de Oliveira e Silva, Vanusia B. de Oliveira Amorim, and Michael Pillay address the nutritional value of banana. Breeding objectives for quality improvement are discussed. The role of biofortification and breeding strategies for developing biofortified cultivars with improved nutritional quality is highlighted.

Cherukatu K. Narayana and Michael Pillay list some of the various postharvest products obtained from banana in Chapter 14. The need for new products from banana to reduce large postharvest losses is discussed. The authors conclude by stating that bananas represent a great potential raw material for food and nonfood processing industries.

Chapter 15 by Michael Pillay, Christopher A. Cullis, David Talengera, and Leena Tripathi reviews various ways of propagating banana. Embryo culture of hybrid seeds from breeding programs is discussed. The role of micropropagation is reviewed. Low-cost techniques to rapidly multiply banana

seedlings are reviewed. Since micropropagation is usually associated with somaclonal variation, molecular methods to detect somaclonal variants are outlined.

The success of plant breeding programs is measured by the extent to which the breeding products are adopted and used by the growers, profitably and durably. Beyond the genetic products, perhaps the more challenging task for the breeders is to understand and help put in place the complex battery of institutional and transactional measures that create a conducive delivery framework. These issues are discussed by Abdou Tenkouano, Michael Pillay, and Ousmane Coulibaly in Chapter 16. The authors also elaborate on the asymmetric nature of cultivar-based transactions in an evolving market within domestic, regional, and international contexts.

Molecular breeding in banana has not been as progressive as that of other crops. In Chapter 17 Michael Pillay, Abdou Tenkouano, and Rodomiro Ortiz review some aspects of molecular breeding in potato, cassava, and sugarcane. The breeding challenges, production constraints, and breeding objectives of these crops are similar to those of banana. Greater progress has been made in the search for molecular markers, mapping, and developing transgenics for a number of traits in potato, cassava, and sugarcane. These are useful lessons for banana scientists.

Chapter 18, by Rodomiro Ortiz, Michael Pillay, and Abdou Tenkouano, is a brief chapter on future prospects in *Musa* research.

We trust that those interested in banana and plantain will find the information in this book useful and stimulating. This book is intended for students, teachers, and banana breeders. We hope that academics throughout the world interested in developing tropical crops will also find use for this book.

We thank all the authors for their valuable contributions and for sharing their knowledge to make this book a success.

Editors



Michael Pillay (BSc, UHDE, BEd, BA, BSc [Hons] MS, PhD) is a professor in the Department of Biosciences at Vaal University of Technology, Vanderbijlpark, South Africa. He completed a BSc degree in botany and zoology and a university higher diploma in education at the University of Durban-Westville (now the University of KwaZulu–Natal), a BEd and BA from the University of South Africa (UNISA), a BSc (Hons) at the University of Durban-Westville, an MS (agronomy) at Louisiana State University, and a PhD at Virginia Polytechnic Institute and State University.

Dr. Pillay is the author and coauthor of many articles and book chapters. He served as an editor for the *American Journal of Agronomy* and is on the editorial board of the *Journal of Crop Improvement*. Dr. Pillay's research interests are biotechnology, breeding, molecular genetics, genetics, plant sciences, plant systematics, cytogenetics, tissue culture, and germplasm conservation of crop plants. Dr. Pillay started his career as an educator (1974–1984) before obtaining a scholarship to Louisiana State University, in the United States. After completing three postdoctoral fellowships in the United States, he joined the International Institute of Tropical Agriculture (IITA) in Nigeria as an associate scientist to work on cytogenetics and molecular biology of bananas and plantains. He was then transferred to Uganda as a scientist and banana breeder/molecular biologist.

He joined Vaal University of Technology in 2007 as an associate professor, was employed at UNISA as professor in 2009, and rejoined Vaal University of Technology in 2010, where his main interests are research and teaching.



Abdou Tenkouano (BSc, MSc, PhD) is the director of the Regional Center for Africa, AVRDC—The World Vegetable Center in Arusha, Tanzania, and formerly a banana and plantain breeder at the International Institute of Tropical Agriculture. Dr. Tenkouano obtained his MSc in plant breeding and his PhD in genetics from the Department of Soil and Crop Sciences, Texas A&M University, College Station, Texas, and his BSc in agronomy and *ingénieur agronome* in rural development (agricultural planning and resource management) from the University of Ouagadougou, Burkina Faso.

Dr. Tenkouano is the author of numerous articles and book chapters in a wide range of topics on banana and plantain. His research interests lie in genetics, breeding, and improvement of crop plants, with a particular focus on improving nutritional quality and host-plant reaction to biotic and abiotic stress factors.

Dr. Tenkouano worked as a researcher at the Institut de l'Environnement et de Recherches Agricoles (INERA) and as a lecturer at the University of Ouagadougou in Burkina Faso before joining the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT, Mali)

as coordinator, West and Central Africa Sorghum Research Network. He then started employment at the International Institute of Tropical Agriculture (IITA, Nigeria) where he was the research team coordinator, Plantain and Banana Research, Genetic Improvement Group, and thereafter became the program coordinator, Plantain and Banana Research.

He moved to Cameroon where he assumed the role of program leader, Diversification of Agricultural Systems in Humid and Sub-Humid Agro-Ecologies for IITA. He was elected councilor, Research for Development Council (RDC), at IITA. Dr. Tenkouano has been involved in the supervision of many MSc and PhD students.

Contributors

Edson Perito Amorim, PhD

Embrapa Cassava and Tropical Fruits
Cruz das Almas, Bahia, Brazil

Vanusia Batista de Oliveira Amorim, PhD

Embrapa Cassava and Tropical Fruits
Cruz das Almas, Bahia, Brazil

Guy Blomme, PhD

Bioversity International
Kampala, Uganda

Ousmane Coulibaly, PhD

International Institute of Tropical Agriculture
(IITA)
Biological Control Center for Africa
Cotonou, Benin

Daniel Leigh Coyne, PhD

International Institute of Tropical Agriculture
(IITA)
Dar es Salaam, Tanzania

Christopher Ashley Cullis, PhD

Department of Biology
Case Western Reserve University
Cleveland, Ohio, USA

Thomas Dubois, PhD

International Institute of Tropical Agriculture
(IITA)
Kampala, Uganda

Simon Eden-Green, PhD

EG Consulting
Larkfield, Kent, UK

Jeanie Anne Fortescue, PhD

School of Plant Biology
Faculty of Natural and Agricultural Sciences
University of Western Australia
Crawley, Australia

Markku Anton Häkkinen, PhD

Finnish Museum of Natural History
Botanic Garden, University of Helsinki
Jyrängöntie, Finland

Shri Mohan Jain, PhD

Department of Agricultural Sciences
University of Helsinki
Helsinki, Finland

Deborah Karamura, PhD

Bioversity International
Kampala, Uganda

Eldad Karamura, PhD

Bioversity International
Kampala, Uganda

Eli Khayat, PhD

Department of R&D
Rahan Meristem (1998) Ltd.
Rosh Hanikra, Israel

Mohammed Mustaffa, PhD

National Research Centre for Banana
(ICAR)
Tamil Nadu, India

Cherukatu Kalathil Narayana, PhD

Division of Post Harvest Technology
Indian Institute of Horticultural Research
Karnataka, India

Bartholomew Nwauzoma, PhD

Department of Applied & Environmental
Biology
Faculty of Science
Rivers State University of Science &
Technology
Port Harcourt, Nigeria

Rodomiro Ortiz, PhD

Sociedad Anomia
Lima, Peru

Michael Pillay, PhD

Biosciences Department
Vaal University of Technology
Vanderbijlpark, South Africa

Nicolas Roux, PhD

Commodities for Livelihoods Programme
Bioversity International
Montpellier, France

Sebastião de Oliveira e Silva, PhD

Embrapa Cassava and Tropical Fruits
Cruz das Almas, Bahia, Brazil

Marimuthu S. Saraswathi, PhD

National Research Center for Banana
(ICAR)
Tamil Nadu, India

Uma Subbaraya, PhD

National Research Center for Banana
(ICAR)
Tamil Nadu, India

Prasanna Suprasanna, PhD

Plant Cell Culture Technology Section
Nuclear Agriculture and Biotechnology
Division
Bhabha Atomic Research Centre
Mumbai, India

David Talengera, MSc

International Institute of Tropical Agriculture
(IITA)
Kampala, Uganda

Abdou Tenkouano, PhD

Regional Center for Africa, AVRDC—The
World Vegetable Center
Duluti, Arusha, Tanzania

