Baffour Badu-Apraku · M.A.B. Fakorede

Advances in Genetic Enhancement of Early and Extra-Early Maize for Sub-Saharan Africa

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Foreword

About 300 million people of sub-Saharan Africa (SSA) depend on maize as a staple food. During the last three decades, there have been tremendous strides in increasing maize production and productivity in the region due to the development of early, extra-early, intermediate-, and late-maturing maize varieties with improved resistance to *Striga hermonthica*, the maize streak virus (MSV), downy mildew, and stem borers along with tolerance to drought for the forest, forest–savanna transition, and savanna agroecological zones. Reviewed in this book are the breeding methodologies and strategies that have been adopted for the improvement of the early and extra-early varieties that have largely contributed to the phenomenal increases in maize production and productivity in the savannas, especially the northern fringes of the Guinea savanna and the Sudan savannas.

Even though there are many books on the principles and practices of maize breeding and improvement, the major focus of these books has been on temperate maize. This book focuses on the principles and practices of maize improvement of tropical maize with special emphasis on early and extra-early maize. This book should therefore be of great interest to maize breeders, graduate students, and professors of maize breeding interested in the genetic enhancement of maize to feed the increasing population of sub-Saharan Africa. The book should also be useful to national agricultural research and extension systems, nongovernmental organizations (NGOs), seed companies, community-based seed organizations, and policymakers interested in generating wealth from agriculture and providing agricultural solutions to alleviate hunger and poverty in the sub-region.

The material in this book is based on the wealth of knowledge accumulated during the last three decades in breeding early and extra-early maize for tolerance/resistance to biotic and abiotic stresses in SSA and the experience gained over the years in offering training courses in maize improvement and seed production to young scientists and technicians of the sub-region. Thus, this book on maize improvement is unique to the extent that it is based on the practical experience and realities in SSA and is also relevant to the situation and circumstances of the maize breeders and farmers of the sub-region.

Director General, IITA, Ibadan, Nigeria N. Sanginga

Preface

Maize production in SSA has been greatly constrained by many biotic and abiotic stresses. Most of these constraints cut across countries with similar agroecological zones, the most important being drought, low soil fertility, *Striga* infestation, stem borers, and maize streak virus (MSV). The last two are more important in the more humid southern zones. In addition, farmers face a variety of policy and institutional constraints, such as undeveloped markets, the high cost of farm inputs, high labor requirements for land preparation and weeding, lack of good-quality seed, and difficult access to credit, all of which inhibit increases in maize yields and production. Improved maize varieties grown under controlled and well-managed conditions on research stations can produce average yields of 4–5 t/ha in the forest zone and 5–8 t/ha in the savanna zones, but the average yield in the farmers' fields is currently about 1.5 t/ha, one of the lowest in the developing world. National maize scientists of West and Central Africa (WCA), in collaboration with farmers, identified, in 1998, maize production constraints as the need for improved crop varieties, appropriate natural resource and crop management, plant health, postharvest technologies, socioeconomic practices and conditions, as well as the need to improve human capacity. During the last three decades, maize breeders at IITA in collaboration with national scientists of WCA have addressed ecologically specific adaptive traits, including the varietal development of resistance to MSV, *Helminthosporium* leaf blight (*H. maydis*), *Striga* spp., and stem borers, as well as tolerance to drought and low soil nitrogen (N). Also critical was the development of a vibrant seed sector. In spite of the substantial effort in breeding and the large number of new varieties released in WCA since the 1990s, impacts of maize research and development have not been as high as expected, partly due to the nonavailability of good-quality improved seeds for farmers. Public sector production and marketing of seeds have achieved mixed results but have often been limited by inadequate resources and poor management.

The early and extra-early maturing varieties are used for filling the hunger gap in the savannas of SSA, and this has allowed the early and extra-early varieties to spread into the shorter rainfall areas which for a long time had been precluded from maize production. Within the framework of the IITA Maize Improvement Program, the ultimate goal of the early and extra-early maturing breeding unit has been to improve maize in the two maturity groups for biotic and abiotic stress tolerance. This program, undertaken in collaboration with NARS scientists of WCA, focused on developing breeding materials with resistance/tolerance to the major biotic and abiotic stress factors, including *Striga*, drought/heat stress, low soil N, MSV, rust, and leaf blight, as appropriate in all agroecologies. The program has since inception focused on four strategies for the two maize maturity groups: development of stress-tolerant (*Striga* resistant, drought and low-N tolerant) maize source populations for recurrent selection; improvement of source populations using recurrent selection with reliable artificial field infestation and screening methods to increase resistance to relevant stresses in the breeding materials; extraction of open-pollinated varieties (OPVs), inbred lines, and hybrids from source populations; and germplasm enhancement.

This book reviews the methodologies, strategies, and advances in maize improvement in SSA during the last three decades with special emphasis on the early and extra-early maize. Some aspects of research activities relevant to the intermediate- and late-maturing maize in which substantial progress has been made in improving resistance to downy mildew, stem borers, and aflatoxin-producing fungi by IITA maize breeders during the last three decades have also been reviewed in the book. Despite the tremendous progress made in developing and promoting maize varieties and hybrids, over one-third of the maize area in WCA is still planted with farmer-saved, low-yielding varieties (Arega et al. 2009). At the same time, many farmers continue to use seed saved from their farms because improved varieties are either not accessible to them or they regard improved seed as too costly. Since maize is an open-pollinated crop, farm-saved seed can quickly lose its genetic purity, implying that farmers who wish to grow improved varieties must replace their seed regularly, annually in the case of hybrid varieties and every 2–3 years in the case of OPVs. The development and dissemination of maize varieties and hybrids adapted to the increasingly drought-prone conditions and *Striga* endemic savannas require ongoing support to avert hunger and malnutrition in SSA.

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June 2017

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Contents

Part I Introduction

Part II Maize Breeding Procedures in Sub-Saharan Africa

Part III Breeding for Specific Traits

Part IV Improving Breeding Efficiency

Part V Potential Role of Early and Extra-Early Maize in Sustainable Food Security in Sub-Saharan Africa

Abbreviations and Acronyms

AMMI	Additive main effect and multiplicative interaction
ANOVA	Analysis of variance
ASI	Anthesis–silking interval
GGE	Genotype–genotype environment
CGIAR	Consultative Group on International Agricultural Research
CIMMYT	(Centro Internacional de Mejoramiento de Maíz y Trigo) International Maize and Wheat Improvement Center
CRI	Crops Research Institute
DA	Days to anthesis
DAS	Days after mid-silk
DAP	Days after planting
DC	Double cross
DH	Doubled haploids
DS	Days to silking
DTC	Double topcross
DT	Drought tolerant
DUS	Distinctness, uniformity, stability
DTMA	Drought-Tolerant Maize for Africa
E%	Emergence percentage
EASP	Ear aspect
EFPD	Effective filling period duration
EI	Emergence index
EPP	Number of ears per plant
ERI	Emergence rate index
ESA	East and Southern Africa
EV	Experimental variety
FAOSTAT	Food and Agriculture Organization Corporate Statistical Database
G%	Germination percentage
GCA	General combining ability
GEI	Genotype by environment interaction
GI	Germination index

GR	Growth rate
GS	Genomic selection
GWS	Genome-wide selection
HST	Hybrid seed technology
HSGCA	Heterotic groups' specific and general combining ability
ICIPE	International Center for Insect Physiology and Ecology
IITA	International Institute of Tropical Agriculture
IPTT	International Progeny Testing Trial
LSD	Least significant difference
KARI	Kenya Agricultural Research Institute
MAS	Mid-altitude savanna
MAS	Marker-assisted selection
MABC	Marker-assisted backcrossing
MARS	Marker-assisted recurrent selection
MB	Marker-assisted breeding
MCMC	Markov chain Monte Carlo algorithms
MH	Mid-parent heterosis
MI	Multiple stress tolerance base index
MLN	Maize lethal necrosis
MSC	Modified single cross
MSV	Maize streak virus
MTWC	Modified three-way cross
NARIs	National Agricultural Research Institutes
NARS	National Agricultural Research Systems
NARES	National research and extension system
NIP	Noninbred parent
NGS	Northern Guinea savanna
OPVs	Open-pollinated varieties
PASP	Plant aspect
PCR	Polymerase chain reaction
PHMD	Plant Health Management Division
PLHT	Plant height
PM	Physiological maturity
QEI	QTL by environment interaction
QPM	Quality protein maize
QTL	Quantitative trait locus
RAPD	Random amplified polymorphic DNA
RFLP	Restriction fragment length polymorphisms
RGR	Relative growth rate
RILs	Recombinant inbred lines
SCA	Specific combining ability
SAFGRAD	Semi-Arid Food Grain Research and Development
SNP	Single nucleotide polymorphism
SSLP	Simple sequence length polymorphism
SSA	Sub-Saharan Africa

SSR	Simple sequence repeat
STRs	Short tandem repeats
TC	Topcross
TWC	Three-way cross
USA	United States
VC	Varietal cross
WA	West Africa
WAP	Week after planting
WARDA	West Africa Rice Development Association
WCA	West and Central Africa
WECAMAN	West and Central Africa Collaborative Maize Research Network

List of Figures

List of Tables

List of Plates

Part I
Introduction

Chapter 1
Maize in Sub-Saharan Africa: Importance and Production Constraints

1.1 Production and Role of Maize in Sub-Saharan Africa

Maize (*Zea mays* L.) is one of the most important food crops worldwide. It is also the most important staple food in sub-Saharan Africa (SSA) and is critical to food security with more than 300 million Africans depending on it as their main staple food. It is the staple food for 24 million households in East and Southern Africa and is annually planted over an area of 15.5 million hectares (Thorne et al. 2002), and it is a major cereal crop in all countries of SSA. In West and Central Africa (WCA), for example, it has a remarkable production potential and produces higher yield than other cereal crops. From the time of its introduction to SSA about 500 years ago, it has risen to become a staple crop with numerous varieties developed for the various agroecological zones in SSA. Maize currently covers 25 million hectares in SSA, largely on smallholder farms, and it accounts for about 20% of the calorie intake of 50% of the population. It was domesticated in Mesoamerica during prehistoric times. In the late fifteenth century, explorers and traders introduced it to other countries. Maize spread to the rest of the world due to its ability to thrive in diverse climates. Maize and rice are the second most widely grown crops in the world with wheat as number one. No other crop produces more grain than maize. Industrialized countries largely use it as livestock feed. In sub-Saharan Africa, maize is the most widely grown crop and is a staple food for an estimated 50% of the population. Out of 53 countries in SSA, 46 grow maize—only Equatorial Guinea, Liberia, St. Helena, Seychelles, Western Sahara, Mayotte, and British Indian Ocean Territories do not grow it. Maize production covers the largest land area in Nigeria (7th in the world and 2.4% of the total), followed by Tanzania and South Africa. The top producers are South Africa (9th in the world but only 1.5% of the total), Nigeria, and Ethiopia. About 10% of South Africa's maize is exported. In terms of food security, it is the most important cereal crop in sub-Saharan Africa. Maize is well integrated into the farming system, and a number of maize-based cropping systems are

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prominent throughout the region. It is now cultivated in the drier traditional sorghum (*Sorghum bicolor* L.) and millet (*Penisetumtyphoides* L.) niches in the savannas of West and Central Africa (WCA), a feat made possible by the development and availability of extra-early and early-maturing varieties. These varieties help to fill the hunger gap that occurs toward the end of the dry season. They are not only able to escape drought but are also tolerant to drought that occurs sporadically during the growing season. These varieties are therefore capable of giving reasonable yield in dry environments where intermediate cycle maize varieties fail. Early and extra-early maize cultivars are more responsive to fertilizer application, are faster in maturity, and can be harvested much earlier in the season than the adapted sorghum and millet crops. There is also a high demand for the early and extra-early maize in the WA forest zone for peri-urban maize consumers because they allow farmers to market the early crop at a premium price in addition to being compatible with cassava (*Manihot esculenta* Crantz), cowpea [*Vigna unguiculata* (L.) Walp.], and soybean [*Glycine max* (L.) Merr.] for intercropping (IITA, 1992). Another important advantage of the early and extra-early maize is that they provide farmers in the various agroecological zones with flexibility in the dates of planting. The varieties can be planted when the rains are delayed or could be used for early plantings when the rainfall distribution is normal (Badu-Apraku et al. 2012, 2017).

In addition, through collaboration between the National Agricultural Research Institutes (NARIs) and the International Institute of Tropical Agriculture (IITA), many of the varieties have been developed with resistance to prevalent diseases, including maize streak virus, rust, and blight. Some varieties have been developed for high productivity under infestation by the parasitic weed, *Striga hermonthica* (Del.) Benth, and low soil nitrogen that are characteristic of the production systems in the savannas of the sub-region. Fakorede et al. (2007) analyzed maize production trends in the WCA sub-region using FAO data from 1980 to 2003 and found an increasing trend at the rate of 0.363 million tons per annum. Between 1987 and 2007, the area cultivated to maize increased from about 8 to 12 million ha (FAO 2009). The diversity of food uses and expanding opportunities for commercial and industrial utilization of maize ensure its continued eminence among cereals and other important food crops in the sub-region. The rising profile of maize and the impact generated by the crop in WCA have been aptly described as a revolution (Fakorede et al. 2003). The crop is widely considered to be the vehicle for a green revolution that has already commenced (Abalu 2003).

In SSA, a considerable proportion of the maize produced is used for human food in various forms. Physiologically immature field maize, known as “green maize,” is consumed as a snack after roasting or boiling as “corn on the cob.” Dried maize grain is milled and consumed as a starchy base in a wide variety of gruels, porridges, soups, and pastes. Dough made from the milled grain can also be cooked or fried in oil. The importance of maize as food is associated with the nutritive value of the kernels, and research has revealed large genetic variability for nutritive values of maize in WCA. Depending on the maize type, an average of 70–75% of the kernel is composed of carbohydrate, which is present mostly as starch and sugar. Because of its high carbohydrate content, maize is a major source of calories.

The kernel also contains protein (8–15%); about 80% of the protein is in the endosperm, while the remaining 20% is contained in the germ. Other components of the kernels are fat (or oil), minerals, and vitamins. The vitamins in maize kernels occur mostly in the germ and in the outermost layer of the endosperm. Carotenoids, which are precursors of vitamin A, are present in yellow but absent in white maize. The quality of the protein in maize kernels is relatively poor due to the low content of lysine and tryptophan—two amino acids that are essential for human nutrition. Years of research by maize breeders at the International Maize and Wheat Improvement Center (CIMMYT), the IITA, and the Crops Research Institute (CRI) of Ghana have resulted in the development of quality protein maize (QPM) which contains twice the quantity of lysine and tryptophan in normal maize. "Obatanpa," a Ghanaian word that means *good nursing mother*, was the first QPM variety developed and released in SSA by the CRI, Ghana. This variety is widely grown by farmers, not only in Ghana but in most other SSA countries and beyond. IITA research scientists, in collaboration with scientists from other parts of the world, have been developing nutrient-dense maize varieties, with funding support from the Challenge Project of the Consultative Group for International Agricultural Research (CGIAR).

1.2 Industrial Uses of Maize in Sub-Saharan Africa

Various alcoholic drinks are prepared from maize. It is also important as feed for poultry and other livestock industries, constituting up to 40–75% of feed rations. The dry grain of popcorn types will swell and burst when heated, forming a popular snack food. Dry milling of maize grain produces corn meal, corn flour, and corn oil. Cornstarch, obtained from the wet milling process, is used for food, textile and paper sizing, laundry starch, dextrines, and adhesives such as the gums used for stamps and envelopes. Corn syrup, used as a sweetener, is also made from cornstarch. Other industrial products obtained from maize through distillation and fermentation include ethyl alcohol, butyl alcohol, propyl alcohol, acetaldehyde, acetic acid, acetone, lactic acid, citric acid, glycerol, and whisky. Ethanol is now mixed with gasoline to create ethanol fuels for vehicles. The demand for maize as food, feed, and industrial raw material continues to increase in WCA. This increasing demand is fueled by expanding populations and rising incomes in all countries of the sub-region. The yearly per capita consumption of maize is greatest in Benin Republic (87 kg), followed by Togo (70 kg) and Ghana (45 kg).

1.3 Constraints of Maize Production in Sub-Saharan Africa

The constraints to maize production in SSA can be grouped into two broad categories—biotic and abiotic. Among the biotic constraints are maize streak virus; weeds, including parasitic weeds such as *Striga* (notably *Striga hermonthica*) and noxious weeds such as *Imperata cylindrica*; insect pests, particularly stem borers; ear rot organisms, the *Bipolaris maydis* and *Exserohilum turcicum*; the gray leaf spot; downy mildew; and the maize lethal necrosis (MLN). *Striga* is considered a major biotic constraint to cereal crop production in SSA. Yield losses due to *Striga* may be as high as 100%, depending on a number of factors. Cereal yield loss due to *Striga* has not been estimated in recent times, but in 1986, it was estimated at US$7 billion per annum (M'Boob 1989). Stem borers are a serious threat to maize production in the humid forest and mid-altitude agroecologies of WCA. Several ear rot pathogens can produce mycotoxins on maize in the field and in storage that are known to be carcinogenic when consumed by humans and animals. Prominent types of mycotoxins include aflatoxin produced by *Aspergillus* spp. and fumonisin produced by *Fusarium* spp.

The most important abiotic constraints in the SSA are low soil fertility and drought. Particular soils of the savanna, where maize potential is greatest, are low in fertility and soil organic matter. However, as land use intensifies, a complex of other problems may develop including soil erosion, reduced water retention capacity, and an increase in persistent weeds and *Striga* infestation. The different stresses often occur together, inflicting severe damage and yield losses to the maize crop. For example, the adverse effects of *Striga* infestation are exacerbated by low nitrogen and drought. Maize yield losses due to drought depend on the stage of the crop during which the drought occurs. The crop is most susceptible to drought from a few days before tassel emergence to the beginning of grain filling; drought at this stage may reduce grain yield by as much as 90% (NeSmith and Ritchie 1992). In the savanna of WCA, annual yield loss due to drought has been estimated at 15%. Table 1.1 shows the ecological zones in SSA with their maize production constraints (MIP 1996).

1.4 Improving Maize Productivity in Sub-Saharan Africa

Breeding goals need to be prioritized based on the relative importance of the biotic and abiotic constraints in each agroecological zone. Although specific goals must be established for each agroecological zone, high-yield potential with good post harvest quality remains a general objective for the sub-region. High-yield stability is ensured by incorporating multiple genetic defenses against important pests and diseases.

Effective management of the production constraints may require crop diversification. For example, crops that are nonhosts to *Striga* may play a role in the long-term control of the parasite. Plant breeding is not the only strategy that is needed to solve the myriads of problems that occur in maize production environments. Improved soil and water management and agronomic practices that improve soil fertility are also required. In addition, it is possible to develop integrated strategies for management of mycotoxins, especially aflatoxins. Improved maize productivity also requires the development of improved processing methods.

Table 1.1 Relative importance of biotic and abiotic constraints to maize production in the agroecological zones of sub-Saharan Africa

Constraint	NG	SGS	SS	MA	HF	HA
Downy mildew	x	xx		x	xxx	
Maize streak virus	x	x	x	x	x	x
Puccinia polysora		x			xx	xx
Puccinia sorghi				xx		x
Bipolaris maydis		x			xx	xx
Exserohilum turcicum				xx		xxx
Gray leaf spot				x		xxx
Maize lethal necrosis				x		xx
Aspergillus flavus	x	x	x	x	x	x
Striga spp.	xxx	xxx	xxx	xx		x
Eldana saccharina					xxx	x
Sesamia calamistis					xxx	x
Busseola fusca						xx
Low-N fertility	xxx	xx	xx	xx		xxx
Drought	xx		xxx			xxx

Source: MIP (1996)

NG northern Guinea savanna, *SGS* southern Guinea savanna, *SS* Sudan savanna, *MA* mid-altitude, *HF* humid forest, *HA* high altitude

x = low, xx = moderate, xxx = severe

Beyond the challenge of developing germplasm with multiple resistances to the important biotic constraints and tolerance to abiotic stresses, improving maize productivity in SSA requires a well-developed seed industry to ensure that farmers have access to improved varieties and hybrids. There is therefore the need to increase farmers' awareness of the economic benefits of using improved seeds. The seed industry in SSA is not well developed due to a number of factors including (i) the lack of seed policy in many countries of the sub-region, (ii) long delays between variety development and variety registration and release, (iii) lack of an enabling environment for private sector participation and survival, (iv) low levels of human and material resources in the public seed sector agencies for effective seed production and marketing, (v) inadequate attention devoted to variety maintenance as well as breeder and foundation seeds by NARS, (vi) lack of effective and sustainable national seed systems in most countries of WCA, and (vii) weak regional seed trade development and weak seed market information systems. In spite of the problems currently confronting the seed industry, tremendous opportunities exist, given that many high-yielding improved varieties have already been developed by international and national agricultural research systems. These varieties are available for exploitation by the emerging formal and informal, small- to medium-sized seed enterprises in the region.

There are also socioeconomic constraints that limit maize productivity in SSA, including (i) nonavailability of complementary inputs such as fertilizers and chemicals which limit the rate of adoption of improved maize technologies, (ii) inefficient markets for agricultural inputs and outputs leading to poor pricing which is a major disincentive to high maize production by farmers, (iii) lack of credit facilities for the purchase of needed production inputs, (iv) absence of market information systems leading to inefficient marketing, (v) lack of farmers' organization to facilitate access to markets, (vi) inconsistent governmental production and trade policies which discourage local production, and (vii) poor processing and storage facilities resulting in loss of agricultural produce. Each of these constraints, in addition to the abiotic and biotic constraints, is formidable and requires much research for effective control measures.

For many years, efforts have been invested into maize research and development at the individual country level in SSA. Many of the production constraints have been too formidable for individual countries to solve. Foreign interventions have been put into maize research programs, along with capacity building to ensure sustainability of the improvement of the crop. The interventions have become more prominent since the middle of the twentieth century with the establishment of international agricultural research centers, notably CIMMYT and IITA in Mexico and Nigeria, respectively. These two centers have positively impacted maize research and development in East, Southern, and Western Africa, and much progress has been made in improving maize production in the region. One notable indication of progress is the feedback from farmers, the ultimate end users of the technologies emanating from the research and development efforts. At the initial stages of maize improvement programs in SSA, the farmers had little or no knowledge of desirable traits to expect in maize. As time went on, farmers' awareness of what to expect in maize increased and has now reached a level that they interact with researchers and technology transfer specialists to specify the traits they desire in varieties released to them for cultivation. An example is found in the savanna agroecology of WCA where farmers are wary of varieties not having multiple tolerance/resistance to *S. hermonthica*, drought, and low soil nitrogen. This is a clear indication that, despite the much encouraging progress achieved in maize improvement in SSA, considerable challenges remain to be faced in order to sustain maize production and productivity in the region. In addition to incorporating multiple disease resistance to varieties, maize researchers must prepare to meet the challenge of unknown diseases that may surface in the future. Similar preparation must be made for insect pests as well as weeds, including parasitic weeds. Much work has been done to improve maize germplasm in Africa for tolerance to the abiotic stresses such as low soil N and drought. Varieties containing the precursor to vitamin A have been developed and are available for cultivation. Future breeding efforts must build on this foundation to improve nutrition, food security, income, and well-being of people in SSA. Hybrid maize has been convincingly established globally as the best type of variety for farmers. A large proportion of SSA farmers are yet to adopt hybrids for cultivation. In many instances, farmers continue to use farm-saved seed not because new maize varieties and improved seeds are unavailable but the farmers are small scale, are subsistence oriented, and are located in isolated rural areas making it difficult for them to be well integrated into the market economy. All stakeholders in maize research and development must face this challenge and come up with creative approaches to reach the millions of small-scale farmers to fully enjoy the benefits of national and international interventions into maize improvement. A major effort has been devoted to the establishment of a well-functioning research for development pipeline to ensure the production and dissemination of improved maize germplasm and to build the capacity of national maize research scientists and seed company staff. The mentoring, the capacity building, and the strong partnerships have been effective in building the critical mass of competent maize scientists and technicians in the NARS and the private seed companies while at the same time enhancing the quality of partners' research activities across both public and private sector maize breeding programs in the region. Besides enhancing the scientific/technical capacity of scientists and technicians of partner institution's joint regional planning, on-site backstopping visits, graduate student project supervision, and breeding and dissemination team awards have been used as strategies to improve the research capacity and technology dissemination capabilities of maize researchers. Technician training course has been a critical element in improving trial quality, as is monitoring. The availability of the early and extra-early OPVs and hybrids, good-quality seed, improved research capacity and capability of NARS partners, and support to NARS for the testing and commercialization of the hybrids and OPVs have significantly contributed to phenomenal increase in maize production and productivity in SSA.

1.5 Conclusions

Maize, an introduced crop to SSA, has become a major food crop that is highly more productive than other cereal crops in the continent. Increased yield has been made possible by the availability of varieties adapted to specific agroclimatic zones and of different maturity classes, along with resistance or tolerance to abiotic and biotic stresses, some of which are crosscutting all over SSA, while others are endemic in specific agroclimatological zones. Genetic enhancement of the crop has been made possible by interventions from the national governments, regional organizations, and international donor agencies. Execution of the research programs has been actualized by scientists in national research institutions; regional bodies; international research institutes, specifically IITA and CIMMYT; maize networks; and nongovernmental and community-based organizations. Maize has a high-yield potential yet to be fully exploited; therefore, research work is still being carried on and must continue if food security in SSA is to be achieved and sustained.

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Chapter 2
Climatology of Maize in Sub-Saharan Africa

2.1 Agroclimatic Zones of West and Central Africa

The West Africa (WA) sub-region of SSA is endowed with several tropical agroclimatic zones, ranging from the forests, usually at the coastline, through the savannas to the Sahara desert in the northern parts. Maize is produced in most of the climatic zones, at least for consumption. Much of the climatic belts are in lowlands with relatively small proportion of the sub-region in mid-altitude agroecology. A striking feature of the WCA climatic zones is their crosscutting nature. Unlike East Africa, high altitudes are completely absent in WA. Each climatic zone occupies about the same belt across the countries of the sub-region (Fig. 2.1) thereby making it relatively easy to study the environmental factors affecting crop production in a few locations within a climatic zone, with possible reliable extrapolation to other locations within the zone. Each climatic zone is distinct from the viewpoint of weather factors and the concomitant flora and fauna. In this chapter, the agroclimatic zones are described followed by a presentation of the effect of the climatic factors on the different growth stages of maize and its production and productivity.

2.1.1 Forest Zone

The forest zone runs along the southern coast of West Africa, from Guinea, through Sierra Leone, Liberia, Cote d'Ivoire, Ghana, Togo, and Nigeria, and on to Cameroon in Central Africa, covering about 40 million ha. The zone is characterized by high rainfall 8–10 months of the year, except in some coastal areas where rain falls throughout the year.

Total annual rainfall in the forest is high, ranging from 1000 to 1500 mm, but may be as high as 3000 mm in some coastal locations, such as Calabar in the

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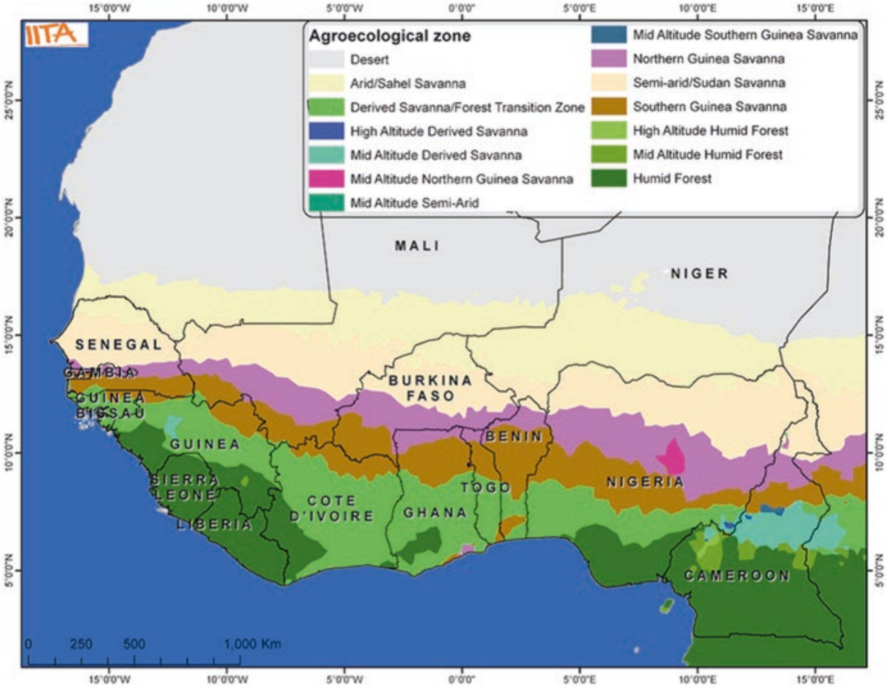

Fig. 2.1 Agroclimatic zones of West Africa

southeastern part of Nigeria. Based on rainfall and vegetation patterns, the forest zone may be divided into three subzones: mangrove saline water swamp, mangrove freshwater swamp, and rainforest (also called high forest). The swamp forests are not conducive to commercial maize production and are, therefore, not discussed any further here. Maize production in WA started from the rainforest (RF) from where it gradually moved northward to the savanna ecology. In the rainforest, the rain season starts in March and continues until late October or early November, in a bimodal distribution with peaks in June/July and September. A short dry spell usually occurs in August (Fig. 2.2), although in some years and along the coast, the dry spell is not sharply defined. For purposes of crop production in most of the RF zone, there are two rain seasons, the *early* (March to early August) and *late* (late August to October/early November) seasons. A 3–4-month near-perfect dry season follows the late season to complete the cycle. Mean monthly rainfall varies from <20 mm in January to 100–300 mm in June and July. Relative humidity is generally high (80% in January/February and over 90% in June/July). The average annual mean temperature is 25–28 °C, with a mean maximum of 37 °C and a mean minimum of 21 °C (WARDA 2002).

Because of higher solar radiation and more favorable rainfall distribution during the growing season, the subhumid savanna regions in the northern parts of West Africa are better food grain-producing areas than the humid forest zones in the

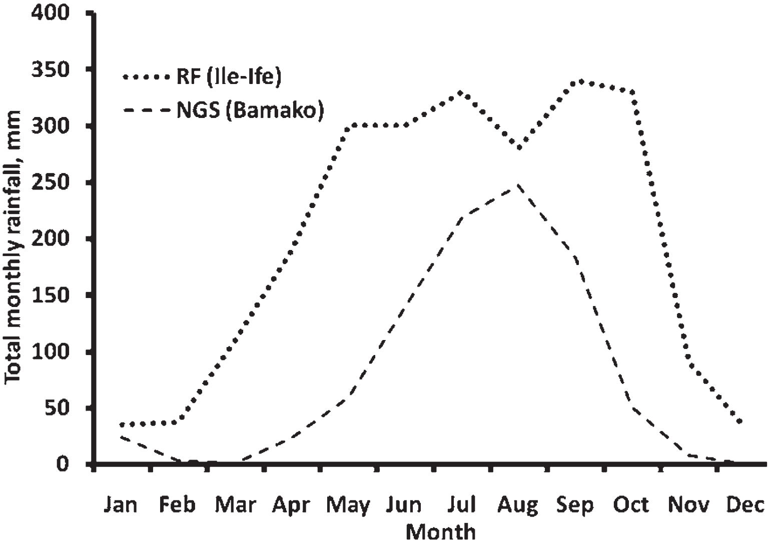

Fig. 2.2 Mean monthly rainfall in the forest (*RF*) and northern Guinea savanna (*NGS*) agroecologies of West Africa

south. In spite of this, however, maize is the commonest and easiest crop to grow in the south, and every farmer (and nonfarmer alike) makes an effort to grow some maize, if only for home consumption. Indeed, extensive maize hectares, as in the Guinea savanna, are exceptions rather than the rule in the forest ecology, but the small areas here and there add up to substantial "much" in the final analysis. The bimodal rainfall pattern in the best maize areas of the RF, for example, Ile-Ife (Fig. 2.2), permits the raising of two maize crops under natural rains per annum: the early-season crop sown from mid-March to early April and the late-season crop sown in places where sufficient rainfall permits, from about mid-August, after the usual 2–3-week dry spell, till sometime in early September. The early maize crop, largely harvested when the ear is still green (referred to as green maize), puts an end to food scarcity and hunger which had prevailed over the dry season, and green maize forms an important item of food for all classes of people from about May of each year. It can be seen roasted or boiled and sold everywhere—along town streets or within compounds, along highways, and even in villages. A late-season crop is sown. This crop invariably is much less successful than the early-season crop. The rains stop often before vegetative growth or flowering is completed or, at best, early during the grain-filling period. There is also the problem of maize streak virus (MSV) which is a scourge in the late season on nonresistant varieties. Luxuriant growth of weeds is a challenge as it competes with the crop for available nitrogen.

High humidity, persistent rains, and less hours of sunshine in between the two seasons in the RF make the production of good-quality dry grains difficult in the first cropping season. The soils in the RF are loams or sandy loams with generally low moisture retention capacity. Much of the decomposed organic matter from the short fallow between cropping seasons is rapidly utilized by the emerging corn plants, but the heavy rains soon come to leach away much of the essential nutrients, especially nitrogen (N). Split application of nitrogen during the growing season is often recommended to reduce this problem. Studies have shown, however, that where leaching losses have been minimal, there is no significant yield difference between maize receiving all of its N fertilizer at planting (whole N) and maize receiving its N in splits (Alofe and Okeleye 1991). These researchers also found that in the forest ecology, maize with whole N application at planting stayed green longer than under the other methods of application.

Based on the abiotic stresses resulting from unfavorable climatic and soil conditions common to all agroecologies of WA, IITA, and NARS, maize scientists, individually and collaboratively, have been working on short- (agronomic practices) and medium- to long-term (genetic enhancement) solutions to the maize production constraints resulting from drought and low soil N. Maize breeders have developed genotypes that are not only adapted to the different agroecologies but, among other qualities, are also drought and low N tolerant. For the forest agroecology, both international and national maize breeders are conscientiously working on specific varieties of medium, early, and extra-early maturity for the short, late season. If the appropriate varieties are developed and released for commercial production, the forest ecology would have the advantage of increased maize yields through the additional late-season harvest. Theoretically, the sum of both yields is expected to even surpass the only single harvest possible in a year in the savanna zones.

2.1.2 Savanna Zone

The savanna is basically a subhumid or semiarid tropical woodland or grassland comprising of about 75% of the total land mass of WA. Of all climatic variables, rainfall is the most important determinant of agricultural activity. The timing of planting operations, the number and type of crops grown, and the overall ecology are greatly influenced by rainfall seasonality and onset, duration of the regime, and the number of months with less than 100 mm, the minimum amount of moisture that can support plant life. Characteristically, rainfall pattern is monomodal (Fig. 2.2), and the different zones within the savanna are determined by the duration, intensity, and total rainfall, along with the duration of the dry season. The patterns of rainfall distribution are quite similar, but the onset of rains, which marks the beginning of the growing season, the amount of rainfall, and the duration of the growing season vary widely within and among the different savanna zones (Fig. 2.3). Based on the assumption that 100 mm rainfall in a month is the minimum required to support plant life, the estimated duration of the growing season in the different ecologies is summarized in Table 2.1. Incoming solar radiation increases with latitude (Kassam et al. 1975) for all months of the year with the lowest radiation received in August at the peak of rains. For example, sunshine hours (SHR) are consistently lower at Ibadan (latitude 7° 23′ N) than Kano (latitude 11° 59′ N), although in each case, the SHR decreases during the cropping season relative to the dry season (Fig. 2.4).