Raman Thangavelu, PhD, PDF

National Research Centre for Banana
Tamil Nadu, India

Bradley Till, PhD

Plant Breeding Unit
FAO/IAEA Agricultural and Biotechnology
Laboratory
International Atomic Energy Agency
Vienna, Austria

Leena Tripathi, PhD

International Institute of Tropical Agriculture
(IITA)
Kampala, Uganda

David William Turner, PhD

School of Plant Biology
Faculty of Natural and Agricultural Sciences
University of Western Australia
Crawley, Australia

Richard Henry Wallace, PhD

Department of Chemistry and Physics
Armstrong Atlantic State University
Savannah, Georgia, USA

1 General Plant Morphology of *Musa*

Deborah Karamura, Eldad Karamura, and Guy Blomme

CONTENTS

1.1	Introduction	1
1.2	Botanical Description	2
1.2.1	The Aerial Shoot.....	2
1.2.2	The Pseudostem	2
1.2.3	The Suckers	3
1.2.4	The Leaves.....	3
1.2.5	The Inflorescence.....	5
1.2.6	Bunch Morphology	6
1.2.7	Fruit Morphology.....	8
1.3	The Underground System	9
1.3.1	The Corm.....	9
1.3.2	Root Systems	9
1.3.2.1	The Considerable Size of the <i>Musa</i> Root System	9
1.3.2.2	The Effect of Soil and Climate on Root Systems	10
1.3.2.3	Root Branching: The Lateral Roots.....	11
1.3.2.4	Allocation of Dry Matter to the Shoot and Root System.....	11
1.3.2.5	Genetic Variability in Root Growth and Relationships with Shoot Growth: Refining the Ideotype	13
1.3.2.6	Alternative Methods for Root System Assessment.....	14
1.4	Value of Morphological Variation	15
1.4.1	Introduction	15
1.4.2	Sources of Morphological Variation in Cultivated <i>Musa</i>	15
1.4.2.1	Mutations	15
1.4.2.2	Selection.....	16
1.5	Ecological Adaptation	16
	References.....	17

1.1 INTRODUCTION

In this chapter, *Musa* stands for the genus and musa for the crop that includes both bananas and plantains. This chapter describes the morphology of the musa plant and discusses the potential benefits of morphological diversity. The morphology of *Musa* has been extensively described by Cheesman (1947, 1948a, 1948b, 1950), Simmonds and Shepherd (1955), Champion (1961), De Langhe (1964), Simmonds (1962, 1966), Purseglove (1972), Stover and Simmonds (1987), and Karamura and Karamura (1995). These authors focused on the aerial parts of the plant, but an understanding of the root morphology is also critical, given its role in plant nutrition and anchorage. Root architecture

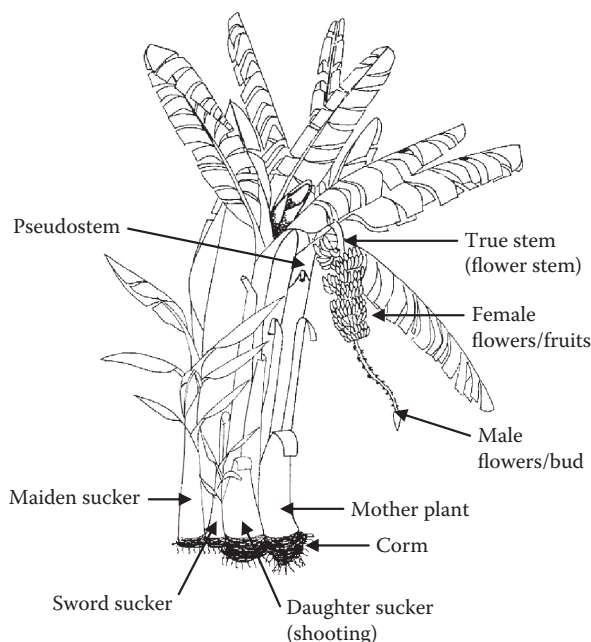


FIGURE 1.1 The morphology of the *Musa* plant: a mat or stool.

has been studied by Champion (1961, 1963), Swennen et al. (1984), Stover and Simmonds (1987), Price (1995), Blomme (2000), and Blomme et al. (2003).

The *Musa* plants constitute some of the largest herbaceous perennial plants that range from 2–9 m in height in cultivated plants and 10–15 m in some wild species. Basically, the *Musa* plant consists of a subterranean stem or corm, an aerial pseudostem, the leaves, and the inflorescence (Figure 1.1). The corm is the true stem to which are attached developing suckers (that perpetuate the life cycle of the plant) and roots; the corm supports the pseudostem, the leaves, and the inflorescence that bears the flowers and subsequently the fruit. The plants are monocarpic, that is, the shoots flower only once and die after fruiting. Together, the corm and attached structures form a stool or a mat.

1.2 BOTANICAL DESCRIPTION

1.2.1 THE AERIAL SHOOT

The aerial shoot is the above-ground part of the *Musa* plant, consisting of the pseudostem, leaves, and the inflorescence. The aerial shoot has the greatest utility and value.

1.2.2 THE PSEUDOSTEM

The pseudostem is made of large overlapping leaf sheaths that are tightly rolled on each other to form a firm cylindrical structure (Purseglove, 1972; Stover and Simmonds, 1987). The aerial stem entirely depends on the leaf sheaths for mechanical support and it essentially provides vascular connection between the leaves, the roots, and the fruit (Stover and Simmonds, 1987). Considerable variation in height, color, and disposition of the pseudostem occurs and is used to distinguish banana cultivars. Thus, the pseudostems of *Musa* AB (e.g., ‘Kisubi’), the AAB (plantains, ‘Silk,’ ‘Mysore,’ and ‘Sukali Ndizi’), and the ABB (‘Bluggoes’ and ‘Pisang Awak’) groups are predominantly yellow-green with little or no pink pigmentation on the undersheaths; the AA (‘Sucrier’) and the AAA (‘Gros Michel’) groups are generally multicolored (Figure 1.2). The pseudostem of the



FIGURE 1.2 Variation in color of the underlying pseudostem in the different *Musa* groups.

AA group tends to be rich chocolate-brown at the junction of the pseudostem–petiole region while the AAA has dull green to green-brown pink-flushed uppersheaths, and a rich mix of green, pink, and rust-brown background with black mottling along the pseudostem length. The East African Highland bananas (AAA-EA), also considered as the Lujugira-Mutika subgroup, display a very variable pseudostem color, the intensity of which varies with environmental conditions. Thus, in the Lujugira-Mutika subgroup, the pseudostem and leaf petioles tend to get darker as altitude increases. Pseudostem height also varies across cultivars and agro-ecological conditions, for example, from 4 m on the plains to 8 m in sheltered valleys for the AAA cultivar ‘Gros Michel’ (Purseglove, 1972). Likewise, Cavendish cultivars may be relatively tall in lowlands where conditions are ideal but shorter at higher altitudes. In the Lujugira-Mutika, the cultivar ‘Nakyetengu’ usually grows up to 2 m and is early maturing, but it can reach 3 m under some conditions and takes then longer to shoot. In general short-stemmed cultivars are susceptible to drought while the tall ones are tolerant (Stover and Simmonds, 1987). Most cultivars have a straight and erect pseudostem, but some cultivars of the Lujugira-Mutika subgroup, such as ‘Mukazi-aranda,’ distinctly display a “creeping” habit from which it derives its name (meaning “crawling lady” in Luganda dialect).

1.2.3 THE SUCKERS

The suckers are lateral shoots that emerge from buds located opposite the base of leaves on the corm. Only 3–4 buds develop into shoots or suckers. Continuous emergence of new suckers perpetuates the corm’s life, giving *Musa* its perennial status. There are two types of suckers: the broad-leaved suckers from superficially placed buds (usually due to damaged corms) and the sword-leaved suckers from deep-lying buds. Thus, unless they are removed for propagation purposes, the aerial part of a plant consists of a large number of shoots forming a clump and the rate of production of shoots varies from a few to several tens, depending on the clone. The growth of suckers is also greatly influenced by the stage of maturity reached by the parent plant, and field operations like pruning or manure/mulch application may also affect sucker production.