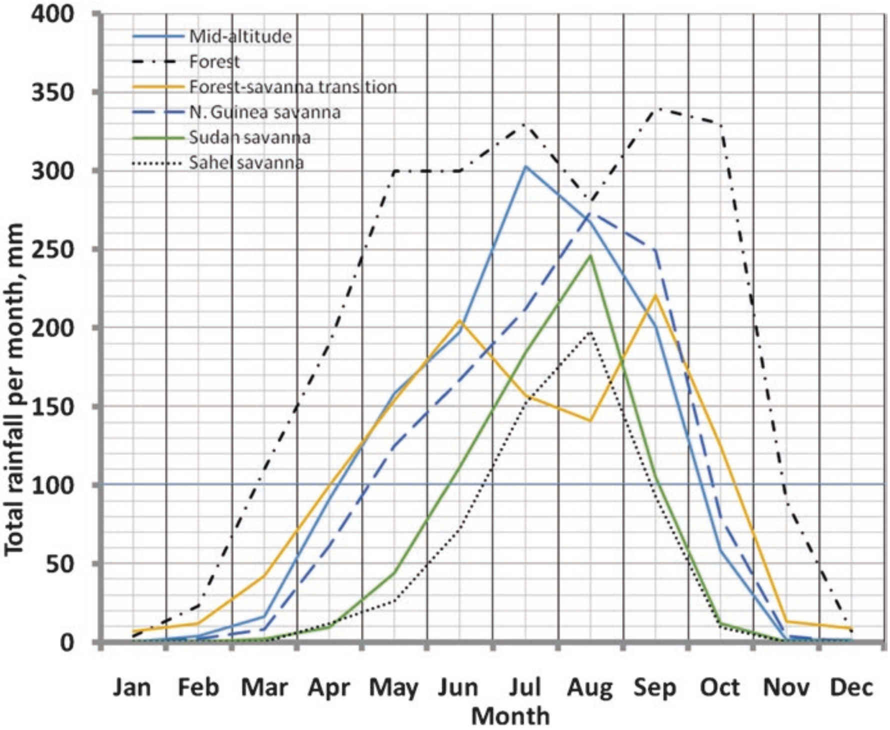

Fig. 2.3 Rainfall pattern for the different agroecologies of West Africa. The horizontal line at 100 mm marks the minimum moisture for maize growth

Table 2.1 Estimated onset, recession, and total duration of the growing season in the different agroecologies of West Africa

	Growing season		
Savanna zone	Onset	Recession	Duration, days
Forest	Mid-March/early April	Early Nov.	215–230
Forest–savanna transition	Late March/early April	Late Oct.	200–220
Southern Guinea	Late April	Mid-Oct.	185–200
Northern Guinea	May	Early Oct.	160–180
Sudan	Mid-June	Late Sept.	107–120
Sahel	Late June/early July	Late Sept.	90–100
Mid-altitude	Late April/early May	Late Oct.	184–210

Net photosynthesis therefore increases with latitude; dry matter production and grain yield of maize would be expected to be greater in the northern drier areas than the southern forest zones. Kassam and Kowal (1973) found that the net potential photosynthesis is 20–40% greater in the savanna than in the forest zone. Rates of dry matter and economic production of maize in the savanna were found to be twice

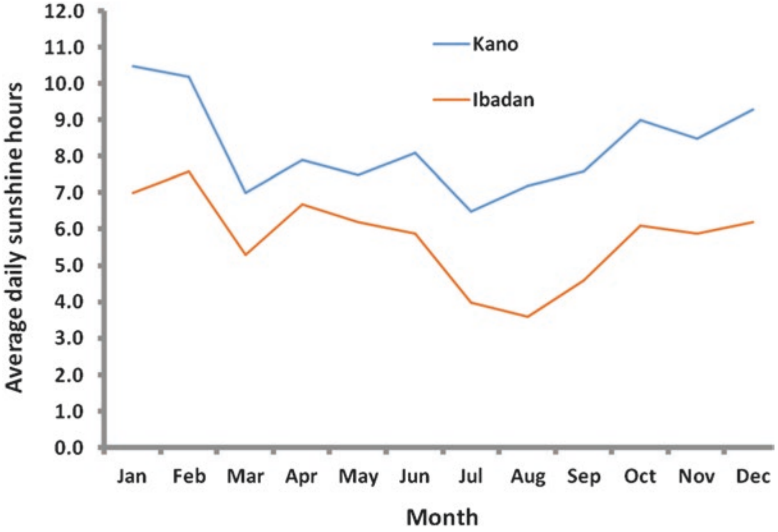

Fig. 2.4 Average daily sunshine hours received per month at Ibadan (lat 7° 23′ N) and Kano (lat 11° 59′ N)

as high as in the forest environment. In addition, daytime temperature is higher and nighttime temperature lower in the savanna than in the forest zone, a combination that increases maize production.

Most of the savanna soils belong to the ferruginous tropical soil group developed on sand parent materials, crystalline acid rock, or undifferentiated materials. Depending on hydrology, parent material, and age, other soils such as vertisols; entropic, ferralitic, hydromorphic, and halomorphic soils; brown soils of subarid regions; and weakly developed soils are also found (Klinkenberg and Higgins 1968; Kowal and Kassam 1978; Agboola 1979; Baker 1980; Norman et al. 1982). The clay content of savanna topsoils is generally low due to geological and pedological factors. Low clay content with sparse vegetation associated with extended period of dry season results in low soil organic matter content, and phosphorus levels are also low (Jones 1974, 1973; Jones and Wild 1975; Mokwunye 1974; Bache and Rogers 1970). Because of the dominant kaolinitic type of clay which is due to the type of parent material, the cation exchange capacity (CEC) is very low resulting in poor buffering capacity. Most of the soils are rich in potassium, calcium, and magnesium to a level that could support adequate plant growth. Nevertheless, there are few vertisols developed in sites with impeded drainage which are rich in clay minerals and high in CEC, exchangeable calcium, and trace elements. Organic matter is low to moderate, but poor physical properties (swelling–shrinking, low macroporosity, poor structure, etc.) call for special management practices to maintain crop production. Hydromorphic soils are scattered all over the WA savanna and occupy about 7.3% of the total area (Klinkenberg and Higgins 1968). These soils, which are high in organic matter content and chemical fertility, are used for intensive cultivation of rice in the rainy season and irrigated sugarcane, wheat, vegetables, and maize in the dry season.

The savanna zone consists of six distinguishable agroecologies: the derived savanna (forest–savanna mosaic), southern Guinea, northern Guinea, Sudan, and Sahel agroecological zones in that order northward of the RF, along with the mid-altitude ecology, a somewhat unique zone in the NGS.

Derived savanna There are two types of derived savanna (DS). The first is a belt of land that lies between the southern Guinea savanna and the RF. Because of human activity, the trees and vegetation that originally grew in the belt have been removed and naturally replaced by vegetation thinner and more deciduous than in the RF. The second is the coastal savanna found in parts of Ghana, Togo, Benin, and Nigeria. Annual rainfall is 1300–2000 mm, with rains falling from April to October. Relative humidity is generally high (about 80% or higher in the morning), and nights are hot. Crops and cropping patterns are closely related to those of the adjoining zones (WARDA 2002).

Southern Guinea savanna Vegetation in the southern Guinea savanna (SGS) zone consists of open forest interspersed with tall, dense grasses such as the elephant grass. This is a result of years of fire and other devastations that have kept the plants in a constant state of struggling to adapt to the environment. Trees and grasses have structures that enable them to survive the dry season and resist bushfires. The zone is found in all countries of the region except Mauritania and Mali. In countries such as Nigeria, Benin, Togo, Ghana, and Cote d'Ivoire, the zone occupies more than half of the land area, covering over 40 million hectares. Total annual rainfall is about 1200–1500 mm, and the wet season lasts for 6–8 months. Mean monthly temperature ranges from 23 to 35 °C, with the hot months recording a high of 37 °C and the cool months a low of 18 °C.

Northern Guinea savanna The northern Guinea savanna (NGS) extends across the region from Senegal in the west to Chad in the east. Typically, it consists of tall grasses (3–4 m) and more trees in comparison to the Sudan savanna. The zone has monomodal rainfall of 1000–1200 mm per year, most of which falls from April to October. The moisture deficit is moderate in the south to high in the north. The mean monthly temperature ranges from 15 to 48 °C, with highs during the peak of the dry season (November to March). The tall grasses and woody species are subjected to bushfires most years. Thus, the grasses are deep rooted, enabling them to sprout with the onset of the rains.

Sudan savanna The Sudan savanna (SS) is a transition zone between the NGS and Sahel zones. It is found in Senegal, Mali, Burkina Faso, Niger, Nigeria, and Chad, with patches in the northern parts of Cameroon and Benin. The drier, northern parts of the zone are characterized by the sparse savanna grasses and woody species of the Sahel zone, while the wetter southern parts contain more grasses and woody species. The vegetation is mostly short (1.5–2.0 m) grasses and scattered, stunted trees (mainly *Acacia* spp., silk cotton, and baobab). The silk cotton is the tallest of the group, growing to a height of 10–15 m. The zone has monomodal rainfall of

600–1000 mm per year. The high variability in annual rainfall causes drought damage to rainfed upland crops. Relative humidity is generally below 40%, except in the few wet months when it reaches about 60%. The dry season lasts roughly 6–8 months. Monthly mean temperature varies between 12 and 45 °C, with highs of 45–48 °C in the hot months and lows of 10–12 °C in the cool mornings of the harmattan months.

Sahel savanna The Sahel savanna extends from the extreme north of the region bordering the Sahara desert to the semiarid Sudan savanna. It covers most of the land areas of Chad, Niger, Mali, Senegal, and Mauritania and is found to a lesser extent in Nigeria, northern Cameroon, and Burkina Faso. Savanna-type vegetation, mainly grasses (*Andropogon* spp., etc.) and sparse woody plants, dominates the landscape. Annual rainfall varies from less than 200 mm in the north to 500 mm in the south of the zone. Most of the rain falls in 2 months (mid-July to mid-September). Temperatures range from 40 to 48 °C during the day and could be <12 °C at night during the cool harmattan months (October to February). Severe sandstorms as well as cold, dry winds from the Sahara occur during the harmattan. Eighty percent of the upland soils are regosols, while the rest are mainly arenosols. The soils are characterized by low organic matter content (1–2%) and high pH (6.5–7.5). Because of its low rainfall and very high relative humidity, 90% of the Sahel requires irrigation for crop production.

Mid-altitude savanna Areas on an elevation >800 m above sea level in WCA primarily found only in Nigeria (about 1300–1500 m), in Cameroon (1300–1650 m), and, to a lesser extent, in Guinea (about 900 m) are referred to as mid-altitude ecology. The mid-altitude ecology, especially in Nigeria and Cameroon, is a high-potential maize production zone, usually performing much higher than the lowlands if appropriate varieties are planted. Some of the advantages are the less weathered, more fertile soils, high-incident solar radiation, and lower temperatures which extend the crop's growth cycle giving it more time for assimilation of carbohydrates and, thus, higher yields. Special adaptation is, however, required for maize developed for the ecology, including resistance to the prevailing highland rust, *Puccinia sorghi*, and highland blight, *Exserohilum turcicum* (formerly known as *Helminthosporium turcicum*).

2.2 Improved Classification of WA Agroecological Zones for Maize Production

Classification of the WA agroecological zones started long ago, at the time fine tools and facilities for precise data collection and analysis were not readily available. Maize researchers in the sub-region loosely stratified the environments for purposes of germplasm evaluation, screening for resistance to diseases, and release of varieties for farmers. In the early stages of maize breeding in Nigeria, for example, results of national variety trials conducted at Ibadan, Mokwa, and Zaria were used as basis

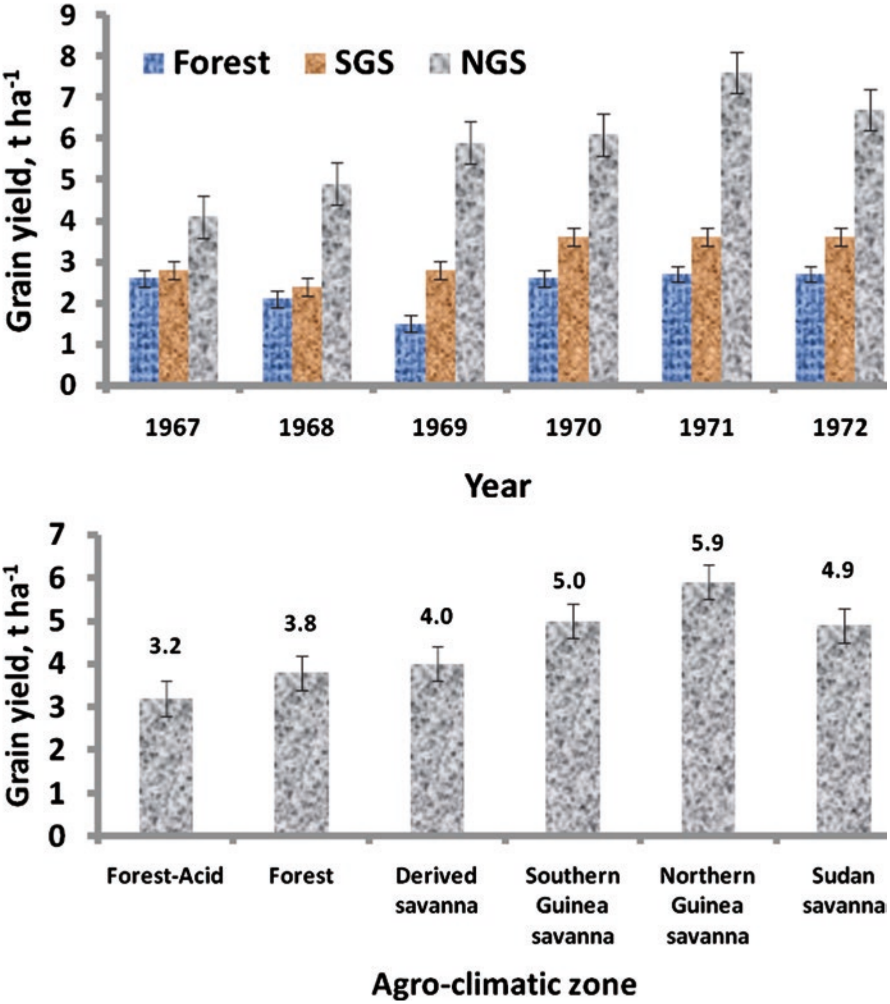

Fig. 2.5 Grain yield (t ha^{-1}) of open-pollinated varieties (*upper graph*, 1967–1972) and the first set of IITA hybrids (*lower graph*, 1985–1988) evaluated in the different agroecological zones of Nigeria. Vertical lines on the bars are standard errors

for classifying the country to forest, SGS, and NGS (Fig. 2.5). The NGS was more favorable to maize production than the other two zones, which were not consistently different from each other.

Recent advances in digital (e.g., computers), spatial (e.g., geo-positioning systems, GPS), and geographic information system (GIS) have opened up an unprecedented limitless opportunity to use massive agricultural and climatic data to define agro-climatic zones of WA with greater precision and finesse. Fakorede et al. (1989) subjected the 4-year (1985–1988) grain-yield data of the Nationally Coordinated

Maize Research Program (NCMRP) of Nigeria to principal component factor analysis with varimax rotation for orthogonality of similarity grouping of the test locations and adaptation of the varieties. Analysis of variance involving only the locations grouped into each factor eliminated or at least considerably reduced the genotype × environment interaction (GEI). Average grain yield in the zones ranged from 4.1 t ha^{-1} in the RF agroecology to 5.8 t ha^{-1} in the NGS (Fig. 2.5), which was thereafter declared the Corn Belt of Nigeria (Fakorede et al. 1993).

On the basis of the multivariate statistical grouping, Fakorede et al. (1989) identified four distinct zones and suggested testing of maize in only these zones: (i) forest/forest–savanna transition/southern Guinea savanna, (ii) northern Guinea savanna, (iii) Sudan savanna, and (iv) mid-altitude. Similar conclusions were reached by Ajibade et al. (2003) who evaluated early and late OPVs in 18 locations across these agroclimatological zones, along with 2 others, the forest with acidic soil and mangrove forest. Maize trials for early and extra-early germplasm are now conducted primarily in the forest, SGS, NGS, and Sudan savanna. Varieties in these maturity groups are yet to be developed for the mid-altitude ecology.

A more comprehensive study, involving real climatic data, was conducted by the maize researchers and climatologists at IITA (Menkir et al. 2000; Menkir 2003). The study involved GIS spatial climatic data of 114 maize testing sites in SSA, 75 of which were in WA. The data were subjected to cluster analysis, followed by principal component analyses (PCA), using the correlation matrix generated from the original data to extract linear combinations of the climatic variables that could best describe the differences among clusters. For each site, estimates of the growing season, along with the relevant climatic data, were obtained from a computerized resource information system (RIS) developed by IITA (Jagtap 1995). The RIS is a compendium of spatial data in the form of digitized maps and extensive soil, climatic, elevation, population density, and other data. The database has the capability to combine different layers of spatial data for characterization of a region.

The sites were grouped into four regions similar to but not exactly the same as had been known before for the WA sub-region (Table 2.2). For the WA sites, the deviations occurred primarily in region 2 (forest and forest + savanna zones) and region 3 (northern + southern Guinea savanna zones). For region 2, Broykou in Togo and Man in Côte d'Ivoire that were SGS in the original classification, and Ferke also in Côte d'Ivoire previously in NGS, were grouped into the forest + forest–savanna zone in the new study. For region 3, Angaradebou in Benin Republic and Massantola in Mali, originally in Sudan savanna, along with Sotuba in Mali (NGS–SS transition) and Saminaka in Nigeria (NGS–MA transition) were properly grouped into SGS + NGS. The crop growth periods in the agroecological zones determined from the GIS classification were also strikingly close to those based on the rainfall distribution (Fig. 2.3).

Multivariate statistical analysis of the GIS and RIS data has put the SGS and the NGS together, contrary to the earlier classification based on maize yield performance in the different ecological zones in which the two zones were separate entities (Fakorede et al. 1989). The two zones are now generally referred to together as Guinea savanna.

Table 2.2 Grouping of maize testing locations in West Africa based on agroclimatic variables from GIS and RIS developed at IITA, Ibadan

Variable	Region 1	Region 2	Region 3	Region 4
Total number of sites (114)	24	37	33	20
Number from WA (75)	3	29	27	16
No. of WA sites at variance	0	3	4	0
Annual rainfall, mm	1293 ± 372	1690 ± 476	1184 ± 202	795 ± 164
Seasonal total rainfall, mm	1220 ± 376	1612 ± 481	1085 ± 209	699 ± 169
Seasonal PET, mm	818 ± 198	1024 ± 116	1085 ± 209	513 ± 101
Ave. seasonal max. temp, °C	26 ± 2	30 ± 1	31 ± 1	32 ± 1
Ave. seasonal min. temp, °C	15 ± 2	21 ± 2	21 ± 1	22 ± 1
Elevation, m	1347 ± 245	308 ± 238	360 ± 163	275 ± 172
Crop growing period, months	7 ± 2	9 ± 1	6 ± 1	4 ± 1
Suggested name of region[a]	MA	F & FST	N&S GS	SS

Adapted from Menkir (2003)

[a] *MA* mid-altitude, *F* forest, *FST* forest–savanna transition, *N* northern, *S* southern, *GS* Guinea savanna, *SS* Sudan savanna

2.3 Some Empirical Evidences of the Impact of Climate Change

Presently, there is a global focus of attention on climatic change occurring in the whole world. The Intergovernmental Panel on Climate Change (IPCC 2001) defined climatic change as statistically significant variations in weather pattern that persist for an extended period, typically decades. It is a complex biophysical process attributed to increased concentration of greenhouse gases in the atmosphere. The greenhouse gases include carbon dioxide ($CO_{2)}$, methane ($CH_{4)}$, nitrous oxide (N_2O), and fluorinated gases. Long-term or permanent changes in the pattern and intensity of manifestation of weather factors are characteristics of climatic change. Such changes destabilize the equilibrium state of crop production, including crop varieties, sowing dates, crop duration, management practices, and crop yield. Therefore, climatic change negatively impacts agriculture by increasing the risk of crop production and the threat to food security in SSA.

In contrast to climatic change, climatic variation involves short-term changes in the manifestation of weather factors from one location to another or from year to year in a location. Climatic variation is a frequently occurring phenomenon well known to and normally expected by crop scientists and farmers. Effects of short-term weather fluctuations on maize production systems have been well recognized for a long time. Indeed, plant breeders are constantly working to cope with a phenomenon called genotype x environment interaction (GEI), which is the failure of crop varieties to perform consistently in variable environments.

Climatic change has manifested in WA in several ways, including recurrent drought since the 1950s, consistent decrease in total annual rainfall over time, delayed onset and early recession of the rains resulting in reduced duration of the

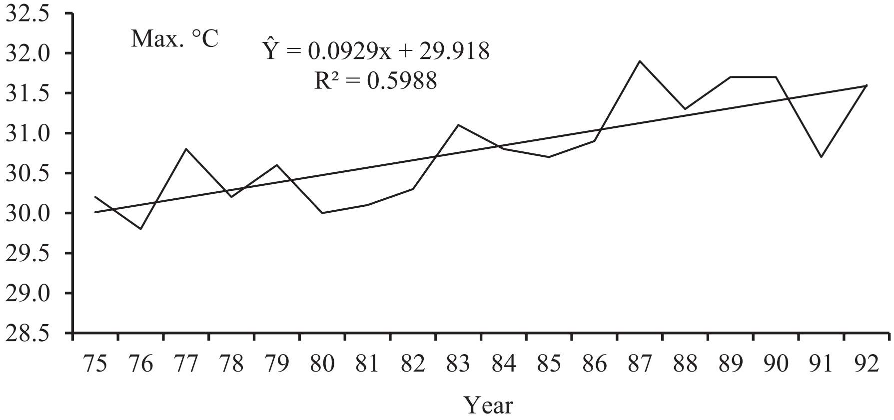

Fig. 2.6 Mean annual maximum temperature at the Teaching and Research Farm of Obafemi Awolowo University, Ile-Ife, Nigeria, 1975–1992

Table 2.3 Parameters from the regression of monthly maximum temperature at the Teaching and Research Farm of Obafemi Awolowo University, Ile-Ife, Nigeria, on years from 1975 to 1995

Month	Regression model	Coefficient of determination, r^2
January	**$\hat{Y}$ = 32.757 – 0.077×**	0.049
February	$\hat{Y}$ = 33.845 + 0.027×	0.008
March	$\hat{Y}$ = 33.604 – 0.011×	0.001
April	$\hat{Y}$ = 32.259–0.017×	0.005
May	$\hat{Y}$ = 30.749 + 0.005×	0.000
June	$\hat{Y}$ = 29.192 – 0.001×	0.000
July	$\hat{Y}$ = 27.261 + 0.013×	0.003
August	$\hat{Y}$ = 26.060 + 0.074×	0.109
September	$\hat{Y}$ = 27.688 + 0.056×	0.115
October	$\hat{Y}$ = 29.207 + 0.053×	0.119
November	$\hat{Y}$ = 30.478 + 0.134×	0.377
December	$\hat{Y}$ = 31.262 + 0.038×	0.021

cropping season, false start of the rainy season, increased drought probability during the cropping season, and increased annual maximum temperature (Jagtap 1995; Fakorede and Akinyemiju 2003). In the rainforest agroecology of Nigeria, for example, Fakorede and Akinyemiju (2003) found that the mean annual maximum temperature increased from 1975 to 1992 at the rate of 0.09 °C per annum (Fig. 2.6).

Monthly maximum temperatures remained more or less the same for February to July each year (Table 2.3). For August to December, however, there was an increasing trend with the largest increase occurring in November, at about 0.13 °C per annum (Table 2.3).

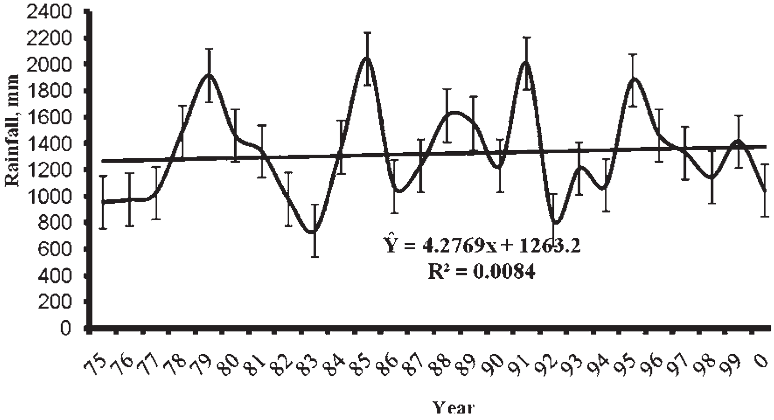

Fig. 2.7 Total annual rainfall at the Teaching and Research Farm of Obafemi Awolowo University, Ile-Ife, Nigeria, 1975–2000

Total annual rainfall varied from 740 mm to 2040 mm with peaks (maxima) occurring at fairly regular interval of 5–6 years (Fig. 2.7). The overall annual mean rainfall was 1263.2 mm. However, regression of total rainfall for early cropping season (March, April, and May) on years gave a linear regression equation $\hat{Y} = 541.4–22.14\times$ with a coefficient of determination of 76%.

In other words, rainfall during the first 3 months of the cropping season consistently decreased significantly from about 500 mm in 1981 to <100 mm in 2000 at the rate of about 22 mm per year. This exposes maize planted early in the season to moisture stress at the seedling and early vegetative growth stages. For this reason, genetic enhancement for drought tolerance at these growth stages has been initiated in the region.

In another study, Fakorede et al. (2004) quantified drought per day (termed drought day, DD) and used the value to compute drought probability of each day for the 1975–2000 climatic data of the T&R Farm at Ile-Ife, a typical rainforest location. It was hypothesized that, for a 24-h period, a DD has occurred if potential evaporation is greater than the total rainfall. Drought probability, P, for a period, t, was then calculated as

$$P = \left(\sum DD\right) / t$$

Rainfall data were obtained with a manual rain gauge and PE data from a shielded Piche evaporimeter in a Stevenson's screen of standard height. The results showed that P was very high in March (from week 1), the conventional beginning of the cropping season, decreased to about 0.2–0.3 during the first week in May (week 9), and remained at about that level till the beginning of October (week 29), except for a slight upsurge during the second week in August (week 22), which corresponds to the peak of the August dry spell (Fig. 2.8).

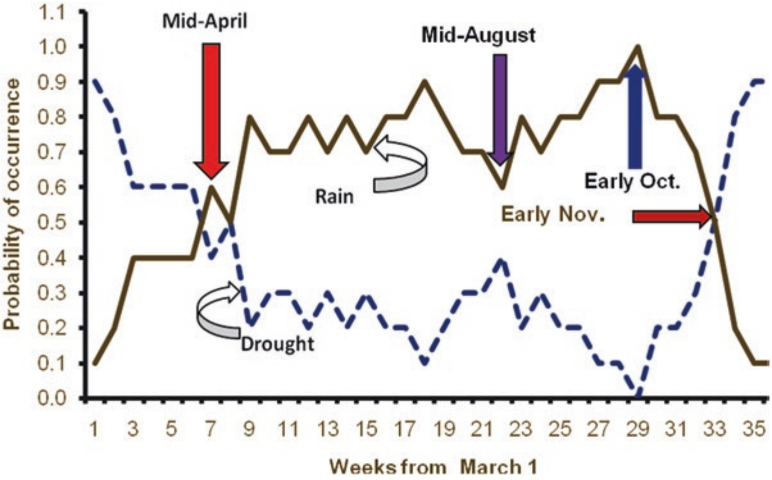

Fig. 2.8 Probability of drought and rain from the first week in March till the end of November at the Teaching and Research Farm of Obafemi Awolowo University, Ile-Ife, Nigeria, 1975–2000

From the viewpoint of moisture availability, therefore, the effective maize planting in the early season starts about the middle of April, and the late-season crop must complete flowering about the middle of October to avoid the chances of terminal drought adversely affecting maize production at this location. In effect, the duration of the season has now reduced to 6–7 months from the long-established 8–9 months, a definite negative impact of the climate change. This is the advantage of developing early/extra-early and/or drought-tolerant varieties that can escape or withstand the unpredictable terminal drought characteristic of all agroclimatic zones of WA, in addition to sporadic dry spells that may occur at any growth stage of the crop.

2.4 Response of Maize to Climatic Factors Under WA Agroclimatic Conditions

Studies in the savanna agroecology showed that, for a 120-day maturity cycle maize, the pattern of crop water requirement during the growing season was well matched to the pattern of crop water availability (Kassam et al. 1975). The highest period of water requirement by the crop occurred when the leaf area index was greater than 2.1 and coincided with the period when the amount and frequency of rainfall were greatest. With potential evapotranspiration rate of 4–6 mm per day, the crop experienced water stress when there was no rain for a period of 5 days or more. Crop growth rate was found to be drastically reduced when soil water potential decreased

Table 2.4 Moisture requirement of an early-maturing maize variety at different growth stages

Growth stage	DAP	No. of days	Water required, mm	
			Total	Per day
Emergence	5	5	10	2
Seedling	16	11	27.5	2.5
Early vegetative	30	14	63	4.5
Late vegetative	40	10	65	6.5
Tasseling	45	5	40	8
Anthesis/silking	55	10	80	8
Grain filling, lag phase	65	10	80	8
Grain filling, linear phase	80	15	90	6
Grain filling, physiological maturity	90	10	50	5
Dry down	100	10	25	2.5
	Total water required = 530.5 mm			

below 0.5 bar. Averaged for the growing season, crop water use was 353 g per gram of dry matter. In a more recent study (Fakorede, 2015, unpublished), the amount of water required at the different growth stages of maize was determined for an early-maturing variety in a pot experiment (Table 2.4). Total moisture required for the crop from planting to maturity was 530 mm. The greatest demand for water was from about 5 days before tasseling, reaching a climax at tassel emergence and remaining high during anthesis, silking, and the early part of grain filling (the lag phase)—a total of about 25 days. Nearly 40% of total moisture required for the growth cycle of maize must be available at this time. Moisture stress at this period has been found to cause greater reduction in grain yield than at any other growth stage. Based on the water-use efficiency (WUE) results, Kassam et al. (1975) recommended a 120-day maize (late maturity) for the NGS and 90-day maize (early maturity) for the Sudan savanna.

The WUE of maize at the seedling/early vegetative and grain-filling stages was evaluated under marginal and normal rainfall conditions in 2015 at the T&R Farm of OAU, Ile-Ife, Nigeria (Ajani et al. 2016). Nine drought-tolerant, early-maturing cultivars plus a check were evaluated in the two environments.

Total water use (TWU) and WUE at both vegetative and grain-filling stages were significantly higher, but grain yield was lower under drought stress than under normal rainfall conditions (Table 2.5). Neither of the two traits had significant correlation with grain yield, but total moisture use (TMU) had significant positive correlation with dry weight (DWT) in the vegetative stage under drought stress and negative correlation at the grain-filling stage under normal rainfall (Table 2.6). Also at the grain-filling stage, WUE was a near-perfect predictor of DWT under stress ($r = 0.99$) but not under the vegetative phase for the two environmental conditions.

Table 2.5 Total water use (TWU), water-use efficiency (WUE), and grain yield of ten maize varieties evaluated under drought and normal rainfall conditions at the Teaching and Research Farm, Obafemi Awolowo University, Ile-Ife, Nigeria, 2015

	Vegetative stage		Grain-filling stage		
Environment	TWU, mm	WUE	TWU, mm	WUE	Grain yield, t ha^{-1}
Drought	100.25	0.11	179.04	0.42	2.08
Normal rainfall	84.18	0.07	168.6	0.33	2.98
LSD0.05	7.72	0.01	7.95	0.05	0.48

Table 2.6 Correlation coefficients among water-use traits and dry matter at the vegetative and grain-filling stages, along with grain yield of ten maize varieties evaluated under drought stress (upper diagonal) and normal rain (lower diagonal) environments at the T&R Farm, OAU, Ile-Ife, Nigeria, 2015

	Vegetative stage			Grain-filling stage			
	TWU, mm	WUE	DWT, g pl^{-1}	TWU, mm	WUE	DWT, g pl^{-1}	Grain yield, t ha^{-1}
Vegetative TMU	–	−0.04	0.73*	0.33	0.25	0.34	0.52
WUE	−0.81**		0.56	0.01	−0.14	−0.07	−0.26
DWT, g pl^{-1}	0.79**	−0.33		0.36	0.15	0.27	0.17
Grain-fill TMU	−0.84**	0.65*	−0.69*		0.41	0.45	0.37
WUE	0.52	−0.31	0.49	0.55		0.99**	0.52
DWT, g pl^{-1}	−0.22	0.27	−0.14	−0.06	0.55		0.54
Grain yield, t ha^{-1}	0.02	−0.20	−0.08	−0.14	0.10	−0.09	

*, ** r-value significantly different from zero at 0.05 and 0.01 level of probability, respectively

2.5 Effects of Climatic Factors on Growth and Grain Yield of Maize in West Africa

Several studies have been conducted in other parts of the world to determine the growth stage most vulnerable to moisture stress in maize (Shaw 1988; Mugo et al. 1998). Results of these studies led to the conclusion that stress from about 2 weeks before to 2 weeks after flowering most drastically reduced maize yield. Moisture stress during the grain-filling period, to a lesser extent, also reduced grain yield. Effect of moisture stress at the seedling and early vegetative growth stages was relatively small.

In a study conducted for 12 years at the Teaching and Research Farm of Obafemi Awolowo University, Ile-Ife, Nigeria (Fakorede and Akinyemiju 2003), total rainfall, number of rain days, and temperature at different stages of maize growth and development had no significant correlation with grain yield (Table 2.7). Preseason weather did not affect the performance of maize during the early season. During this season, total rainfall, number of rain days, and maximum temperature at the different stages and the whole growth cycle did not influence maize yield. However, the number of rain days during the early vegetative stage showed a negative relationship

Table 2.7 Correlation coefficients of climatic variables at different growth stages with grain yield of maize during the early and late (second) seasons at the Teaching and Research Farm of Obafemi Awolowo University, Ile-Ife, 1978–1990

Climatic variable	Preseason	Planting to emergence	Early vegetative	Late veg to flowering	Grain filling	Whole cycle
			Days after planting (DAP)			
			1–30	31–60	61–100	1–100
Early season						
TR mm	0.06	−0.21	−0.42	0.21	0.03	0.02
No. rain days	0.05	0.00	−0.63*	−0.32	−0.22	−0.37
Drought prob.	0.10	0.62*	0.86**	−0.88**	−0.55*	−0.59*
Max temp. °C	0.38	0.15	−0.17	−0.10	0.16	−0.09
Late season						
TR mm	–	0.06	0.31	0.66*	0.67*	0.58*
No. rain days	–	0.12	0.07	−0.21	−0.15	0.43
Drought prob.	–	0.24	0.24	−0.95**	−0.76**	−0.66*
Max temp. °C	–	0.31	0.45	−0.56*	−0.63*	−0.43

*, **Significantly different from zero at 0.05 and 0.01 level of probability, respectively

with yield. That is, the higher the number of rain days during this growth stage, the lower the grain yield. Conversely, the higher the probability of drought during this growth stage, the higher the yield. Similarly, r-values between drought probability and yield were negative for the late vegetative to flowering and grain-filling stages as well as the whole growth cycle. Therefore, some level of drought during the early vegetative stage was favorable to maize yield, whereas drought during the flowering and grain-filling stages was detrimental. The r-values between grain yield and drought probability at flowering, grain filling, and for the whole cycle during the late (second) season were similar in sign but larger in magnitude than the early season. In other words, the impact of drought was more severe in the late than in the early season. Similarly, maximum temperature effects on yield were higher in the late than early season. Consequently, total rainfall had significant positive r-values with grain yield for the flowering, grain-filling, and total growth periods during this season.

In a more recent study, 25 varieties were planted for 3 years under managed drought stress at Ikenne in the rainforest agroecology, naturally occurring drought at Kadawa in the Sudan savanna, and optimal conditions at Mokwa, southern Guinea savanna. The managed stress was achieved by growing the crop in the dry season and irrigating till 25 days after planting after which it was stopped for the rest of the growth cycle. Results from the study (Table 2.8) showed significant positive correlation between grain yield and total or average daily rainfall from planting to, or during specific phenological stages.