1.2.4 THE LEAVES

The corm also consists of the apical meristem from which the leaves and the flowers are initiated. At emergence the leaf is more or less vertical, gradually becoming horizontal and drooping as it

ages. The lamina develops as a rolled cylinder (hence the name *cigar leaf* or *heart leaf*) during its passage through the pseudostem, with the right half rolled upon itself and the left half rolled over the right and the midrib. Purseglove (1972) has attributed the unfurling process of the leaf and other diurnal lamina movements to growth and turgor changes of specific motor cells of the pulvinar band exerting pressure against rigid structures. The pulvinar bands are found where the two leaf blades join the midrib and appear as two pale lines. The leaf blade gradually expands into a large, oblong lamina with a pronounced supporting midrib and well-marked, pinnately arranged parallel veins. The whole process of leaf blade formation is completed when the leaf sheaths narrow on both sides to form the petiole (leaf stalk), which is rounded beneath and channeled above, retaining the crescent-shaped section of the sheath and enlarging at the tip to form the blade. The petiole is variously colored in many banana cultivars. In the *Musa acuminata* cultivars, the petiole coloration has a predominantly reddish to purplish background, with traces of green. Conversely, in cultivars of *M. balbisiana* the petioles are largely green and in many cases waxy. Hybrids have mixtures of green and purplish colors. However, due to somatic mutations, coloration and waxiness may vary even within the same stool.

Leaf disposition on the plant enables them to receive maximum light for photosynthesis. The blade is often torn by the wind and hangs in ribbons from the midrib. New leaves are continually forced up through the center of the pseudostem and expand at the top, where the leaf blades form a handsome crown or canopy that enables the giant herb to outcompete other herbaceous plants for light. Banana leaves are light green in color, smooth and glossy, and attain a very large size, often being used as a temporary shade for other crops. The final leaf to emerge through the pseudostem is much smaller than the rest and curves to protect the developing inflorescence from direct insolation. In some Lujugira-Mutika cultivars such as 'Nsowe' or 'Kataribwambuzi' (translated as "that which cannot be eaten by goats"), the sword suckers continue to produce scale leaves until the plant is taller than 2 meters. This enables the cultivar to grow without being eaten by herbivores that may devour the foliage of cultivars that unfurl their leaves at lower heights. The lamina is thickest near the midrib and thinnest at the edges. The veins of the lamina are parallel as they leave the midrib but become S-shaped as they approach the margins. Stover and Simmonds (1987), quoting Skutch (1930), have indicated that there are about 17,000 veins near the midrib in one lamina half of a large leaf. This venation offers little or no resistance to transverse tearing of the lamina. When this happens, commissural bundles and some of the ground tissue may be destroyed but the vascular connection between the midrib and margin remains intact.

Splitting of the lamina along the veins is a normal occurrence, which may increase the surface area for cooling the plant while reducing transpiration due to suberization of torn surfaces (Taylor, 1969). This results in higher photosynthetic rates in torn leaves because of favorable temperatures and carbon dioxide exchange (Taylor and Sexton, 1972). However, excessive tearing of the lamina may reduce photosynthetic rates and cause yield losses in highland agro-ecologies that are prone to hailstorms (Karamura and Karamura, 1995). Excessive tearing can be prevented with wind breaks, as is common in Uganda where *Ficus* trees are prominent on banana farms (Davis, 1995).

Purseglove (1972) observed that the number of functioning leaves remains approximately constant at 10–15, with a new leaf emerging every 7–10 days. Leaf emergence is influenced by cultivar and ecological conditions, with a pronounced seasonality effect whereby more leaves are produced in wet than dry seasons. Likewise, leaf retention is affected by prevailing soil fertility and soil moisture levels. Air temperature, day length, plantation age, plant density, and plant stature are also known to influence leaf emergence, notably in the Cavendish and Gros Michel subgroups (Allen et al., 1988). The posture of the leaf varies with age, gradually shifting from a tightly rolled vertical cylinder at emergence to an expanded horizontal posture before drooping as the petiole starts to collapse. The lamina eventually senesces and dies, preceding the decay and shedding of the leaf sheath.

Much variability exists in the color, disposition, and waxiness of musa leaves. In general, diploids tend to have more erect leaves, whereas triploids have broader leaves, more or less drooping, carried on vigorous stems. In plantains and other interspecific hybrids, the leaves are yellow-green

(or display various shades of greenness). Conversely, within the Lujugira-Mutika subgroup, there is a wide variability of colors, including the green but variegated leaves of 'Nasuuna,' the purplish leaves of 'Bitambi,' the glossy leaves of 'Namafura,' and various shades of dirty green of the lamina with or without the red midrib. In general, however, color variation is more pronounced in *M. acuminata*, while *M. balbisiana* tends to be monochromatic green.

Musa plants have a large leaf area, ranging from 1.27 to 2.80 m² in dessert bananas (Stover and Simmonds, 1987; Stover, 1988) and 0.68 to 0.92 m² in plantains (Anojulu, 1992). The total leaf area of Cavendish cultivars at flowering is approximately 16.9 to 25 m², providing a closed canopy that protects the soil from the impact of rain and oxidative insolation (Stover and Simmonds, 1987).

Leaf pigmentation and posture may affect photosynthetic efficiency and transpiration rates as described by Brun (1960, 1961a, 1961b, 1962, 1965) and Turner (1972), but there are surprisingly not many recent studies relating leaf morphology to photosynthetic efficiency or transpiration of the existing cultivars.

1.2.5 THE INFLORESCENCE

The apical meristem and flower initiation have been extensively discussed by Barker and Steward (1962), Ram and Steward (1962), Fahn et al. (1963), and Stover and Simmonds (1987). The time of flowering and fruit maturity are both dependent to a large extent on cultivar and environmental conditions. The following events characterize flowering: elongation of the corm internodes; suppression of leaf development, which is replaced by bract development; and, eventually, initiation and development of the inflorescence. Floral initiation occurs with the apical meristem ceasing to produce leaves (about 30–40 leaves in lowland tropical locations) and elongating through the center of the pseudostem, until the inflorescence bud emerges. Inflorescence emergence is described as shooting, at which stage the purplish green/greenish brown inflorescence appears vertical with a pointed tip and a broader base, but it soon bends over due to its weight. The inflorescence is a complex spike with a stout peduncle on which flowers are arranged in nodal clusters on transverse cushions (crown), subtended by large spathe-like bracts that are nearly ovate and usually purple-red in color (Purseglove, 1972). Each nodal cluster consists of two closely appressed rows of flowers, one above the other, and enclosed in a large subtending bract. The bracts and their axillary groups of flowers are arranged spirally around the axis and the bracts closely overlap each other, forming a tight conical inflorescence. In the cultivar 'Lwezinga' (rolled), however, the spiral is continuous and consequently the bracts form one long strip from the female to the male inflorescences. In other cultivars the spirally arranged bracts overlap in such a way that all bracts and flowers within are enclosed tightly and protected in a large bulbous structure. Each bract is a large red/purplish pointed structure that becomes completely reflexed as the flowers develop and that falls from the axis, leaving a large scar when the fruits start to mature. Some clones—for example, *Musa* (AAA-EA) 'Nakawere'—have yellowish-green bracts with streaks of brown, which makes the emerging inflorescence appear as yellow instead of purple. The flowers are bisexual but mostly unisexual in function and there are three types of flowers. The lower bracts of the inflorescence axis enclose the female flowers, the middle few bracts may enclose neutral or hermaphrodite flowers, whilst at the tip of the inflorescence are the male flowers. The female flower consists of an elongated inferior, trilocular ovary of three fused carpels, on top of which six tepals (five united and one free) are implanted, surrounding a thick style and five or six fleshy and nonfunctional stamens (staminodes). The ovary of female flowers constitutes two thirds of the length of the whole flower, and these are the flowers that eventually develop into individual fruits or fingers of the bunch. In the male flowers, the ovary constitutes one third of the length of the flower, usually deciduous, and contains one slender style, five stamens topped by long anthers that do not, however, produce functional pollen. Neutral or hermaphrodite flowers consist of an ovary that does not develop into fruits but forms short useless fingers. The ovary is about half the length of the flower. The stamens of neutral flowers do not produce pollen.

1.2.6 BUNCH MORPHOLOGY

Continued elongation of the main stalk of the inflorescence causes the bunch to hang over, the bracts open and fall, disclosing the female flower clusters or hands. The female flowers undergo further development without being pollinated or fertilized. Growth of the inflorescence stalk is rapid and the hands become separated by several centimeters of stalk. After the emission of a number of hands of female flowers (1–12 depending on the conditions and cultivar), the bud differentiates hands of hermaphrodite and then male flowers. The bracts and the male flowers open and fall, so that eventually a considerable length of stalk separates the male bud from the bunch proper. Further rapid growth causes the individual fruits to fill, and their increased weight bends the main stalk so that the bunch hangs down vertically, although some bananas have upright bunches. Although the physiology, anatomy, and development of *Musa* cultivars are similar, the morphology tends to be variable, particularly for the Lujugira-Mutika subgroup. Karamura (1999) divided this subgroup of bananas into clone sets based on bunch and rachis characteristics (orientation and compactness), persistence of neutral flowers and bracts, and shape and apex of male bud. The lax pendulous banana bunched clone set is Musakala, whereas the most compacted and subhorizontal bunched clone set is Nakabululu. ‘Nakitembe’ and ‘Nfuuka’ clone sets have compact medium-sized oblique bunches but ‘Nakitembe’ has persistent floral parts on the rachis and fruits as well as imbricated male buds (Figure 1.3).

This bunch/inflorescence orientation is common among the widely grown Cavendish and Plantain subgroups. Within the diploids and other groups, including the highland AAA-EA, two more inflorescence orientations can be recognized. Firstly there are those that are carried obliquely (to the pseudostem). The cultivars ‘Nfuuka’ and ‘Mbwarzirume’ are examples of obliquely oriented inflorescences (Figure 1.3). In the “small-bunched” cultivars such as ‘Nabakululu,’ ‘Endirira,’ and ‘Katabunyonyi,’ the orientation is clearly subhorizontal (Figure 1.3). Purseglove (1972) has implied that geotropism is a factor in determining inflorescence orientation, conferring desirable traits for the export trade as manifested by the AAA Cavendish and Gros Michel cultivars. The weight of the inflorescence too appears to play an important role. Among the Lujugira-Mutika, it can be generalized that the heaviest-bunch cultivars such as ‘Rumenyamagali’ tend to have pendulous orientation, while the small-bunched cultivars tend to have subhorizontal inflorescences. The medium-sized bunch cultivars are carried obliquely on the pseudostem. Another factor that appears to influence inflorescence orientation relates to the presence or absence of the male bud, the big purple terminal protuberance on the bunch. It has been observed that cutting off the male bud at shooting makes the inflorescence peduncle fail to elongate and make the U-downward turn, so that a normally pendulous inflorescence ends up subhorizontal. Among the Lujugira-Mutika, for example, ‘Endirira,’ the only AAA cultivar without a male bud, always carries its inflorescence subhorizontally. It would appear that bananas have a “male-bud factor” that is responsible for inflorescence orientation. In breeding programs where bunch weight is a consideration, attention should be given to the male bud factor’s effects on the fruit characters. Cultivars without male buds may be important sources of traits in breeding programs aimed at controlling *Xanthomonas* wilt disease of bananas (Biruma et al., 2007).

The male bud itself varies in many aspects, which include bract arrangement, color, shape and its apex, and presence and degree of waxiness. In the majority of cultivars, male bud bracts are purple and purplish green considering the external side of the bracts. In cultivars ‘Nakawere’ and ‘Tereza’ of the Lujugira-Mutika subgroup, however, the male bract is greenish-yellow with vertical brown streaks. The majority of *M. balbisiana* clones have a continuous uniform crimson color in the internal surface of the bracts (Figure 1.4), whereas in the *M. acuminata* cultivars the crimson color fades to yellow at the base of the bract (Figure 1.4). Male bracts in many cultivars reflex and roll back after opening and eventually fall off while still fleshy. In some cultivars such as ‘Mbwarzirume,’ ‘Namaliga,’ and ‘Nakitembe,’ the bracts persist and form a “protective” cover over the persistent neutral and male flowers (Figure 1.3). Upon falling, the bracts leave prominent scars. Within the



FIGURE 1.3 Bunch orientation in the Lujugira-Mutika subgroup. (a) Subhorizontal 'Nakabululu,' (b) oblique, with bare rachis 'Bitambi,' (c) oblique, rachis with persistent floral parts 'Mbwazirume,' (d) pendulous 'Musakala.'

Lujugira-Mutika subgroup, male bud shape and apex is variable. In general the cultivars with short and fat fingers, closely packed bunch, and oblique to subhorizontal bunch orientation have obtuse-angled male bud apices. Conversely, the long-fingered, loosely packed, and pendulous bunch cultivars have acute male bud apices.

The compound tepal of the male flower is white to cream but with a flush of pink among the plantains, 'Silks,' 'Mysore,' 'Kamaramasenge,' 'Bluggoes,' 'Pisang Awak,' and the 'Red/Green Red.' The lobes of the compound tepal as well as the stigma range from yellow to orange. The anthers are pink among the Lujugira-Mutika bananas and the 'Pisang Awak,' yellow in the 'Bluggoes,' orange in the Cavendish, and cream in most other groups. The ovule arrangement in the ovary does not vary much except being either two or four rowed in the different groups. This ovule arrangement can be clearly seen in the longitudinal sections of fruits.

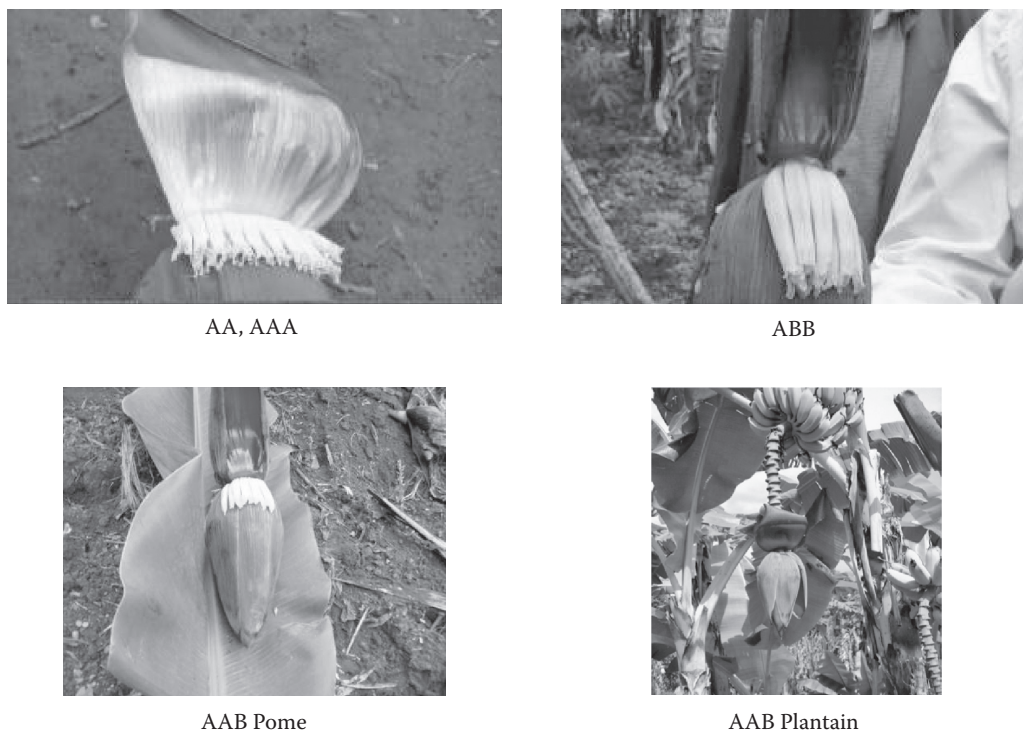


FIGURE 1.4 Variation in the internal bract color: Varieties with a B genome have a homogeneous red color towards the base of the bract.

1.2.7 FRUIT MORPHOLOGY

Both Purseglove (1972) and Stover and Simmonds (1987) provide extensive coverage of the flowers and fruits of the musa plant, based largely on observations made on the Cavendish subgroup and French plantains (AAB), with little reference given to the Lujugira-Mutika subgroup. Seedless fruits develop parthenocarpically from female flowers. However, numerous aborted ovules, carried in an axile placentation in the ovary, can be seen as small brown objects in the center of the fruit. The fruit is elongated, curved, and more or less round in cross-section but with the triangular form of the ovary still visible. At the tip of the fruit, the perianth, androecium, and the style become withered but persist for a short time, separated from the fruit by a brown corky layer. The fruit is protected by an epidermis and an underlying parenchyma layer in which the vascular bundles and a series of latex tubes are found. Inside this “skin” lies the pulp, a tissue of large cells filled with starch that is partially converted to sugars during the ripening process. As the fruit develops, it slowly curves under a negative geotropic response.