Regression analysis showed that grain yield increased as total moisture to anthesis, silking, or grain-filling stages increased (Fig. 2.9). The analysis also showed that high temperature significantly decreased grain yield and increased the ASI

Table 2.8 Correlation coefficients between grain yield and climatic factors at specific phenological stages of 25 early-maturing maize varieties, evaluated from 2012 to 2014 under managed moisture stress, naturally occurring drought, and optimal conditions

	From planting to		During	
Climatic factor	Anthesis	Silking	ASI	Grain filling
Total rainfall, mm	0.761**	0.767**	0.466*	0.824**
Daily rainfall, mm	0.760**	0.767**	0.227	0.682**
Total heat units, °C	−0.513*	0.625**	−0.640**	−0.514*
Daily heat units, °C	−0.437*	−0.448*	−0.689**	−0.663**

*, **Significantly different from zero at 0.05 and 0.01 level of probability, respectively

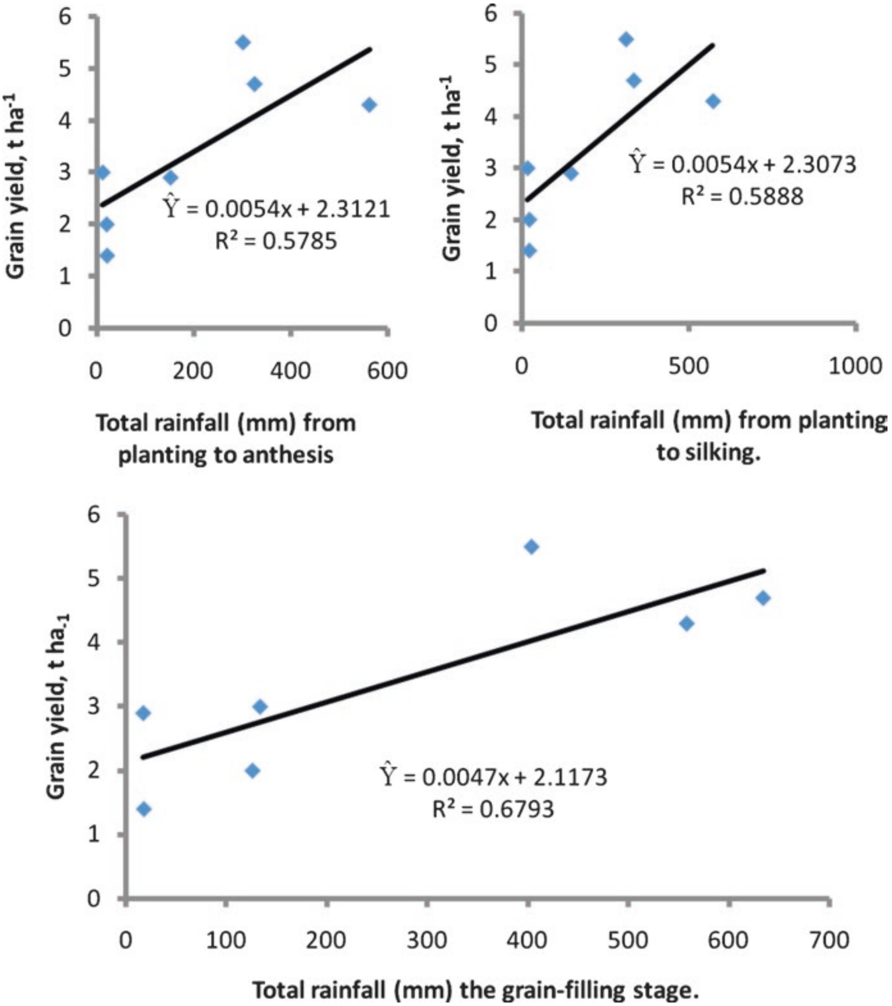

Fig. 2.9 Parameters from the regression of grain yield on total moisture from planting to anthesis and silking and during the grain-filling stage of 25 early-maturing maize varieties, evaluated from 2012 to 2014 under managed moisture stress, naturally occurring drought, and optimal conditions

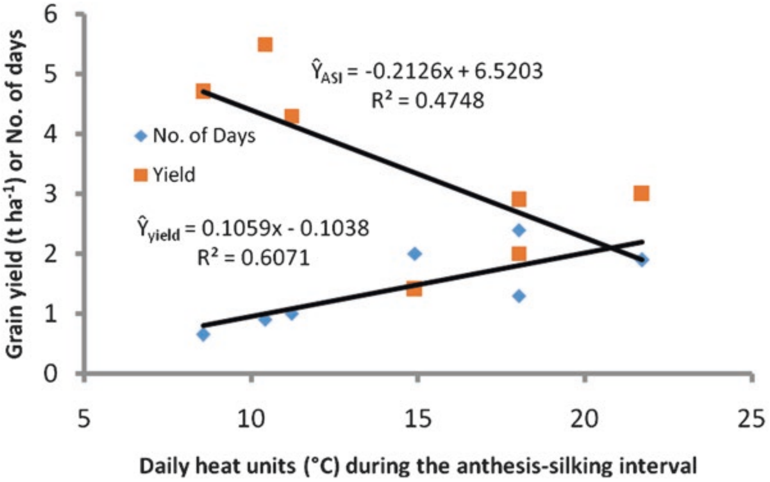

Fig. 2.10 Regression of grain yield on daily heat unit during the anthesis–silking interval of 25 early-maturing maize varieties, evaluated from 2012 to 2014 under managed drought stress, naturally occurring drought, and optimal conditions

(Fig. 2.10), both of which are undesirable. Results of these studies are consistent with those reported by earlier workers (Shaw 1988; Edmeades et al. 1995 inter alia). The implication of the results is that, in breeding for drought tolerance, moisture stress should be imposed during the flowering and grain-filling stages for optimum impact. Maize breeders have, therefore, been screening early and extra-early maize for drought tolerance during the dry season under carefully monitored irrigation and imposed water stress as from 25 or 21 days after planting, respectively, till harvest maturity. The research methods used and the progress made in the application of these findings are discussed in greater details in Chaps. 11 and 12 of this volume.

2.6 Conclusion

There is ample evidence of climatic change in SSA—increasing trends in temperature; delayed onset of the rains without a corresponding delay in the recession, thereby resulting in a shorter cropping season; and increased drought probability or sporadic dry spell even during the rainy season; With the availability of the geographical information system (GIS) and the computerized resource information system (RIS) developed by IITA, along with evidence obtained from maize yield trials, there are four distinct agroclimatic zones for maize in WCA: mid-altitude, forest and forest–savanna transition, northern and southern Guinea savanna, and the Sudan savanna. Results obtained from yield trials conducted in 1967–1972 with OPVs and 1985–1988 with hybrids indicated the NGS as the most favorable agroclimatic zone for maize production in WCA and was thereafter declared the Corn

Belt of West and Central Africa. Field trials conducted with imposed moisture stress as from about 2 weeks before anthesis to the end of the season compared with natural terminal drought and natural optimal conditions showed that drought during the flowering and grain-filling stages was detrimental. In the savannas and the late season in the forest zone, the impacts of drought and high-temperature effects were detrimental to grain yield.

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Chapter 3
Morphology and Physiology of Maize

3.1 Origin of the Maize Plant

Maize (*Zea mays* L.), also known as corn, is a member of the grass family (family: Poaceae, previously Gramineae). Species of *Zea* largely have a chromosome number of $2n = 20$, except for *Z. perennis* (perennial teosinte with $2n = 40$) (Ellneskog-Stam et al. 2007). The widespread distribution of maize, an indication of its great adaptability, makes it one of the most popular crops in the world. The center of origin of maize is Central America, more precisely Mexico with a possible secondary origin in South America. Maize was domesticated about 7000–10,000 years ago, and it is perhaps the most domesticated of all field crops, given that it can no longer exist as a wild plant as it cannot disperse its seed. During its domestication, every region in which it has been cultivated over the centuries has produced a selection of maize cultivars or landraces. The origin of maize has remained controversial. No wild plant is known from which maize could readily have been derived, suggesting that the wild maize plant has become extinct. Perhaps the closest relative of maize is the teosintes, which in addition to sharing several morphological features with maize also hybridize readily with it, producing fertile progeny. The nearest teosinte relative to *Z. mays* is *Z. mays* ssp. *mexicana* (Schrader). This central Mexican annual teosinte is a large flowered, mostly weedy grass with a broad distribution across the central highlands of Mexico. It does not spread readily. It has limited use as a forage and green fodder crop but can be problematic due to weedy tendencies (Doebley 1990; Watson and Dallwitz 1992). Chromosomes of the hybrids pair normally, and crossing-over takes place between the chromosomes of maize and the teosintes. Some studies suggest that maize arose as a natural hybrid between teosinte and gama grass (*Tripsacum* spp.). Other studies, however, suggest that both maize and gama grass arose from an unknown common ancestor by independent lines of descent, while teosinte arose from the natural hybridization of maize and gama grass.

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One of the most important consequences of Columbus' discovery of America in 1492 was the introduction of American food crops to Europe, Asia, and Africa. Included among such crops was maize, which was totally unknown outside the Americas before the time of Columbus. Maize was introduced to West Africa a little over 500 years ago. Two routes of maize introduction to West Africa are known. One is through the introduction of the floury grain type to the island of São Tomé, from where it spread to the West African coast. Flint maize, on the other hand, was introduced to the region by Arab traders crossing the Sahara. To date, these introduction patterns largely influence the distribution of floury and flint maize in West Africa. Flint maize is the dominant maize type in the northern parts of West Africa, while floury maize is more common in the coastal areas. In contrast to the generally grown maize varieties in which kernels are naked, pod corn is a classic morphological mutant of maize in which the mature kernels of the cob are covered by glumes. Pod corn, known since pre-Columbian times, is the result of a dominant gain-of-function mutation at the *Tunicate* (*Tu*) locus, and it shows a striking phenotype. The *Tu* also has a gene dosage effect, as there are several partial phenotypic revertants. Pod corn was described as *Zea mays* var. *tunicata* almost two centuries ago by the French naturalist Saint-Hilaire, who proposed that pod corn represents the natural state of maize. This raised a considerable, long-lasting scientific interest in pod corn. Because the *Tunicate* phenotype is a universal characteristic of wild grasses and is different from naked kernels in maize varieties common today, pod corn is thought to be a progenitor of maize by some researchers, and pod corn has been of religious significance for certain native tribes of American Indians since pre-Columbian times, who believed it to have magical and curative properties.

3.2 Adaptation

Maize is probably the most widely adapted field crop in the world. It is grown from latitude 58°N in Canada and Russia, throughout the tropics, to latitude 40°S in New Zealand and South America. It is grown from below sea level in the Caspian plain up to areas as high as 4000 m in Bolivia and Peru. It is grown in all countries of Africa, from the coast through the savanna to the semiarid regions of West Africa and from sea level to the mid- and high altitudes of East and Central Africa.

The typical maize plant is a tall (1–4 m), determinate annual grass (monocot) which forms a seasonal root system bearing a single erect stem (culm) made up of nodes and internodes, although some cultivars may develop elongated lateral branches (tillers). Among the characteristics maize shares with other grasses are the conspicuous nodes and internodes on the stem and the presence of a single leaf at each node with the leaves arranged distichously (arranged in two opposite ranks). The leaves are long, having parallel venation, and the nodes gradually taper to the top of the plant. Each leaf consists of a sheath surrounding the stalk, an expanded blade connected to the sheath by the blade joint, or collar. The mature maize plant can have up to approximately 30 leaves, with considerable variation in leaf number, size, and orientation. The upper leaves are more responsible for light interception and are major contributors of photosynthate to the grain. Generally, tropical maize plants develop more leaves than the temperate cultivars. Maize is monoecious (having stamens and pistils in separate flowers on the same plant) and allogamous (cross-pollinated). The rate of self-pollination in maize is 5% (Sleper and Poehlman 2006), and as a consequence of its pollination system, natural maize populations are heterogeneous. Maize populations therefore consist of individuals heterozygous at many loci. The most striking difference between maize and related grasses is the pistillate or female inflorescence which develops into the ear. The ear is a modified spike produced from a short lateral branch in the axil of one of the largest foliage leaves, about halfway down the stem. The ear is covered in a number of leaves called husks. These leaves differ in appearance when compared to those on the stalk: they surround and protect the developing ear. In general, the male inflorescence, which is positioned well above the female inflorescence, matures first—about 1–3 days earlier. Thus maize is protandrous, although female flowers may sometimes mature before the male flowers (a situation referred to as protogyny). Initially, the male and female inflorescences have primordial of bisexual flowers. However, during their development, primordial of stamens aborts in the auxillary inflorescences, and primordial of gynoecia aborts in the apical inflorescence. The apical meristem elongates once the leaf primordia are initiated, and it is transformed into a reproductive meristem that develops into the tassel. Maturity of male flowers is indicated by the shedding of pollen grains, which is known as anthesis. The female inflorescences (ears) arise from auxillary buds and bear flowers in rows along the cob. Development of the flowers and the ovules on the ear proceeds from the base upward (acropetal). From each flower, a style begins to elongate toward the tip of the cob, forming long threads or silks. Development of the silk begins from the flowers near the base of the ear and proceeds toward the tip over several days. Silk extrusion signifies maturity of the female inflorescence. Pollen shed on the tassel starts from just below the tip of the central axis and proceeds both upward and downward, reaching the tip of the central axis before it reaches the base. The duration of pollen shed may be up to 1 week or a little longer. The physical separation and asynchronous maturation of male and female inflorescences predispose maize to cross-pollination. Usually there is an overlap in male and female flowering, a phenomenon that is referred to as "nicking." The tassel continues to shed pollen for a few days after the silks are extruded. Under stress (especially water stress), the interval between pollen shedding and silk emergence increases. Maize is a quantitative short-day plant, but some cultivars have low or no sensitivity to day length (Kiniry et al. 1983). In those cultivars that are photoperiod sensitive (mainly those that are late maturing), flowering may be delayed when the photoperiod is greater than a critical threshold value ranging from 10 to 13.5 h. Those adapted to the tropics may show delayed maturity if grown in more temperate areas with longer days (Birch et al. 2003).

Each maize plant produces millions of pollen grains, usually in excess of 2.5 million and potentially as many as 25 million. Pollen shed is facilitated by the extruded anthers borne on the filaments. Pollen is carried away from the plant that produces it by the wind. Receptive silks emerge over the husks over a period of 3–5 days and can grow to more than 30.5 cm length, extending beyond the end of the husks. The silks have short hairs which form an angle to the stylar canals and help harboring pollen grains. Extruded silks are usually pollinated on the first day of extrusion, and silks produced subsequently are pollinated as they extrude. The silks provide the pollen with the moisture required for pollen tube germination. Each ovule in the ear produces a silk. The long silk, which is receptive for most of its length, has sticky hairs for trapping pollen and is capable of continued growth when cut back. Silks from ovules at the base of the ear emerge first. In general, pollination of the silks on each ear is completed in about 3 days. The moist pollen on the silk germinates, producing a pollen tube which may follow the surface of the hair for some distance but eventually enters the silk (Kiesselbach 1980). The pollen tubes grow toward the base of the individual silks. Only the tube of one pollen grain normally reaches the micropyle where it grows between cells of the nucellus until it enters the embryo sac, ruptures, and releases the two sperms. The nucleus of one sperm fuses with that of the egg to form the zygote, restoring the diploid number of chromosomes (20) in the cell nucleus. This number persists thereafter in the somatic cells of the sporophyte, all of which are formed by mitotic division. The other sperm fuses with one of the two polar nuclei which in turn fuse with the other polar nucleus to form the primary endosperm nucleus which has 30 chromosomes (10 derived from each of the polar nucleus and 10 from the sperm nucleus).The fertilized egg develops into the embryo, while the primary endosperm nucleus develops into the endosperm which comprises the bulk of the mature kernel. These processes are collectively known as double fertilization. Assuming an ear with 1000 kernels, between 2500 and 25,000 pollen grains are produced for every kernel, although only one usually functions in fertilization. The structure of maize grain is commonly referred to by a number of interchangeable terms— fruit, kernel, grain, and seed. The kernels are composed of three main parts— the embryo, the endosperm, and the fruit wall. The number of kernels per ear and the number of ears developed are established at or shortly after pollination (Duncan 1975).

Maize is one of the easiest crops to pollinate manually. This is due mainly to the separation in space of the staminate and pistillate flowers and the abundance of pollen produced. These attributes facilitate controlled pollination which can be achieved by detasseling or covering/bagging of the inflorescences. The former is important in the commercial production of hybrids. Selfing and crossing are easy to accomplish with a considerable number of kernels produced. However, because maize is naturally cross-pollinated, selfing is usually deleterious, manifested as a reduction in vigor, fecundity, and the appearance of sub-vital types. Maize researchers refer to this as inbreeding depression. Inbreeding in maize is discussed in greater details in Chap. 6.

Maize kernels are arranged in even numbers of rows on the cob, and the latter is covered with several layers of husk which serve a protective function. Grain filling in maize takes about 8 weeks, and it occurs in three stages, viz., blister (R2) stage, milk stage (R3), and dough stage (R4). The blister stage follows fertilization, wilting, and browning of the silks. It is characterized by a rapid accumulation of carbohydrates in the kernels which now contain a clear fluid. The embryo is visible at the

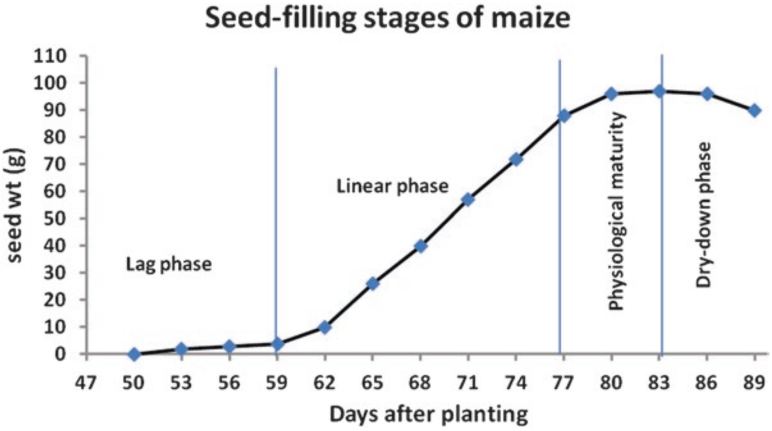

Fig. 3.1 Idealized seed-filling stages in an early-maturing maize cultivar

blister stage. In the milk stage, which is about 3 weeks after silking, the clear fluid in the kernel turns milky. Maize ears can be harvested at this stage for fresh consumption (green maize) due to the high sugar content of the kernels. Thereafter, the quality for fresh consumption declines due to the decline in sugar and water content and an increase in starch content and dry matter. A line known as the milk line is visible on the side of the kernel opposite the germ. The milk line, which moves down as the grain matures, separates the mature starch area from the milky region near the base of the kernel. The dough stage, which is the last stage of grain filling, has two distinct phases, soft dough and hard dough. At the soft-dough stage, the kernels are composed of white paste with the embryo occupying half the width of the kernel. The white paste of the soft-dough stage starts to solidify at the hard-dough stage beginning from the top part of the kernel. At this stage, a dent in the top of the kernel becomes apparent in dent varieties.

At physiological maturity, transport of assimilates to the kernel ceases, the black layer (abscission layer) develops at the base of the kernel, and the milk line disappears. At this stage, the kernels have attained maximum dry weight, with a moisture content of about 35%. The kernels at the tip of the ear mature first. An ear is physiologically mature when 75% of the kernels in the central part of the ear show the black layer. Idealized seed-filling stages in maize are shown in Fig. 3.1. The maize kernel is a caryopsis, a dry indehiscent single-seeded fruit (the grain or fruit of grasses is called a caryopsis).

The kernel is composed of three parts: the pericarp, the endosperm, and the embryo or germ. The pericarp is the protective outer layer of the kernel derived from the matured ovary wall (i.e., the maternal tissue). The pericarp (ovary wall) and testa (seed coat) are fused to form the fruit wall. The tight adhesion between the fruit and the seed makes the two structures to actually appear to be a single structure. The endosperm is the starchy storage part of the kernel constituting between 82% and 84% of the weight of the dry kernel. It contains about 88% starch and about 8–10%

protein. Due to its high starch content, the endosperm provides the energy reserve for developing seedlings.

The embryo constitutes between 10% and 12% of the kernel on a dry weight basis and is enclosed in a shield-shaped organ known as the scutellum. The embryo axis extends from the coleoptile to the coleorhizae. The shoot primordial consists of 5–6 embryogenic leaves, the stem, and growing point (apical meristem). The plumule consists of the embryonic leaves and the stem. The coleoptile is a sheath protecting the first leaf and growing point. The radicle, which is at the root end of the embryo axis, has several lateral root initials. As with the plumule, it is protected by a sheath, which in this case is known as the coleorhiza.

Following imbibition, enzymes released by the aleurone layer convert the starch stored in the endosperm to sugar which is absorbed by the scutellum, providing the energy required for germination. The radicle elongates first. Thereafter, the shoot elongates, and the coleoptile breaks through the seed coat. Depending on environmental conditions (soil texture and soil moisture content), germination takes place in 2–3 days. The first internode elongates, and the shoot emerges from the soil 3–5 days after germination. Germination in maize is hypogeal because the seed structure remains in the soil. After emergence, the seedling begins to photosynthesize. By this time, the food reserve in the endosperm is nearly exhausted. The seminal roots, which had initials in the embryo, develop and function to anchor the seedling and absorb water and nutrients required for early growth. The main root system develops from the crown, just below the soil surface. The seedling develops additional leaves, which together with those present in the seed grow into mature leaves. Many adventitious roots develop from successive nodes of the stem. Adventitious roots arising from nodes above the soil surface are called brace roots or prop roots. The small stem develops into the stalk which attains full size at the time of tasseling.