There is variability in finger length, and consumers generally prefer long fingers to short ones for all uses. This is true for dessert as well as *matooke* (green cooking) bananas. The longer fingers are easily peeled during *matooke* preparation. Among the Lujugira-Mutika subgroup, the cultivars with long fingers—‘Musakala,’ ‘Muvubo,’ and ‘Nakibizzi’ (also called ‘Mpologoma’)—are increasingly becoming commercial cultivars in Uganda. Fruits are glabrous, less angular, sharply pointed or bottle-necked or almost blunt at the apex, without floral relics. Fruit length varies from 5 cm to more than 30 cm. Within the bunch, fruits vary in their arrangement, position, and number in a hand, shape of fruit, apex, waxiness, and rows and shapes of ovule they contain. The fruits may lack ovules like in ‘Kattabunyonyi’ (AAA-EA), or they may have two or four rows of ovules. There is also variation in the color of fruit skin, pulp (ranging from white, cream, ivory, and beige-pink),

and absence or presence of stalk. Fruit characteristics are increasingly becoming important in the banana chips industry as well as in the table-fruit markets.

1.3 THE UNDERGROUND SYSTEM

The underground system of the *musa* plant consists of a subterranean stem or corm that bears the root system and developing suckers.

1.3.1 THE CORM

The corm is the true stem of the plant, with a cultivar-dependent diameter ranging from 20–25 cm for a typical mature Cavendish and about 15–18 cm for most African plantains. It has short internodes that are completely covered by tightly appressed leaf scars. The longitudinal section of the corm looks like an inverted cone; it is differentiated internally into a central parenchymatous cylinder surrounded by a 1–3 cm thick cortex. The top of the cone is dome shaped, with the apical meristem at the crest of the dome (Price, 1995). During the vegetative growth stage of the *musa* plant, the apical meristem has the form of a flattened dome with little internal differentiation. At the transition from the vegetative to the floral stage, a profound change occurs in the growing point: What was more or less a quiescent mass of cells starts showing signs of intense and general mitotic activity so that the meristematic area becomes convex and rises above the surrounding leaf bases. The outermost layer of the central cylinder consists of a cambium-like meristematic tissue from which roots arise.

1.3.2 ROOT SYSTEMS

The *Musa* root system is a complex structure that supports multiple plant functions. For example, it ensures the optimal uptake of water and nutrients, provides anchorage to the plant, and produces plant growth regulators (De Langhe et al., 1983; Swennen et al., 1984; Stover and Simmonds, 1987; Price, 1995). Research on *Musa* roots started some 70 years ago (Skutch, 1932) predominantly on export dessert bananas, such as Gros Michel (Moreau and Le Bourdelles, 1963) and Cavendish cultivars (Beugnon and Champion, 1966; Lassoudière, 1978; Avilan et al., 1982).

Although extensive breeding efforts have been devoted to improve shoot traits of *Musa*, comparatively little has been done for roots, despite the interdependence of shoot growth and root development. For example, nematodes reduce root growth, which often results in yield decline in *Musa* (Swennen et al., 1988; Gowen and Quénehervé, 1990). While the nematode pest has been considered an important priority in breeding programs at the International Institute of Tropical Agriculture (IITA) (IITA, 1997, 1998), the Centre Africain de Recherches sur Bananiers et Plantains (CARBAP) (Fogain et al., 1996, 1998), and the Fundación Hondureña de Investigación Agrícola (FHIA) (Rowe, 1991; FHIA, 1998), no systematic effort has been devoted to developing root systems that are less prone to nematode damage.

A comprehensive study of the root system of a wider gene pool is required to construct an ideotype target for the genetic improvement of plantains and bananas. Such studies were carried out at the International Institute of Tropical Agriculture (IITA) and by Bioversity International in Nigeria and Uganda, respectively. Experiments focused on elucidating relationships between root and shoot traits, assessing variability in root system size, assessing the biophysical effects on root development, and devising alternative methods for root evaluation (Blomme, 2000).

1.3.2.1 The Considerable Size of the *Musa* Root System

The *Musa* root system is adventitious. Cord roots arise, usually in groups of three or four, from a common primordium (Skutch, 1932; Riopel and Steeves, 1964; Turner, 1970). They grow through the cortex where cytolysis takes place to give space. Before the roots penetrate the soil, their

tips broaden abruptly (Skutch, 1932). They are 5–10 mm thick (Riopel and Steeves, 1964), initially white and fleshy before turning somewhat corky with age. The mature roots have prominent lacunae in the cortex and have large vessels and phloem strands in the central portion of the stele. Xylem elements are formed at a level in the root at which elongation has ceased (Riopel and Steeves, 1964).

Champion and Olivier (1961) reported that, for the dessert banana ‘Poyo,’ the zone on the corm on which roots emerge (i.e., root-bearing zone) is negatively geotropic. Swennen et al. (1988) reported both a positive and a negative geotropic movement or widening of the root-bearing zone of sucker-derived plants. However, they found that the center of activity of the root-bearing zone becomes negatively geotropic with time. The number of cord roots varies considerably depending upon the health status of the plant. A healthy corm can bear 200 to 400 primary cord roots with a total length of 230 m (Summerville, 1944; Robin and Champion, 1962; Beugnon and Champion, 1966). Fawcett (1913) noted that growth rates of the tips may reach 60 cm per month, which is in agreement with later studies with ‘Poyo’ in Côte d’Ivoire, where growth rates of 2–3.5 cm a day were recorded (Lassoudière, 1978). Various factors, such as soil properties, climatic conditions, and pest and diseases, influence the root growth rate (Lassoudière, 1971).

Roots generally spread over 2–3 m and may extend up to 5 m from the plant, but most of the root system occurs within 60 cm of the stem (Avilán et al., 1982; Gousseland, 1983). Root distribution down the soil profile is strongly influenced by soil type (Irizarry et al., 1981) and drainage. Compact soils, impermeable soil layers, high clay content, and saturated soil conditions prevent or reduce root growth (Beugnon and Champion, 1966; Champion and Sioussaram, 1970; Godefroy, 1969; Lassoudière, 1971). Root systems are confined mostly to the upper 40 cm of soil because of unfavorable subsoil conditions. Araya et al. (1998) found that 65% of the total root weight was in the upper 30 cm of soil for the clone ‘Valery’ (AAA) growing on a sandy clay loam in Costa Rica. The same authors found not less than 79% and 88% of the roots in the first 45 and 60 cm of the soil profile, respectively. Besides the laterally spreading roots, there are a limited number of roots that grow vertically (Simmonds, 1966; Summerville, 1939).

Cord roots emerge in flushes for sucker-derived plants. Thus, Swennen et al. (1988) reported that, for the False Horn plantain ‘Agbagba,’ 40 cord roots were formed during the first 3 weeks after planting, from preformed roots that were present in the cortex of the sucker. The number of primary roots remained unchanged for the next 4 weeks, at which time another flush of root emergence was observed (Swennen et al., 1988). Similar emergence flushes were reported by Beugnon and Champion (1966) for the ‘Poyo’ dessert banana and Lavigne (1987) for a dessert banana grown in a rhizotron. New roots are formed continuously until flowering occurs (Champion and Olivier, 1961; Beugnon and Champion, 1966; Turner, 1970; Lavigne, 1987). However, roots may remain alive and functional beyond fruit maturity. For example, the roots of a harvested mother corm were still alive (and presumably functioning) during growth and at the harvest of the daughter stem (Walmsey and Twyford, 1968; Lassoudière, 1980).

The upper surface of corms in aging plantain fields can be seen above soil level (Stover, 1972; Swennen et al., 1988; Swennen, 1990), a phenomenon called “high mat,” and causing newly formed roots to only penetrate the topsoil or die off before reaching the soil surface (Moreau and Le Bourdelles, 1963). The plants become weak and tip over easily because they are no longer firmly based in the soil (Swennen, 1990). Earthing up (adding soil around the plant) only slightly enhances root growth and plant vigor. However, mulch protects the roots (which would otherwise dry out) and improves the ramification and stability of the plants (Swennen, 1990).

1.3.2.2 The Effect of Soil and Climate on Root Systems

Studies on the effects of soil and climate on root growth conducted at IITA stations in Nigeria revealed significant influences of substrate type and climate on root growth (Blomme, 2000). Also, field-grown plants had a relatively larger root system (i.e., lower shoot–root ratio) under low-nutrient conditions. These plants might have invested more dry matter in the root system in

order to explore a larger soil volume to produce a vigorous shoot. In addition, a reduction in soil bulk density (during the first months after plowing and harrowing) significantly enhanced root and shoot growth.

1.3.2.3 Root Branching: The Lateral Roots

The banana cord roots bear numerous lateral roots of much smaller diameter. These lateral roots, bearing root hairs, are believed to be primarily responsible for water and mineral uptake by the plant. Lateral root growth, however, is highly influenced by microenvironmental conditions (Blomme et al., 2003) and genotype (Swennen et al., 1986). As a rule, lateral roots are generally abundant on cord roots growing in organic layers in the topsoil and are absent from those growing deeper in the soil.

The first-order laterals usually emerge 12–15 cm from the tip of a cord root and may be as long as 15 cm (Laville, 1964). Second-order and third-order laterals may also be present (Riopel, 1966). When the apex of a primary cord root is damaged, due to biotic or abiotic factors, two or three first-order laterals may develop into secondary cord roots (Lassoudière, 1977). Lavigne (1987) reported that no secondary cord roots are formed if the damage occurs more than 20 cm from the apex. In a study of 10 varieties, Swennen et al. (1986) found lateral roots to account for up to 98% of total root length, with varietal differences for (1) total root length, (2) relative proportions of cord root and first-order and second-order laterals, (3) length of first-order laterals, and (4) proportion of cord roots covered by laterals. This work suggested the existence of genetic variability for these components of the root architecture.

In *Musa*, first-order lateral roots are initiated basipetally in the apical region of the primary axes. Lateral root primordia can be detected in the pericycle within 450–1200 μm of the apical meristem. Their circumferential position in the pericycle is adjacent to protoxylem poles and opposed to proto-phloem (Riopel and Steeves, 1964; Esau, 1965; Charlton, 1982). Therefore, all laterals arising in association with a given protoxylem form a longitudinal series or rank, the number of ranks per root being equivalent to that of protoxylem poles, which varies between 28 and 34 (Riopel and Steeves, 1964).

The distribution of lateral root primordia in the root tip has been analyzed on the basis of longitudinal and circumferential distances between successive primordia and between particular primordia and the apical meristem (Charlton, 1982). Lateral root primordia were rather regularly spaced in a longitudinal pattern within each rank, each lateral arising at a rather constant proportion of the distance between the root tip and the previous lateral. They were also less likely to occur close to each other than would be expected on a random basis. It was concluded that lateral roots are initiated in a nonrandom dispersed pattern (Riopel, 1966).

Root hairs appear 4–6 cm from the apex of the cord roots and reach their mature size at 8–12 cm distally from their place of origin. Their length may exceed 2 mm.

1.3.2.4 Allocation of Dry Matter to the Shoot and Root System

The percentage dry matter allocated to the shoot and the root portion of a *Musa* plant depends on the developmental stage and planting material (Figure 1.5) (Blomme, 2000). For example, juvenile *in vitro*-derived ‘Calcutta 4’ (AA) and ‘FHIA3’ (AAAB) plants allocated up to 45% of dry matter to the root system just after field establishment. Root dry-matter content declined to about 10–15% at flowering. In contrast, less than 20% of dry matter was allocated to the roots of juvenile sucker-derived ‘Mbi Egome’ (AAB) plants, while the corm contained up to 70% of the plant dry matter (Figure 1.5).

Percentage dry matter invested in the mat root system decreased gradually towards flower emergence (Figure 1.5). For example, there was a clear increase in the shoot–root ratio with increasing age for the *in vitro*-derived ‘FHIA3’ mat. The shoot–root ratio of juvenile sucker-derived ‘Mbi Egome’ plants was relatively high, compared to the *in vitro*-derived plants and was caused by the large corm size of the planting material. As for the *in vitro*-derived plants, the highest shoot–root ratio was observed during the late vegetative phase.

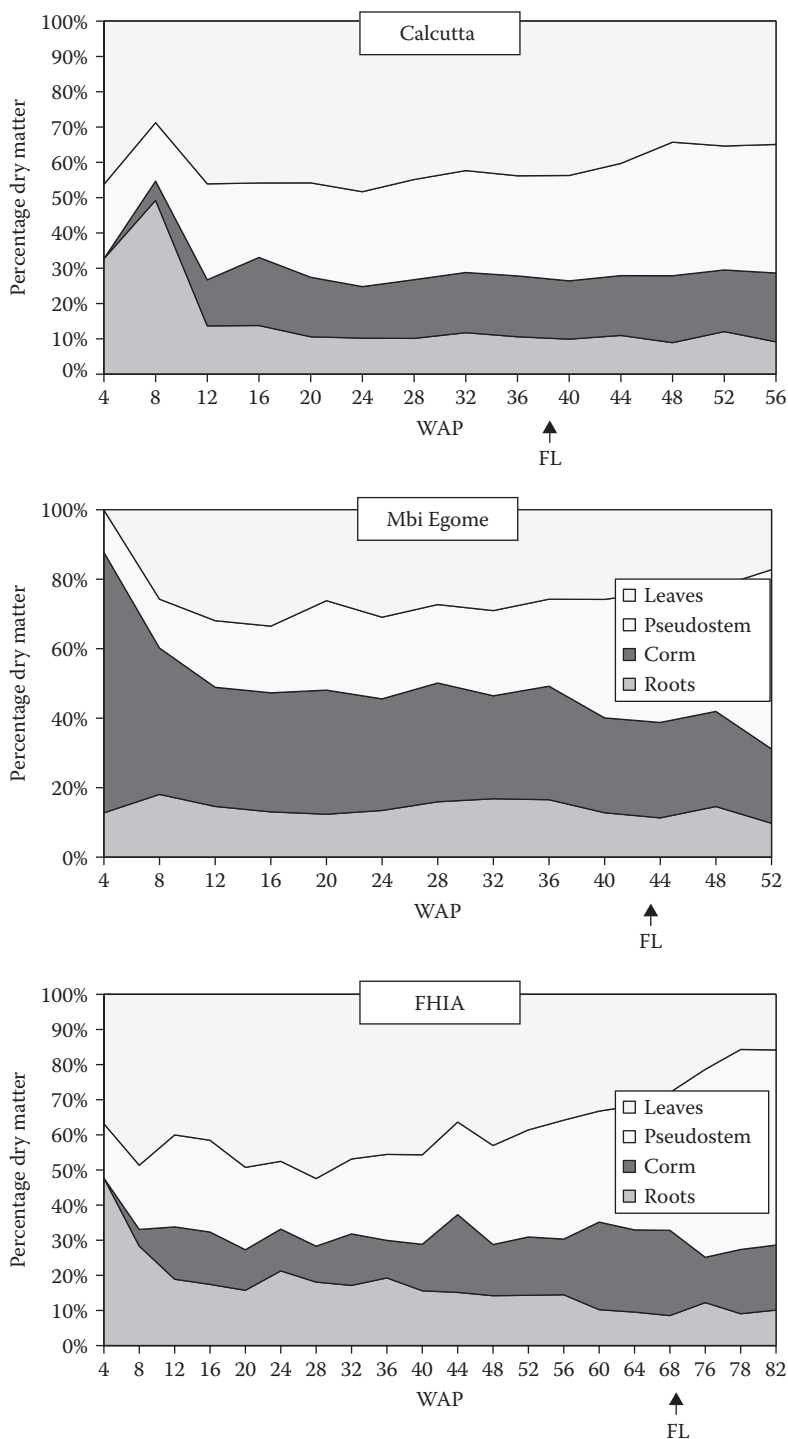


FIGURE 1.5 Dry matter partitioning between roots, corm, pseudostem (including bunch) and leaves in unthinned mats of 'Calcutta 4,' 'Mbi Egome,' and 'FHIA3' from planting until harvest (FL: flower emergence). (From Blomme, G., 2000, The interdependence of root and shoot development in banana (*Musa* spp.) under field conditions and the influence of different biophysical factors on this relationship, PhD diss., K.U. Leuven. Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen, Belgium.)