Maize growth stages are divided into two broad categories: vegetative (V) and reproductive (R). The vegetative stages are defined primarily by the appearance of leaves, while the reproductive stages are based on the female inflorescence and developmental changes in the kernels (Abendroth et al. 2011). The various vegetative and reproductive stages are presented in Table 3.1.

Maize plants of the same population or family will attain these stages at different times due to some differences in their genetic makeup and effects of the environment. Consequently, a family/population is considered to have attained any of these stages when 50% of the plants of the family/population show the characteristics descriptive of the respective stage.

3.3 Classification of Maize

Maize cultivars can be grouped based on the structure of the grain, viz., flint maize, dent maize, sweet (and super sweet) maize, floury maize, popcorn, waxy maize, and pod corn. Grain structure is determined by the distribution of flinty and floury endosperm.

Table 3.1 Vegetative and reproductive stages in maize

Stage	Description
VE	Emergence of the coleoptiles from the soil
V1	Appearance of the collar of the first leaf
V2	Appearance of the collar of the second leaf
V*n*	Appearance of the collar of the *n*th leaf. Leaf number in maize is variable (may be as few as 15 and as many as 23, some of which will have dropped by flowering)
VT	Appearance of the last branch of the tassel signifying the end of vegetative growth
R0	Anthesis or male flowering begins. Pollen is shed
R1	Appearance of the silks
R2	Blister stage; kernels are filled with clear fluid; embryo visible on kernel dissection
R3	Milk stage; kernels are filled with white milky fluid
R4	Dough stage; milky fluid observed in R3 above has thickened to become a white paste; embryo has enlarged to about half the size of the kernel
R5	Dent stage; cap of kernel has become dented in dent types; milk line is close to the base when kernel is viewed from the side of both flint and dent types
R6	Black layer visible at the base of the kernel, signifying physiological maturity. At this stage, moisture content may be as high as 35%

The endosperm consists of starch granules embedded in a protein matrix. Flinty endosperm has a relatively rigid protein structure. In floury endosperm, the starch granules are surrounded by a thinner protein matrix, which may rupture on drying, creating air pockets.

Flint maize The entire outer portion of the kernel in flint maize is composed of hard, flinty endosperm that does not easily form a paste with water. Flint maize produces a good-quality cornmeal (dry milling). It is more resistant to insect attack (Dowswell et al. 1996).

Dent maize Dent maize is the most widely grown type. In dent maize, the flinty endosperm is confined to the sides of the kernel. The floury endosperm that forms the core and cap contracts when the grain is dried, producing the characteristic dent in the top of the kernel. Much of the global production of dent maize is used for livestock feed.

Sweet maize This type is grown primarily as food and is harvested at about 70% moisture before hardening and drying of the grain begins. Sweet corn is a good source of energy. The kernels are high in sugar content due to one or more recessive mutations blocking the conversion of sugar to starch. Twenty percent of the dry matter in sweet corn is sugar compared to 3% in dent maize at the green ear stage. Sweet corn must be processed or eaten quickly after harvest to retain its flavor. The quality of sweet corn can be preserved if the grain is canned or frozen.

Floury maize The kernels of floury maize are composed largely of floury endosperm with little or no flinty endosperm. The kernels are easily ground to make fine flour. It is one of the oldest types of maize, and it is grown in the Andean highlands of South America (e.g., Peru). Some traditional landrace varieties from coastal West Africa are also floury types.

Table 3.2 Maturity groups of maize varieties

Maturity group	Days to maturity
Extra early	80–85
Early	90–95
Intermediate	100–110
Late	120–130
Extra late	>140

Popcorn This is an extreme form of flint maize; the kernels of popcorn are smaller. It is a popular snack in many parts of the world. When heated to about 170 °C, the grains swell and burst, turning inside out. At this temperature, water held in the starch in the kernel tissue turns to steam, and the pressure causes the endosperm to explode.

Waxy maize This type of maize has a waxy (dull) appearance. China was the original source of the waxy gene (wx). Waxy maize starch is composed almost entirely of amylopectin, in contrast to common maize starch, which is approximately 78% amylopectin and 22% amylose. Waxy maize is a raw material for the wet milling starch industry.

Pod corn This is the most primitive form of maize in which the kernels are entirely enclosed in floral bracts or glumes, resembling most grasses. Pod corn has a unique feature of severe reduction in glume size that results in almost naked grains. The predominant phenotypic feature of Tu maize is a foliaceous elongation of the glumes, which cover the kernels in the ears, different from other maize varieties in which glumes are not present or are invisible in the mature ear. The bizarre Tu phenotype is attributable to ectopic expression of the developmental control gene ZMM19 in the maize ear, a gene that is normally expressed only in vegetative tissue.

Maize varieties can also be grouped based on maturity as extra early, early, intermediate, late, and very late (Table 3.2). The number of days to maturity in WCA for each group is indicated below:

Maize breeders also classify maize varieties on the basis of their genetic constitution as open pollinated (landraces, composites, synthetics, experimental varieties) and hybrids (single cross, three-way cross, double cross, and topcross).

Landrace A variety that was developed under a set of farmers' practices of seed selection and field management, without systematic improvement by plant breeders. Landraces have a historical origin and distinct identity and are adapted to local environments but are genetically heterogeneous.

Composite varieties A composite variety is formed by mixing genotypes from several sources with a desired array of characteristics and allowing the genotypes to intermate.

Synthetic A synthetic variety is produced (synthesized) by crossing a number of genotypes developed by inbreeding (referred to as inbred lines) which have been tested and found to exhibit good combining ability among themselves in all possible combinations. Following its synthesis, the synthetic variety is maintained by open pollination.

Experimental variety (EV) This is a variety formed from recombination of genotypes selected for adaptation to a specific set of environments. The selected genotypes may be families from a recurrent selection program or partially inbred lines. Because the resulting open-pollinated variety is intended for release to farmers, it may have greater uniformity and be less genetically diverse than a typical breeding population

Single-cross hybrid A single-cross hybrid is one that is formed by crossing two genotypes, usually inbred lines.

Three-way cross A three-way cross is a hybrid formed from three inbred lines; a single-cross hybrid formed from two inbred lines is crossed to another (a third) inbred line.

Double-cross hybrid This is a hybrid produced from crossing two single-cross hybrids each of which has been produced from two inbred lines.

Topcross hybrid This is a hybrid produced by crossing an inbred line and an open-pollinating variety.

Definitions and description of the different types of hybrids are provided in greater detail in Chap. 6.

3.4 Maize Physiology Studies in SSA

The physiology of maize under the different agroecologies of SSA is little understood. However, studies have been initiated along this line in our programs, and a few case studies are presented in the rest of this chapter, starting from seedling to the grain-filling growth stages.

The resumption of activities by the embryo usually after a resting state is termed germination. The process is triggered with the imbibition of water by the dry seed and is complete when the radicle protrudes. Bewley and Black (1994) classified water imbibition by seeds into three phases: (i) rapid water absorption independent of metabolic activites but dependent on soil texture, structure, and water content in relation to seed-to-soil contact; (ii) point or period of water saturation in the seed with reduced rate of further water imbibition; and (iii) another rapid water uptake for radicle emergence and elongation.

Studies on water imbibition rate by maize seeds are ongoing in the Seed Science Laboratory of Obafemi Awolowo University, Ile-Ife. In one study, seed lots of nine open-pollinated varieties of field corn and one sweet corn variety were weighed and subjected to imbibition test for 72 h in a four-replicate experiment. At hourly interval, ten seeds were removed from each replication and variety, blotted dry with

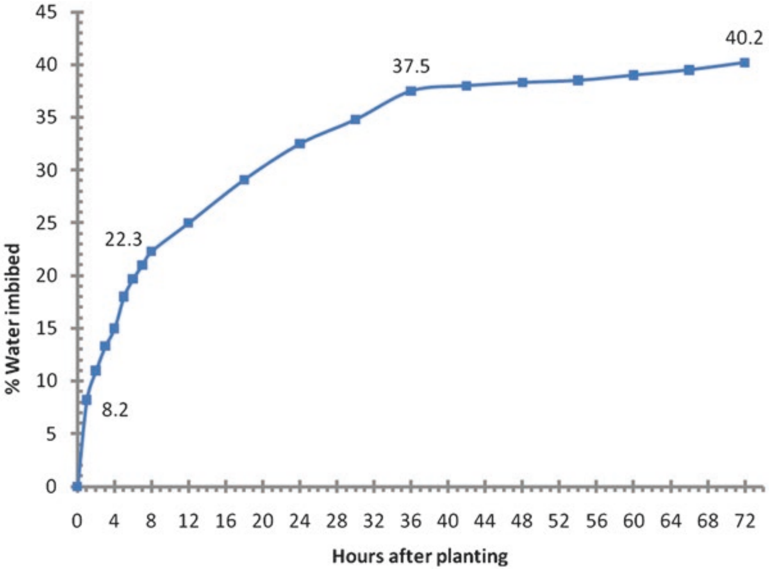

Fig. 3.2 Water imbibition by the seeds of tropical maize varieties during a 72-h period. Each point on the graph is the mean of ten varieties and four replicates

paper towel, and weighed. This was done for the first 8 h after which the process was repeated at 6-h. intervals, starting from 12 h after planting till the termination of the experiment. Standard germination tests were also carried out with daily germination counts from the fourth to the seventh day after planting. On average, water imbibition by the ten varieties was triphasic, and each phase ended at a point of inflection (Fig. 3.2). Within 1 h of planting, the seeds had imbibed additional 8% of their dry weight and, by 8 h, 22%. Together, the first 8 h constituted Phase I with the linear regression equation $Y = 2.495\text{x} + 4.2978$; $R^2 = 0.9204$. For this stage, the seeds imbibed water at the rate of about 2.5% per hour. Water imbibition during Phase II proceeded at a much slower rate of 0.51% per hour, with the linear regression equation $Y = 0.5117x + 19.5$; $R^2 = 0.9868$. Contrary to the submission of Bewley and Black (1994), Phase III had the slowest water imbibition rate of 0.07% per hour with the regression equation $Y = 0.0719x + 34.818$; $R^2 = 0.9613$. Although the values were different, water imbibitions for individual varieties showed trends similar to the one observed for the mean of the ten varieties evaluated in the study, and the variety x – h. interaction was not significant. By the end of the experiment (72 h = 3 days), the seeds on average had imbibed over 40% of their dry weight. However, the rate and amount of water imbibed by the maize varieties were not associated with the germination potential of the varieties.

Studies on maize seedling emergence and early (first 30 days after planting) vegetative growth have received sizable attention in our program. Maize yield can be improved indirectly by improving plant stand. Seedling vigor is an important factor in obtaining near-perfect stands and should be an important consideration in maize breeding programs. Seedling vigor may be boosted by favorable environmental factors, primarily moisture availability. The environment at the beginning of the season in WCA is characterized by inadequate soil moisture; farmers therefore require varieties that are drought tolerant at the seedling and early vegetative stages. This will extend the early (or first) planting season and make it possible for grain filling to coincide with the period of relatively high-incident solar radiation. A similar situation exists in the US Corn Belt except that the environment is characterized by cold, wet conditions. In Iowa, for example, maize breeders and physiologists conducted research into seedling vigor under the cold, wet conditions of early spring with a view to planting the crop early in the season so that grain filling would coincide with the period of high solar intensity and duration in the summer (Mock and Eberhart 1972; Mock and Bakri 1976; Mock and Skrdla 1978; Mock and McNeil 1979). Results from the studies demonstrated that under the cold, wet planting environments, high final stands occurred for vigorous (or cold-tolerant) maize seedlings but seedling vigor had low or nonsignificant correlation with grain yield. Mock and McNeil (1979), however, obtained statistically significant positive correlation between dry matter at the vegetative stage (42 DAP) and grain yield ($r = 0.48$). Similarly, Mock and Erbach (1977) obtained a statistically significant positive association between final stand and grain yield under minimum tillage environments of the early spring maize planting in Iowa.

One approach to evaluating seedling and vegetative vigor is to employ the technique of growth analysis (Radford 1967; Voldeng and Blackman 1973; Arkin and Monk 1979). Employing this technique, Voldeng and Blackman (1973) observed that heterosis was present in the early growth stages of maize. Taking a cue from the experience of maize scientists in the US Corn Belt and elsewhere, research into maize vigor at the seedling and early vegetative stages was initiated at Obafemi Awolowo University, Ile-Ife, Nigeria, in 1978. In all plantings for seedling and vegetative vigor studies, emergence counts were taken at 4 or 5, 7, and 9 days after planting. Beginning at 9 DAP until 29 DAP when six samplings were completed, five seedlings were sampled per plot at 4-day interval and oven-dried to constant weight at 80 °C. The data were used to compute traits for quantifying seedling and vegetative vigor, including emergence percentage ($E\%$), emergence index (EI), emergence rate index (ERI), growth rate (GR), and relative growth rate (RGR). The traits were computed as follows:

$E\%$ = 100(number of seedlings emerged 9 DAP)/total number of seeds planted
EI = [$\sum(N\text{x})(\text{DAP})$]/seedling emerged 9 DAP (Mock and Eberhart 1972)
ERI = EI/$E\%$, with $E\%$ expressed on a 0 to 1 scale (Fakorede and Ayoola 1980; Fakorede and Ojo 1981; Fakorede and Agbana 1983)
GR = $(W_{n+1} - W_n)/(t_{n+1} - t_n)$, mg plant^{-1} day^{-1} (Radford 1967)
RGR = $(log_e\, W_{n+1} - log_e W_n)/(t_{n+1} - t_n)$, mg mg^{-1} day^{-1} (Radford 1967)

Here, Nx is the number of seedlings emerged on day x, W is the dry weight per plant in mg, t is the number of days after planting, and n is the sampling number. In later studies, GR and RGR were estimated by regression approach: $W = a + bt$ and $W_1 = a_1 + b_1 t$ where W and W_1 are dry weight and loge dry weight per plant; a and

Table 3.3 Correlation coefficients of vigor traits with traits of mature maize plants for 7 varieties and 11 variety hybrids evaluated in five locations in 1981

Mature plant trait	*E*%	EI	ERI	GR	RGR
Grain yield	0.65**	−0.54**	−0.60**	0.68**	0.61**
Stand count	0.79**	−0.66**	−0.77**	0.81**	0.76**
Ear number	0.67**	−0.53**	−0.65**	0.70**	0.62**
Kernel weight	−0.60**	0.40	0.49*	−0.36	−0.48*
Tasseling–pollen shed interval	−0.61**	0.43**	0.59**	−0.64**	−0.58**
Tasseling–silking interval	−0.67**	0.58**	0.69**	−0.64**	−0.71**

*,**Significantly different from zero at 0.05 and 0.01 level of probability, respectively

a_1 are the intercepts of the regression line on the *y*-axis; *b* and b_1 are regression coefficients estimating GR and RGR, respectively; and *t* is the time in DAP.

Results from the many studies may be summarized in the following sections:

(i) Emergence starts to occur within 5–6 days of planting, and seeds whose seedlings fail to emerge by 9 DAP must have lost viability or been destroyed by soil organisms.

(ii) Seedling and vegetative vigor are fairly predictable during the normal planting season. In a date of planting study conducted in 1978, 1980, and 1981, Fakorede (1985) found that, regardless of the cultivar, *E*% increased, while EI and ERI reduced as planting was delayed during the early planting season at Ile-Ife. EI is an index of the number of days it took the observed *E*% to occur, while ERI estimates the number of days it would take 100% emergence to occur given the rate of the observed EI. The lower the EI and ERI values, the faster the rate of emergence. Using these criteria, 80–95% of viable maize seeds planted under normal environmental conditions in WCA take about 5.4–5.7 days to emerge, and they require about 5.6–7.2 days to 100% emergence.

(iii) Seedling and vegetative vigor are under genetic control in maize. In a study reported by Fakorede and Agbana (1983) involving 7 varieties and 11 varietal hybrids, statistically significant genotypic differences were observed in the analysis of variance with the genotype source of variation accounting for 53 and 56% of total variation for *E*% and ERI, although only 7, 32, and 23% for EI, GR, and RGR, respectively. Statistically significant mid- and high-parent heterosis were observed for the seedling and vegetative vigor traits in some of the crosses in the study, and the traits had highly significant correlation coefficients with grain yield, flowering intervals, plant stand, ear number per unit land area, and kernel weight (Table 3.3).