1.3.2.5 Genetic Variability in Root Growth and Relationships with Shoot Growth: Refining the Ideotype

Strong positive correlations between shoot and root development of a mat are observed during the vegetative and reproductive phases (Blomme, 2000). Thus, vigorous shoot growth in most plantains and cooking bananas is associated with a large root system. In contrast, the semi-dwarf dessert banana cultivar ‘Valery’ has a small root system. Despite the observed variability in root system size between genotypes, shoot–root dry weight ratios are similar formats of a wide variety of genotypes (Figure 1.6). These results indicate that breeding for an increased root system size, in addition to being cumbersome, goes along with breeding for a larger aerial part. The study of segregating populations should, however, be considered as different shoot–root relationships may be observed at the within-population level.

Strong positive relationships between shoot and root traits are also observed for the lateral shoots (i.e., suckers) (IITA, 1999; Blomme, 2000). Therefore, breeding for a regulated suckering (two to three well-developed lateral shoots present during the reproductive phase) may prove to be more beneficial for plant anchorage and productivity of the crop than breeding for a modified shoot–root ratio or root system size of the main plant. Under regulated suckering, lateral shoots will have a vigorous shoot as well as root development. In addition, their large corm size will give stability to the mat. For example, plantain hybrids with a regulated suckering will be less susceptible to toppling compared to plantain landraces, which predominantly exhibit an inhibited suckering.

Studies carried out in Uganda (Kawanda Agricultural Research Institute and Makerere University Agricultural Research Institute Kabanyolo) also found significant and positive relationships between root, corm, and aerial growth traits of complete mats in East African Highland bananas (AAA-EA) during the vegetative and early reproductive stage (Blomme, Ocan, et al., 2004; Bloome, Sebuwufu, et al., 2004; Sebuwufu et al., 2004a, 2004b). Additionally, on-farm and on-station studies focusing on the highland bananas ‘Mpologoma,’ ‘Lwadungu,’ ‘Nakitembe,’ ‘Mbawazirume,’ and ‘Kibuzi,’ the

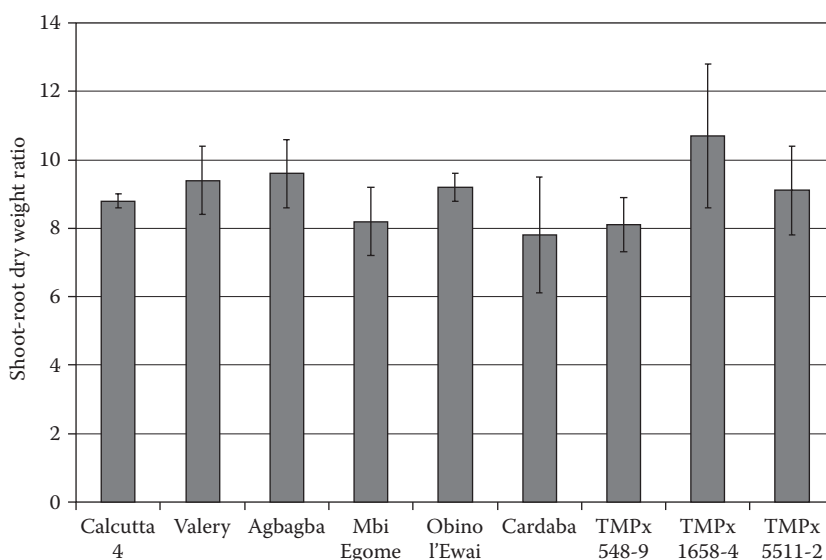


FIGURE 1.6 Shoot–root ratio for the mat of nine *Musa* spp. genotypes at flower emergence of the plant crop [‘Calcutta 4’ (AA); ‘Valery’ (AAA); ‘Agbagba,’ ‘Mbi Egome,’ and ‘Obino l’Ewai’ (AAB); ‘Cardaba’ (ABB); ‘TMPx 548-9,’ ‘TMPx 1658-4,’ and ‘TMPx 5511-2’ (tetraploid plantain hybrids)]. (From Blomme, G., 2000, The interdependence of root and shoot development in banana (*Musa* spp.) under field conditions and the influence of different biophysical factors on this relationship, PhD diss., K.U. Leuven. Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen, Belgium.)

dessert banana ‘Sukali ndizi’ (AAB), the plantain ‘Gonja’ (AAB), and the beer banana ‘Kayinja’ (ABB) revealed strong relationships between bunch weight, root, corm, and aerial growth traits. Hence, poor root development will adversely affect shoot and leaf canopy development and as a result reduce yield. Reciprocally, when leaves are affected by black leaf streak disease, the root system is reduced.

1.3.2.6 Alternative Methods for Root System Assessment

Two man-days are needed to excavate, wash, and assess the root system of one mature *Musa* plant. Also, attempts to correlate root growth of juvenile plants with that of adult plants were inconclusive, indicating that an early assessment of root system growth of juvenile plants may not give sufficient information about the root system size and development of mature plants (Blomme, 2000). Therefore, methodologies for fast and nondestructive root system assessment were developed (IITA, 1999; Blomme, 2000).

Due to the strong relationships between shoot and root traits, regression models were obtained to estimate root traits from easily measurable shoot traits (Table 1.1). More than 90% of the variability in root traits could be explained by the variability observed in shoot traits. However, as the shoot–root ratio is dependent on the developmental stage of a plant and on environmental conditions (Blomme, 2000), fine-tuning of these models will be needed when assessing plants grown under different environments.

Core root samples taken around a plant can also provide adequate information on the variability in mat root system size (Blomme, 2000). This method only takes about 5% of the time needed to excavate and assess the root system of a mature plant. These alternative methods may provide breeders and especially nematologists with adequate information on the roots of a *Musa* plant.

TABLE 1.1
Regression Models to Predict Root System Characteristics

Trait#					
Trait#	LA [^]	PC	HS	PL	R ²
DR	0.001628***	0.596934**	—	—	0.93
NR	0.001459***	1.255633***	—	—	0.93
LR	0.066704***	23.476717**	—	—	0.94
AD	—	0.093835***	—	0.681434***	0.97
TL	0.099478***	—	14.69139***	—	0.92
TD	0.002066***	0.426590	0.17142*	—	0.93

Source: Blomme, G., The Interdependence of Root and Shoot Development in Banana (*Musa* spp.) under Field Conditions and the Influence of Different Biophysical Factors on This Relationship, PhD diss., K. U. Leuven, Faculteit Landbouwkundige en Toegepaste Biologische Wetenschappen, Belgium, 2000.

Note: Plants are 20 weeks old, using aerial growth characteristics and ploidy level as independent variables. #: LA: leaf area (cm²); PC: pseudostem circumference (cm); HS: height of the tallest sucker (cm); PL: ploidy level; DR: root dry weight (g); NR: number of cord roots; LR: cord root length (cm); AD: average basal diameter of the cord roots (mm); TL: cord root length of the mat (mother plant and suckers) (cm); TD: root dry weight of the mat (g). *, **, *** Significant at $P < 0.05$, 0.01, and 0.001, respectively. ^: independent variables.

1.4 VALUE OF MORPHOLOGICAL VARIATION

1.4.1 INTRODUCTION

Musa breeding depends on variations existing within accessions, cultivars, landraces, or wild taxa related to crops. These genetic resources need to be investigated and evaluated to provide information on variation if they are to be utilized efficiently (Pickersgill, 1988). Crop-improvement strategies make use of information on variation with regard to yield, physiology, diseases, and pest responses as well as morphology.

Morphological variation, which is a prerequisite for breeding, constitutes one of the oldest indicators of diversity. Morphological variation is based on the scoring of numerous descriptors that can easily be observed and accessed without any special technical skill and at low cost. However, morphological variation is not a direct expression of the genome and can be influenced by environmental effects so that it expresses more of the phenotype than the genotype (Perrier, 1993).

1.4.2 SOURCES OF MORPHOLOGICAL VARIATION IN CULTIVATED *MUSA*

Variation is the basis of speciation, when acted upon by selection. In nature, variation is a result of basic evolutionary forces—mutation, recombination, genetic drift, and selection acting in different ecologies over time. In clonally propagated populations, however, variation may occur through mutations although other mechanisms can cause variation in banana (Nyine and Pillay, 2010). Selection is largely mediated through environmental factors in different areas or habitats.