(iv) Genotypic variation for seedling and vegetative vigor is quantifiable thereby making selection for its improvement possible. In a study involving 36 maize populations, Fakorede and Ojo (1981) detected large genotypic variances for *E*%, EI, dry matter accumulation, and RGR, with relatively large broad-sense heritability estimates. Opeke and Fakorede (1986) evaluated 169, 169, and 121 S_1 families from three maize populations FARZ 27, FARZ 34, and TZSR-W-1 for genetic variation in *E*%, EI, ERI, and grain yield. Estimates of genetic

Table 3.4 Some genetic parameters for emergence traits and grain yield in three maize populations

Parameter	Population	*E%* (days)	EI (days)	ERI (days)	Grain yield (*t*/ha)
Mean ± s.e.	FARZ 27	77.5 ± 6.84	6.0 ± 0.38	10.10 ± 0.38	3.2 ± 0.71
	FARZ 34	80.3 ± 6.60	5.9 ± 0.41	9.12 ± 2.25	3.7 ± 0.70
	TZSR-W-1	78.9 ± 7.71	6.2 ± 0.37	8.61 ± 1.90	3.0 ± 0.74
σ^2_g ± s.e	FARZ 27	348.8 ± 46.86	0.10 ± 0.02	65.03 ± 9.84	0.53 ± 0.10
	FARZ 34	311.7 ± 45.44	0.13 ± 0.03	57.99 ± 8.39	0.50 ± 0.12
	TZSR-W-1	159.7 ± 21.51	0.08 ± 0.02	8.53 ± 1.41	0.28 ± 0.07
σ^2_{ge}	FARZ 27	30.2	−0.01	19.45	0.06
	FARZ 34	−9.6	0.02	2.11	0.10
	TZSR-W-1	−8.2	0.00	3.38	−0.13
h^2	FARZ 27	0.90	0.59	0.81	0.65
	FARZ 34	0.93	0.56	0.94	0.63
	TZSR-W-1	0.84	0.53	0.71	0.51

Table 3.5 Phenotypic (r_{ph}) and genotypic (r_g) correlation coefficients of seedling emergence traits with grain yield and other traits of adult plants for three maize populations

		E%		EI		ERI	
Trait	Population	r_{ph}	r_g	r_{ph}	r_g	r_{ph}	r_g
Grain yield, *t*/ha	FARZ 27	0.42**	0.18	−0.11	−0.01	−0.45**	−0.12
	FARZ 34	0.61**	0.63	−0.30**	−0.44	−0.63**	−0.17
	TZSR-W-1	0.31**	0.1	−0.08	−0.14	−0.31**	−0.17
Days to tasseling	FARZ 27	−0.22*	−0.09	0.22*	0.12	0.21*	0.05
	FARZ 34	−0.25*	−0.3	0.33**	0.24	0.34**	0.77
	TZSR-W-1	−0.12	0.04	0.24*	0.19	0.23*	−0.03
Days to anthesis	FARZ 27	−0.23*	−0.1	0.22*	0.16	21*	0.05
	FARZ 34	−0.33**	−0.39	0.36**	0.27	34**	0.77
	TZSR-W-1	−0.15	0.02	0.21*	0.14	23*	−0.03
Days to silking	FARZ 27	−0.19*	−0.03	0.22*	0.16	0.16*	0
	FARZ 34	−0.31**	−0.37	0.32**	0.26	0.30**	0.26
	TZSR-W-1	0.13	0	0.20*	0.22	0.19*	0.02
Plant stand	FARZ 27	0.77**	0.28	−0.30*	−0.25	−0.83**	−0.33
	FARZ 34	0.80**	0.78	−0.40**	−0.45	−0.86**	++
	TZSR-W-1	0.59**	0.18	−0.52*	−0.07	−0.62**	−0.33
Ear number	FARZ 27	0.52**	0.2	−0.20*	−0.13	−0.53**	−0.13
	FARZ 34	0.72**	0.73	−0.41**	−0.52	−0.74**	−0.99
	TZSR-W-1	0.42**	0.15	−0.22*	−0.34	−0.43**	−0.31

*,**Significantly different from zero at 0.05 and 0.01 level of probability, respectively
++ Correlation greater than 1

variance, heritability (Table 3.4), and both phenotypic and genotypic correlation coefficients of the seedling traits with grain yield (Table 3.5) were sufficiently high to make genetic improvement of seedling vigor and grain yield in the populations realizable.

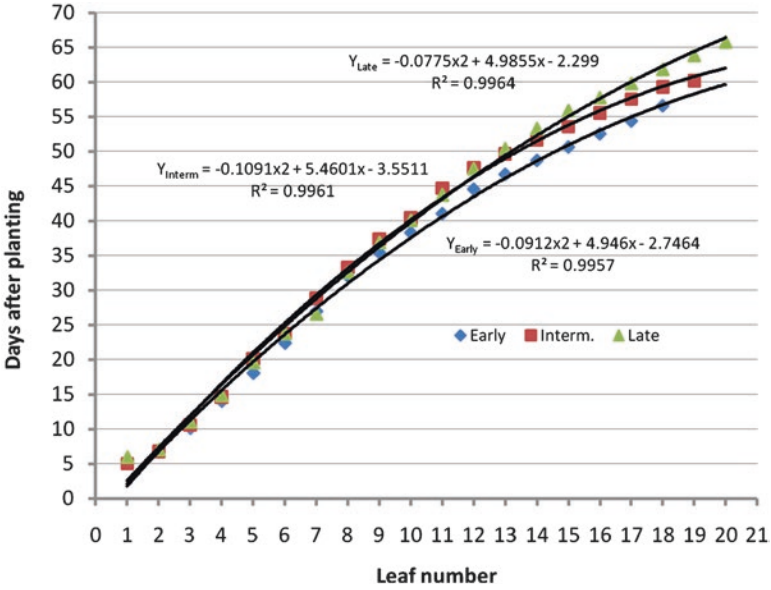

Fig. 3.3 Number of days from planting to leaf formation stages in early-, intermediate-, and late-maturing maize cultivars evaluated at Ile-Ife

One clear distinction among maturity groups of maize is the total number of leaves formed per plant and the rate of leaf formation. Studies conducted in 2009 and 2010 at Ile-Ife, a typical rainforest location, showed that early-, intermediate-, and late-maturing varieties produce about 18, 19, and 20 leaves, respectively (Fig. 3.3).

When grown under similar environmental conditions, seedling emergence and rate of development, as measured by the unfolding and ligule formation of the first four leaves, are not different for the three maturity groups. Thereafter (i.e., as from about 20 DAP), rate of leaf formation proceeds faster in early than the other two maturity groups. Intermediate and late varieties continue at similar rate until about the formation of the 15th leaf when the rate becomes faster in intermediate- than late-maturing varieties (Fig. 3.3). Transition from vegetative to reproductive growth stages (tasseling) occurred about 57, 61, and 66 DAP for the three maturity groups, respectively.

Oluwaranti et al. (2013) evaluated 100 maize varieties during the late and early cropping seasons of 2007/2008 and 2008/2009 at the Teaching and Research Farm of Obafemi Awolowo University (7° 28′ N, 4° 33′ E, 244 m asl). As expected, statistically significant variety differences occurred. There were also significant variety x season and variety x year interactions for the flowering traits (days to 50% tasseling, anthesis, and silking). The earliest varieties to flower in the early season were 97 TZEE-Y2C1 and TZEE-Y POPSTRC0 with 48–55 days to tasseling, anthesis, and silking, while Oba Supa 2 and ACR96DMR-LSRW, which took 64–71 days to the flowering events, were the latest. In the late cropping seasons, 2004 TZEE-W

Table 3.6 Relationships of grain yield (*t*/ha) with days to phenological events in 226 maize varieties evaluated at Ile-Ife, Nigeria

Trait	*r*-value	*b*-value	Trait	*r*-value	*b*-value
Emergence (E)	−0.60	−0.33	TS–PS	−0.48	−0.37
Tasseling (TS)	0.47	0.10	TS–SK	−0.57	−0.33
Pollen shed (PS)	0.39	0.09	TS–MT	0.22	0.12
Silking (SK)	0.32	0.08	PS–SK	−0.37	−0.37
Maturity (MT)	0.45	0.08	PS–MT	0.50	0.24
E–TS	0.58	0.10	SK–MT	0.64	0.29
E–PS	0.52	0.10	TS interval	−0.25	−0.17
E–SK	0.47	0.10	PS interval	−0.16	−0.10
E–MT	0.54	0.08	SK interval	-0.03^{NS}	-0.02^{NS}

NS not significant at 0.05 level of probability. All other values are statistically significant at 0.01 level of probability

Table 3.7 Direct (on the diagonal) and indirect (off diagonal) path coefficients of five traits (variables) on the grain yield of 226 maize varieties evaluated in Nigeria

	Variable							
Variable	1	2	3	4	5	Total corr	Effect corr	Residual
1 Silking to maturity	**0.462**	−0.702	0.744	−0.015	0.148	0.635**	0.636	0.001
2 Silking	0.365	**−0.889**	0.736	−0.031	0.133	0.321**	0.314	0.006
3 Emergence to taselling	0.411	−0.782	**0.836**	−0.015	0.131	0.582**	0.581	−0.001
4 Pollen shed interval	0.051	−0.204	0.092	**−0.133**	0.035	−0.156**	−0.159	0.003
5 Polleshed to maturity	0.407	−0.702	0.660	−0.028	**0.168**	0.503**	0.505	−0.005

** *r*-value significantly larger than zero at 0.01 level of probability

POP STR C4, TZEE POP STR C0, SINET-EE-WSR, and TZE-W POP DT STR C4 F2 with 42–47 days were the earliest to flower, while BUSOLA STR, TZL COMP CO, 9021-18STR, and Oba Supa 2, with 61–68 days, were latest to flower. Fakorede (1993) summarized the data obtained from several studies involving 226 varieties evaluated from 1981 to 1990 at Ile-Ife to determine the relationship of grain yield with specific phenological events in maize under tropical conditions. Wide ranges were observed in the mean performance of the traits determined in the trials. For example, grain yield ranged from 0.5 to 4.5 *t*/ha. The days to and between most of the phenological events had statistically significant correlation coefficients with grain yield (Table 3.6). However, the *r*-value and/or *b*-value for most of the traits was too low to be of much practical use in maize selection programs.

Whereas *r*-value indicated that silking to maturity (SK–MT), which is the grain-filling period, had the largest correlation with grain yield, path analysis showed that emergence to tasseling (vegetative growth phase) made the largest direct contribution to grain yield followed by silking to maturity (Table 3.7). Delayed silking had

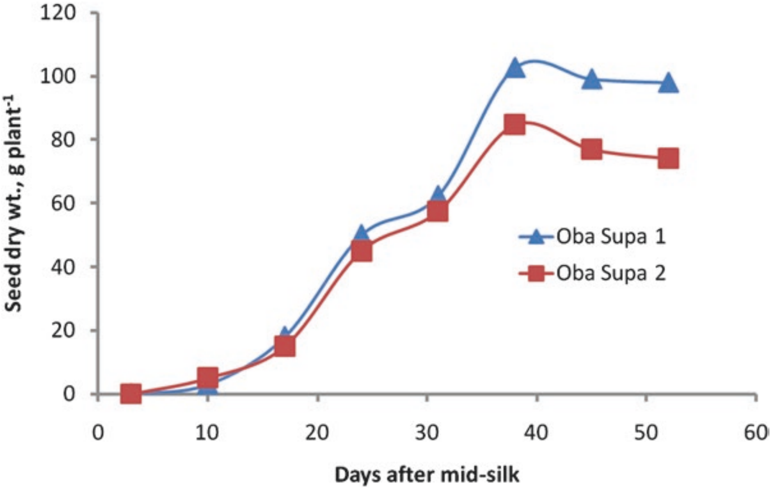

Fig. 3.4 Dry matter accumulation in the seeds of two maize hybrids evaluated in the rainforest agroecology of Nigeria

a large negative direct effect on grain yield. The study led to the conclusion that fast emergence plus vigorous vegetative growth, followed by rapid completion of flowering and extended grain-filling period, would give high grain yield.

Physiological maturity (PM), defined as the point of maximum dry matter accumulation in seed, has been associated with maximum seed quality by researchers and seed producers. However, germination of maize seed on the cob frequently occurs in the field long before PM. Several studies were conducted to determine the effect of seed maturity stage on seed quality.

Two hybrids, Oba Supa 1 and Oba Supa 2, were monitored at weekly interval for three PM indices: milk line, black layer formation, and dry matter accumulation beginning 3–59 days after mid-silk (DAS). Seed samples were taken at the different maturity stages starting from 31 DAS (Ajayi and Fakorede 2000, 2001). The seeds were evaluated in the laboratory for germination percentage (*G%*), germination index (GI), number of abnormal seedlings, and dry weights of roots and shoots. The seeds were also planted in the field, and data were collected on *E%*, EI, ERI, GR, and RGR during the first 30 days of growth along with flowering dates, plant and ear heights, and grain yield per plot.

Seed filling followed very much the expected trend for both hybrids with lag phase lasting about 10 days from mid-silk, linear phase of about 30 days, and the effective filling period duration (EFPD) about 40–45 days at which time the plants reached PM (Fig. 3.4). Mid-silk took about 60 DAP; therefore, the two hybrids are of intermediate maturity, taking about 100–105 days to PM as determined by dry matter accumulation in the seed. Estimates of PM obtained by the three indices were not the same, contrary to studies conducted under temperate conditions where PM rated by milk line and black layer was well correlated with that determined by seed dry weight accumulation (Hunter et al. 1991; TeKrony and Hunter 1995).

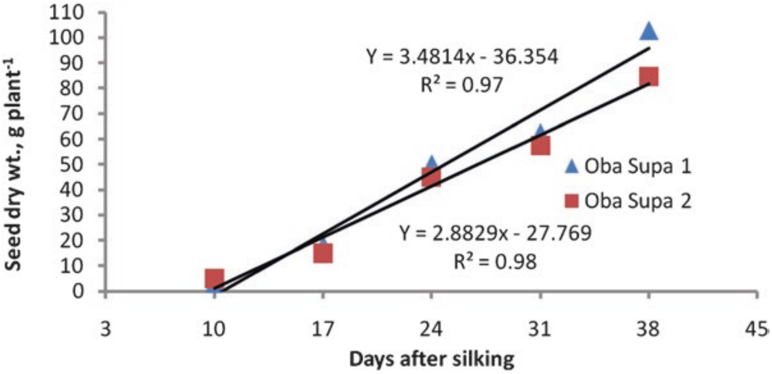

Fig. 3.5 Grain-filling rate during the linear phase in two maize hybrids evaluated in the rainforest agroecology of Nigeria

The two hybrids in Ajayi and Fakorede's studies were different for grain-filling rate: 3.5 versus 2.9 g plant^{-1} per day for Oba Supa 1 and Oba Supa 2, respectively, with about 21% difference (Fig. 3.5).

This result provides a possible explanation for the consistent lower-yielding ability of Oba Supa 2 (and perhaps other yellow hybrids) relative to Oba Supa 1 (and other white hybrids). In a study involving 44 hybrids carried out at CIMMYT-Zimbabwe to investigate the possibility of using grain-filling rate and duration for improving grain yield in early-maturing tropical maize (Gasura et al. 2013), high-yielding hybrids had grain-filling rate of 2.40 g plant^{-1} per day, which was 18% higher than those of the low-yielding hybrids, and a relatively longer EFPD, both of which had positive correlations with grain yield. In another study, Wang et al. (1999) found that general combining ability (GCA) was more important than specific combining ability (SCA) for both grain-filling rate and EFPD, an indication of preponderance to additive gene action in the mode of inheritance for the two traits. It should be possible, therefore, to improve maize grain yield by recurrent selection for these traits.

Ajayi and Fakorede's (2001) studies further confirmed that maize embryo was physiologically mature before maximum dry matter accumulation in the endosperm. Both maximum germination in the laboratory and emergence in field tests occurred in seeds harvested at 31 DAS and remained constant for seeds harvested thereafter. Apart from seed weight that was significantly different among the seed sampling stages, seedling emergence, seedling vigor, and traits of mature plants were remarkably similar for all maturity stages from 31 to 59 DAS (Table 3.8).

The concept of PM arose out of the need for timely harvesting of seed to ensure maximum quality. Studies in several crops, however, have shown that maximum accumulation of dry matter (i.e., PM) alone is not sufficient to determine maximum seed quality. In some cases, such as in barley (*Hordeum vulgare* L.) and rice (*Oryza sativa* L.), maximum seed quality was not achieved until 12 to 30 days after PM (Pieta-Filho and Ellis 1991; Ellis et al. 1993). In some other cases, such as the common bean (*Phaseolus vulgaris* L.), castor bean (*Ricinus communis* L.), and

Table 3.8 Laboratory and field test performances of maize seeds harvested at different maturity stages

	Maturity stage (days after mid-silk)+				
Trait	31	38	45	52	59
Laboratory performance					
Germination %	99.6 a	96.1 a	98.3 a	81.8 b	96.1 a
Germination index, days	5.1 a	5.1 a	5.1 a	5.8 b	5.4 c
Abnormal seedlings, %	1.5 a	1.4 a	1.8 a	9.3 b	0.9 a
Root dry wt, mg seedling^{-1}	47.8 a	56.5 bc	57.5 b	49.5 ac	57.8 b
Shoot dry wt, mg seedling^{-1}	48.5 a	51.3 ab	54.8 b	50.5 ab	50.0 ab
Field performance					
Emergence %	91.4 a	93.0 ab	94.0 ab	65.4 c	95.5 b
Emergence index, days	5.2 a	5.2 a	5.2 a	5.7 b	5.2 a
Emergence rate index, days	5.6 a	5.6 a	5.5 a	8.7 b	5.4 a
Growth rate, g plant^{-1} day^{-1}	0.25 ab	0.26 ab	0.23 bc	0.19 c	0.30 a
Relative growth rate, g g^{-1} day^{-1}	0.17 a	0.17 a	0.17 a	0.16 a	0.17 a
Days to 50% tasseling	58.0 a	58.4 ab	57.9 a	59.1 b	58.0 a
Days to 50% anthesis	59.6 ab	59.7 ab	59.3 a	60.3 b	59.5 ab
Days to 50% silking	61.6 abc	61.8 ab	61.1 bc	62.6 a	60.7 c
Ear height to plant height ratio	0.51 a	0.51 a	0.51 a	0.51 a	0.53 a
Grain wt, kg plot^{-1}	481.7 a	523.5 a	533.9 a	516.0 a	552.8 a

+Values in the same row with different letters are significantly different at 0.05 level of probability

wheat (*Triticum aestivum* L.), maximum seed quality was achieved before PM (Kermode et al. 1986; Rasyad et al. 1990). Using the cold test and seed leachate conductivity to determine seed vigor, TeKrony and Hunter (1995) found maximum seed quality at PM for single-cross and double-cross hybrids but after PM for inbred lines.

Most of the widely used indicators of harvest maturity of the maize seed crop in the temperate regions are greatly influenced by environmental factors; therefore, they need to be evaluated in the tropics in order to establish their relationships with key seed quality indicators.

Considering the results of their study, along with those of earlier workers, Ajayi and Fakorede (2001) called for a redefinition of PM in the context of maize seed quality and the resultant crop. In the tropics which characteristically has wide weather fluctuations, stable indicators of PM that are associated with the physiological and biochemical changes occurring during seed development need to be identified.

3.5 Summary

There are seven maize groups, based on the structure of the grain: flint maize, dent maize, sweet (and super sweet) maize, floury maize, popcorn, waxy maize, and pod corn. In SSA, research is based primarily on flint, dent, and floury types with minor efforts on pop and sweet corns. In WCA, flint maize is the dominant maize type in the northern parts, while floury maize is more common in the coastal areas, following more or less the pattern of maize introduction to the sub-region. Maize emerges 4–5 days after planting, depending on environmental conditions, moisture availability in particular. Seeds whose seedlings have not emerged by 9 days after planting must have lost viability or been destroyed by soil pests. Seedling vigor and early vegetative growth demonstrate significant correlations with grain yield and some agronomic traits, an indication that good and timely application of agronomic inputs such as fertilizer and weed control will lead to increased grain yield. Emergence and seedling vigor traits are under genetic control and may be improved by selection procedures. Apart from differences in attaining the flowering stage, rate of leaf formation and number of leaves are different among maize maturity groups. Studies conducted on grain-filling rate and duration led to a call for redefinition of physiological maturity in maize, to be based on when the embryo is able to germinate rather than maximum dry matter accumulation in the seed.

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Chapter 4
Pollination Techniques

4.1 Introduction

Controlled pollination has probably been carried out in maize than any other crop. In addition to the development of improved cultivars, maize is favored for controlled pollination for scientific investigation because of the ease with which selfing and crossing are made. Unlike most other cereal crops, pollination of one ear shoot may produce many seeds, sufficient for replicated field trials in several locations.