1.4.2.1 Mutations

Bananas and plantains are clonally propagated and it is generally known that clonal propagation reduces variation within a population because relatively few genotypes are selected for conservation and use. However, clonal propagation can conserve heterozygotes as well as homozygotes, and the only source of variation in these *musa* plants has been mutations. One example of a group of bananas is the Lujugira-Mutika subgroup found in East Africa. These bananas were introduced in the region by Arab traders from India, through Madagascar on the eastern coast during the 15th century (Simmonds, 1962). Like all other cultivated bananas, they are vegetatively propagated and there is hardly any variation in the suckers being produced by the mother plant except through mutations and the chimerical nature of the plant, a condition that is not yet well understood. When a banana plant is propagated, it is considered to be genetically the same but in reality, among the AAA-EA cultivars, not all suckers produced on the same mat are always phenotypically identical (Karamura et al., 2004). The meristematic tissues of the mother plant may be giving rise to highly variable suckers. Plants composed of two or more genetically distinct tissues have been called chimera (Huxley, 1940; Crane and Laurence, 1956). Although chimerism has been observed in bananas for a long time, not only is its frequency of occurrence not well understood (De Langhe, 1964; Simmonds, 1966) but also not many in-depth studies have been attempted. However, the phenomenon is believed to be a major source of variation within the crop, a process that generates genetic and phenotypic variation that farmers have continued to exploit through selection breeding.

A number of morphological characters are prone to mutations, including plant stature, bunch and fruit shapes, and astringency in fruit pulp. The implications of chimerism are not usually obvious, depending on which traits of the plant have been affected. In the Lujugira-Mutika subgroup, the phenomenon varies, and its implication for genetic variability and conservation on farm has not been elucidated. It is not known how chimeric traits are selected by a given community and subsequently conserved on farm in banana-based farming systems (Karamura et al., 2008). Yet the farmers' role in initiating and adjusting the numbers and proportions of cultivars on farm based on different cultivar traits is fundamentally important to the way landraces should be evaluated and maintained in *ex situ* and *in situ* collections.

All Lujugira-Mutika bananas are resistant to *Fusarium* wilt races 1 and 2. Conversely, with regard to black Sigatoka, banana weevils, and nematodes, there is variation in resistance even within the same clone set. Similarly within the same subgroup, variation with regard to female pollen fertility exists, with the 'Nfuuka' clone set being the most fertile and the 'Musakala' clone set the least fertile; 'Nakitembe' and 'Nakabululu' clone sets fall in between. All these variability options can and have been exploited for both selection and crossbreeding as well as for commercial purposes.

1.4.2.2 Selection

The process of selection produces patterns of variation in crop populations as well as patterns of individual variation that would be useful to breeders. The former is of primary importance in evolution and the latter in identification. The example of the East African Highland bananas (EAHB) again illustrates this. Since their introduction in the East African region, the EAHB have diversified in this region, not only because of mutations but also due to continuous natural and farmers' selection. The morphological variation pattern existing in these bananas has been as a result of the action of selective forces on the genotypes, and such variation would presumably have an evolutionary significance to ensure survival of the selected types and lead to ultimate improvement and spread of these bananas. Some variation patterns might have little or no evolutionary significance. Bunch and fruit characters experience great selection pressure, particularly the compactness and shape of the bunch and fingers, since these are very important to farmers and other consumers for whom compactness and shape of the bunch in addition to fruit size and shape are known commercial traits. A compact, medium, shaped bunch can easily be packed, transported to market, and sold quite easily in that respect. Cylindrical or very lax bunches or variegated and astringent fruits are not preferred by traders, although they have also arisen through mutations (Rubaihayo and Gold, 1993). This farmers' selection breeding has been based largely on continuously changing morphological characteristics attributed to chimerism, and this has been the basis for plant identification and nomenclature since cultivar names are mainly based on the phenotypic characteristics of cultivars. If, for example, a new mat produces suckers whose characteristics differ from those of the mother mat, farmers can either discard the "different" suckers, or maintain them as mutants of the mother plant or as a different cultivar to which they give a name depending on whether the differences between mother and daughter are major or minor. The major differences with acceptable qualities will readily be selected and adopted widely by farmers and subsequently by traders and consumers. Hence a daughter plant may receive a name different from the mother if a major and consistent difference occurs. At the farm level, the major phenotypic and nomenclature changes are always associated with the floral parts, probably because these are most used by the farmers. Minor changes that do not normally alter nomenclature include changes in the color of the pseudostem, petioles, and midribs. In this case, the daughter plant retains the name of the mother plant but receives a second part of the name to indicate the minor change. The identities of these cultivars become crucially important tools in selection breeding and conservation efforts because the value, potential, and limitations of each clone will very much be influenced by their characters and correct identity. In summary the structure and morphological variation pattern in a crop varies according to its breeding system and the amount, intensity, and direction of selection to which they have been subjected (Pickersgill, 1994).

1.5 ECOLOGICAL ADAPTATION

The variability within a clonal population is more phenotypic than genotypic and many times is caused by slight environmental differences within the habitat. Clonal material is ideal for the study of morphological and physiological effects of diverse environmental factors on plants from different areas or habitats. When breeders deal with clones, particularly with those coming out as new materials from their breeding programs, it is important that they are able to recognize

differences in one cultivar from another. Distinction of one cultivar to another has increasingly gained emphasis in connection with legislation about breeders' rights in different countries. The requirement is further accentuated by traders and buyers who must, in many instances, exercise care in selecting the correct cultivar for their needs. In addition, different growing conditions impose different characteristics to essentially the same clone. For example, 'Sukali Ndizi' (AAB) from dry regions is smaller in both finger and bunch sizes than that from wetter regions but the consumer markets prefer the former to the latter. Furthermore, the farmer wants to get the right price for the particular cultivar he grows. Thus, primarily for economic reasons, identification based on morphology is most important at the cultivar level and is only possible when morphological variation allows it in various types of environments. Since breeders tend to look much more for resistance and yields, it is not yet fully understood whether the observed phenotypic variability in their new materials imparts resistance or tolerance to biotic and edaphic constraints that threaten the very existence of the crop. Morphological variability seen in a new cultivar may be a reflection of genetic elasticity, and its understanding will advance efforts to exploit its potential. It therefore follows that breeders need to focus on the interrelationships between morphological variability on one hand and the plant's ability to survive environmental constraints on the other. The following examples briefly explain such interrelationships between morphological variability, food texture, and distribution incidences.

The Lujugira-Mutika bananas have been divided into four morphologically distinct clone sets, and the clone sets bring together clones that share characteristics important to farmers and consumers, though these characteristics were not used in grouping the clone sets (Pickersgill and Karamura, 1999). The clones in 'Nakabululu' and 'Nakitembe' clone sets sucker profusely, mature quickly, produce soft-textured/flavored food, and are widely distributed but not rich in diversity. Most clones in 'Nfuuka' are slow to produce suckers, take a long time to mature, and produce hard-textured food, not evenly distributed but rich in diversity. However, one subcluster of 'Nfuuka' shares with 'Nakabululu' and 'Nakitembe' the characteristics of rapid maturity and production of some textured food. 'Nfuuka' is more heterogeneous than other clone sets and overlaps with most of them. Its name means "I am changing" and reflects the farmers' perception that somatic mutations are particularly frequent in these clones. The final clone set, 'Musakala,' contains the higher-yielding clones (e.g., 'Lumenyamagali,' which means "I break bicycles"), grown on a commercial scale to supply urban markets. Clones in this set tend to be intermediate with regard to time to maturity and in quality of their food.

In conclusion, morphological variation in clonal crops such as bananas is mediated through mutation (though there is an increasing number of a crossbreeding program), thought to be somatic in nature, and through a phenomenon called chimerism. Both chimeric and somatic mutation variants are then subjected to natural and farmer selection in response to the changing environment and/or economic conditions to widen the variation and exploit its potential.

REFERENCES

- Allen, R.N., E.B. Dettman, G.G. Johns, and D.W. Turner. 1988. Estimation of leaf emergence rates of bananas. *Aust. J. Agric. Res.* 39:53–62.
- Anojulu, C.C. 1992. The role of plantain in environment (Monograph) IITA, Plantain Programme.
- Araya, M., A. Vargas, and A. Cheves. 1998. Changes in distribution of roots of banana (*Musa* AAA cv. Valery) with plant height, distance from the pseudostem, and soil depth. *J. Hort. Sci. Biotechnol.* 73(4):437–440.
- Avilán, R.L., R. Meneses, and R.E. Sucre. 1982. Distribución radical del banano bajo diferentes sistema de manejo de suelos. *Fruits* 37:103–109.
- Barker, W.G. and F.C. Steward. 1962. Growth and development of the banana plant. *Ann. Bot.* 26, 389–423.
- Beugnon, M. and J. Champion. 1966. Etude sur les racines du bananier. *Fruits* 21:309–327.