4.2 Pollination Control

4.2.1 Bagging Ear Shoot

On average, maize plants shed pollen 2–5 days before silk extrusion. Each maize plant produces millions of pollen grains. Expectedly, the atmosphere in a field of flowering maize plants is full of maize pollen. Only pollen that is intercepted by fresh silks can germinate. While one or more pollen may germinate on the same silk, only one is able to effect fertilization. The hairs on the silks function to trap the shed pollen. Moisture required for the pollen to germinate is provided by the silk. Thereafter, the moistened pollen germinates by sending out a pollen tube which may travel some distance on the surface of the hair but ultimately navigates between the cells of the hairs through which it enters the silk. The process of double fertilization in maize has been described in Chap. 3. The large number of pollen produced by maize plants relative to the number of silks is to ensure a high chance of fertilization.

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Plate 4.1 Shoot bagging

Ear shoots, a form of lateral branches in maize, become obvious at tasseling or at the beginning of pollen shed. A maize plant may produce one or two ear shoots. The tip of the first ear shoot may be visible in the axil of the sixth or seventh leaf (counting from the top of the plant). Silk (style) extrusion becomes observable few days later. Once the silks extrude and become exposed, they are expected to have received pollen randomly from flowering plants in the maize field. Consequently, ear shoots must be covered or bagged before the silks emerge (Plate 4.1). The silks of such ears are left covered until the desired pollen are available. Shoot bagging in maize is typically done using Lawson 317 (dimension 3″ × 7″) bags made of glassine. The bag is waterproof. Bagging should begin when the first tassel appears in the field, and this operation is carried out daily during the pollination period.

The Lawson shoot bag is longer at one end. The shoot is covered by placing the bag over the tip of the shoot with the long lip of the bag next to the stem (culm) so that the short tip of the bag slides over the top of the ear. The edge of the bag should be pulled round the ear so that the bag takes the shape of the culm. The bag is given a sharp downward pull to firmly attach it between the main stem and the ear shoot. Bags made locally using transparent polythene have been used with considerable success. One advantage of the latter is that the number of extruded silks can be readily assessed, especially since the number of silks can be equated with the number of potential kernels, provided the silks still remain receptive when pollinated and pollen used are viable. Ideally, silks are receptive for about 3 days after extrusion after which the chance for successful pollination rapidly diminishes. During daily shoot covering and pollination, ears covered on previous days and for which the covering bags are loose must be pulled down to make them more securely positioned. Special attention needs to be paid to lines with leafy husks at the tip (referred to as crazy ears) during the pollination season. This is because the developing husk leaves often push up the shoot bags, leading to the exposure of silks to pollen from unknown source and loss of ears for pollination. Unpollinated silks continue to grow and may reach a length of 15–20 cm. Failure of unpollinated cutback silks to regrow indicates that such silks had already passed their most receptive stage (Sheridan 1982).

4.2.2 Cutting Back of Ear Shoots

When silk extrusion is delayed and the pollen parent is nearing the end of pollen production, the ears without silks can be cut back. Cutting back of ears ensures the uniform exposure of silks 1 or 2 days earlier than they normally would be extruded. Cutting back of ears is done with a knife or secateur. Ears at the right stage for cutting back are those which have extruded few silks about 1 day earlier. The ear is cut at the tip of the husk, as far down the husk as possible without cutting off the tip of the cob inside. Since the wet ends of freshly cut silks are not receptive, they are protected from stray pollen which may fall on them during this operation.

Thereafter, the cut ear is again covered. Shoot bags covering cut ears are usually marked by folding the corner. Usually, by the next day, the silks which have by now grown and emerged from the cut surface and are usually of similar length are ready for pollination. The application of pollen at this time ensures that all the silks are pollinated, resulting in good kernel set. Pollinated silks stop growing in about an hour following which they become darker. Some inbred lines have been bred for tight husk tip. While the tight husk tip protects the matured kernels in the cob from bird damage, it can hinder the extrusion of silks. Usually, lines with such husks need to have their husks cut back since the mass of silk would have long passed the receptive stage before they are able to push through the tight husk (Sheridan 1982).

4.2.3 Pollen Shed and Controlled Pollination

On a warm sunny day, fresh anthers begin to extrude from the florets by elongation of the filament at about 7.00 a.m. The anthers open up about 30 min later to allow for pollen dispersal. Additional anthers continue to be extruded until about 10.00 a.m. Thereafter, no new anthers appear until the next morning. On cloudy or cool days, time of anther extrusion is delayed and may occur toward the evening.

Plate 4.2 Tassel bagging

Pollen shedding proceeds more rapidly in hot and dry environments. Pollen collection is usually done with Lawson waterproof (brown paper) tassel bags (No. 402), although this can be improvised using locally available brown paper cut to size, folded appropriately, and glued. The latter is, however, not usually reusable, while the Lawson pollination bags can be reused.

Tassels that have already attained the stage of pollen shed can be bagged and stapled early in the morning after drying up of the dew before pollen shed for the day commences or even in the evening of the previous day (Plate 4.2). This is important because moisture trapped in the tassel bag raises the humidity within the bag, which prevents the anthers from opening to shed pollen. The pollen released from the anthers remains in the bag enclosing the tassel. Information on the pollen parent and date of pollination must be written on the bag at the time of bagging. If the pollen collected from one bag needs to be used to pollinate more than one ear, then additional bags must be inscribed with the pollen parent and date of pollination as the silks are dusted with pollen and the pollinated ears covered with pollination bags. To facilitate tasks to be undertaken the following day, additional pollination bags can be labeled and kept for the next day.

To bag the tassel, bring the tassel to a near-horizontal position, taking care not to snap the tassel. Allow the tassel to return to the vertical position. Thereafter, pull the bag down past the lowest branch of the tassel. The tassel bag, held at the edges, is then folded at the base firmly around the stem of the tassel and finally secured with a regular paper clip or stapler (Plate 4.2). If tassels were bagged the day before, pollination can begin as soon as nearby unbagged tassels are observed to be shedding pollen. If bags have been soaked by heavy rain during the previous night or early that morning and they do not dry up before pollen shed begins, the bags can be replaced with dry bags (Aldrich et al. 1986).

To collect pollen for pollination, the plant is carefully bent close to the tassel so that the open end of the bag is placed higher than the sealed end. The paper clip or staple pin is removed and the tassel shaken within the bag so that pollen grains held in the anthers are released into the pollination bag. The tassel is thereafter removed from the pollination bag, keeping the open end of the bag higher than the sealed end to prevent pollen falling out of the bag. Maize pollen can be seen in the bag as light yellow to yellow powdery substance. Collected pollen can be dusted on silks of the same plant for self-pollination or to other desired silks or other desired lines/families to be used as female. While taking the pollination bag containing collected pollen to the plant(s) to serve as female, it is important to fold the open end of the bag to prevent contamination (Sheridan 1982).

For pollination, the stalk and tassel of the female parent are bent and placed under the pollinator's arm such that the tassel is positioned at the pollinator's back with the ear in his/her front. This helps to protect the ear to be pollinated from being contaminated with pollen from the tassel of the plant whose ear is being pollinated. The shoot bag is raised, and pollination bag containing the pollen is opened and pollen poured on the silks as fast as possible (Plates 4.3). The pollinated ear is covered with a labeled pollination bag, which is usually longer on one side than the other. The longer side is slid between the stalk and the ear, while the shorter side is positioned loosely to the outside of the ear. The two edges of the pollination bag are then pulled round the stalk opposite the ear, securing the bag to the stalk but allowing the ear to enlarge as it develops within the bag.

Whether it is for selfing or cross-pollination, controlled pollination must minimize contamination. The pollinator must be aware that pollen will be on leaves and on the pollinator's clothing and hands and also airborne. Although most of these may not be viable, enough will be viable to make contamination a serious problem.

Maize pollen is viable for less than 20 min after leaving the anther. The time is even less in hot dry weather but longer in cool humid weather. Loss of pollen viability is usually accompanied by a change in color. Fertilization is impaired if the temperature at pollen shedding and after pollination is above 35 °C. Fertilization is also impaired if temperature is lower than 13 °C (Poehlman and Sleper 1995).

4.3 Diallel Crossing

Crossing in a diallel involves making all possible crosses among a given number of lines or genotypes. For 10 lines, 45 crosses are possible, excluding reciprocals. For crossing in a diallel, it is convenient to have paired rows of each cross—one row per

Plate 4.3 Controlled pollination

parent. Consequently, the 45 crosses of a 10-parent diallel would require 90 rows. When reciprocals are not important, seeds formed from the two rows of a cross can be bulked.

4.4 Bulk Pollination or Half-Sibbing

Bulk pollination involves the use of pollen collected from many plants of a population for pollination. For instance, for topcross evaluation, requiring an open-pollinated variety as tester, pollen are collected from a large number of plants of the population, bulked, and used for pollination. It is important that the field is divided into two parts and pollen is collected from one portion of the field and then carried to another part of the field for the pollination in order to prevent selfing. It should be noted that it is best to collect pollen from one part of the field and bulk and use for pollination of plants in another part of the field.

4.5 Full-Sibbing

For full-sibbing, plant-to-plant crosses are made using each plant once as the male parent. The plant used as the male is detasselled so that it could not be used as the male or pollen parent more than once.

4.6 Emperical Studies on Maize Pollination

Research on different aspects of maize pollination has been carried out rather extensively in temperate environments but to a limited extent in SSA. Results of some of the studies are reviewed herein. In India, Gurumurthy (2005) investigated the effect of pollination methods on seed quality in several open-pollinated varieties of maize. Isolated half-sib nursery mating and reciprocal full-sib mating were significantly superior to other methods with respect to maintenance of genetic purity. There was no significant effect of pollination method on laboratory germination test, field emergence, seedling vigor, plant and ear heights, flowering, grain yield, and yield components. Similarly, pollination method had no significant effect on accelerated aging, electrical conductivity of seed leachate, and cold germination test. A study was conducted at the Seed Science Laboratory of Obafemi Awolowo University, Ile-Ife, Nigeria, to determine the effect of pollination method on seed number and weight in an early-maturing maize population (Okoye et al. 2014). The maize population was planted into a large experimental plot, which was divided into 20 strata, and from each stratum, 15 progenies were produced by each of 3 different pollination methods: S_1 (self-pollination of 15 plants), half-sibbing (each of 3 males used to pollinate 5 females), and bulk-sibbing (bulk pollen used to pollinate 15 detasseled plants as female). The ear per progeny was harvested and shelled manually for each stratum. Seeds from each ear for each pollination method per stratum were counted and weighed, and the data were analyzed using descriptive statistics. Results showed no significant difference in seed number for S_1 (332 ± 5.70) and bulk-sib (327 ± 7.45) progenies, but half-sib progenies had significantly lower seed number (277 ± 7.35) than the other two methods. The trend was similar for seed weight; half-sib was significantly lower (65.1 ± 1.80 g) than both bulk-sib (79.2 ± 2.49 g) and S_1 (78.2 ± 1.69 g) progenies. Stratum, a measure of the microenvironment, had no effect on the two traits. Production of lower seed yield per plant (both number and weight) by half-sibbing relative to the other pollination methods could be attributed to insufficient pollen from only one male plant on five female plants. This is perhaps one reason the genetic studies based on progenies produced by this method (e.g., North Carolina Designs I and II) are evaluated in relatively few environments.

Returns on investment of hybrid seed production are directly related to the quantity (yield) and quality of seed obtained per hectare from the female parent. It is also important to consider the effects that a male parent can exert on the development of hybrid seed in the female parent. This effect is known as xenia. The underlying cause is the fertilization of the diploid polar nucleus by the haploid vegetative sperm nucleus, resulting in triploid endosperm cells. Endosperm characteristics that exhibit xenia include endosperm color (e.g., yellow vs white), waxy vs non-waxy endosperm, aleurone color (purple vs white), non-shrunken vs shrunken endosperm, and starchy vs sugary endosperm. Xenia effect on practical or commercial seed production has been the subject of several studies, especially by seed companies. In a 2-year study in Switzerland, the cross-pollination of maize was investigated by using the occurrence of yellow grains in 13 white-grain maize fields as a marker of cross-pollination from neighboring yellow-grain fields (Bannert and Stamp 2007). Distances of 50–4500 m between pollen-donor and pollen-receptor fields were investigated. Xenia effect of the whole field for each white seeded variety was 0.02% or less. Location of the varieties in relation to wind direction had an effect. For example, four of the white-grain maize fields, located in downwind distances of 50–371 m in the main wind direction, showed marked cross-pollination at the field border exposed to the nearest yellow-grain maize field. The study showed potential horizontal pollen dispersal distance of up to 55 m with a few cases occurring over longer distances, and these were attributed to gusts or vertical movements of the wind (e.g., thermal or turbulence effects). The effect of gradients of 3.4–6.8° on cross-pollination was investigated for 2 years (2005 and 2006) in the canton of Zurich, Switzerland (Vogler et al. 2009). Cross-pollination was determined by the presence of yellow grains on a white-grain hybrid at distances up to 17.5 m from the yellow-grain pollen-donor hybrid. The measurements of the inclination of the slope were based on aerial images data taken by an unmanned Global Positioning System/Inertial Navigation System (GPS/INS)-based and GPS/INS-stabilized model helicopter, which delivered precise altitude-based data for sampling points at maize tassel height. The rate of cross-pollination increased significantly with decreasing altitude of the receptor field ($r = 0.36$–0.64). However, the effect seems to be weaker than that of wind direction and velocity. Results of the studies from Switzerland seem to be in agreement with our unquantified observations; that is, maize planted in isolation fields surrounded by hills or tall forests are relatively free of contamination even when lower than the recommended isolation distance from another maize variety is used. Existence of natural barriers in isolation fields is a definite advantage in maize seed production where land is limiting.

4.7 Conclusions

Although pollination is basically the transfer of pollen grains from the tassel to the silk of maize plants, the method used will be dictated by the type of progeny the breeder wishes to produce, that is, selfed, half-sib, full-sib, bulk, or different types of hybrids. Studies of the effect of pollination methods on quantity and quality of seed production are lacking in SSA. It is desirable also to investigate the role of natural barriers, such as tall vegetation or forests and hills in the determination of isolation distances and xenia effects on seed production. Similarly, studies are needed on male/female number of rows in topcross and testcross nurseries and in the production of different types of hybrids.

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Part II
Maize Breeding Procedures in Sub-Saharan Africa

Chapter 5
Population Improvement and Development of Open-Pollinated Varieties

5.1 Maize Breeding Objectives

Maize breeding programs, like all plant breeding programs, usually have defined objectives. The objectives, which could be short term, medium term, or long term, address the constraints to production and productivity in the various ecological zones where the crop is cultivated. In general, maize breeding programs target high yield and the development of cultivars of different maturity durations, with resistance to important local pests and diseases and acceptable end-use quality for consumers.

In the short term, maize breeding programs may exploit new introductions, which may be open-pollinated varieties, synthetics, or hybrids. Such materials developed in other breeding programs are evaluated under local environmental conditions, and the promising ones are released to overcome immediate challenges and satisfy urgent needs. For medium-term objectives, crosses are made among identified materials to create new and better genotypes with improved target traits that overcome the shortcomings of currently cultivated cultivars. Long-term objectives include the identification of promising germplasm with stable performance. This requires many years of extensive testing. Such materials are used to develop source populations which are thereafter improved through various recurrent selection programs. Also, in the long term, inbred lines could be developed for the production of hybrids or open-pollinated varieties extracted from source populations for use by farmers.

5.2 Choice of Germplasm

Where information is available on maize germplasm, choices can be made directly on the basis of the information. In other instances, however, materials may need to be collected or developed, following which evaluation is carried out before a choice

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can be made. Choosing germplasm for breeding work is a critical decision that requires considerable thought. This is because the germplasm selected will form the basic materials the plant breeder may have to work with for his/her lifetime. The germplasm selected will determine the maximum potential improvement that can be obtained by breeding, while the breeding method to be employed for improvement will determine how much of that potential can be realized.

5.3 Development of Breeding Populations

After selecting germplasm, which may consist of a few to several populations, varieties, or other materials, the selected materials may need to be intermated to ensure that the populations or materials lose their individual identities and become one population. This is achieved by three to four cycles of random mating using a half-sib recombination technique. Usually little or no selection is imposed during the cycles of recombination or compositing. It is helpful to recombine selected germplasm based on heterotic groups. Germplasm belonging to similar heterotic groups are recombined. Thus, materials belonging to different heterotic groups are kept separate. This is to ensure that the source populations developed are heterotic to each other. When this is achieved, inbred lines extracted from the source populations are also expected to be heterotic, thus resulting in high-yielding hybrids.

5.4 Heterotic Populations and Inbreds

The concept of heterosis is applicable to both populations and inbred lines. When the performance of the cross between two populations A and B is superior to either of the parent populations, heterosis is evident, and the two populations are said to be heterotic to each other. For example, if population A is crossed to population B and the performance of the resulting F_1 is better than the average of the performance of the two parental populations, then F_1 is said to exhibit mid-parent heterosis. If F_1 performs better than the high parent, it is said to exhibit high-parent heterosis. In both cases, the breeder is assured of making progress from selection for improvement of the particular trait exhibiting the desirable heterosis. Inbred lines derived from the two heterotic populations are also expected to show heterosis, an indication of high specific combining ability. Such inbreds have the potential for use as parents of commercial hybrids.

5.5 Recurrent Selection

All population improvement methods use some form of recurrent selection. Plant traits are conditioned by genes, which may, to some extent, be influenced by the environment. The influence of the environment is greater with quantitative traits—the class of traits to which many agronomic traits belong. When all the plants in a population carry the gene for a trait, gene frequency is one, while it is zero when none of the plants carry the gene. Recurrent selection aims to increase the frequency of genes for desirable traits in the population.

Recurrent selection, which may be based on the phenotype of individual plants (mass selection) or on the mean of progenies, has three distinct stages:

(i) Generating desired families from a population
(ii) Evaluating generated families for important agronomic traits (e.g., days to maturity, resistance to pests and diseases, root and stalk lodging, and grain yield) and selecting families with superior performance
(iii) Recombining selected superior families by intermating

The last stage represents a major distinction between recurrent selection and mass selection, especially as used for self-pollinating species. No selection is considered recurrent, except when it involves the recombination of selected families to generate a new population from which further selection can be made. Several cycles of recurrent selection are usually carried out. Thus, improvement in the population is cyclical with each improved cycle expected to be of better performance than the previous cycle. A population improved by recurrent selection can be used in several ways. It may be the source of open-pollinated varieties or inbred lines that would be parents of hybrids.

Population improvement methods can be divided into two broad categories:

(i) Intrapopulation improvement methods
(ii) Interpopulation improvement methods

Intrapopulation improvement methods aim to improve the performance of a particular population and ultimately inbred lines derived from it. Interpopulation improvement methods, which usually involve two populations, maximize improvement in the performance of the population cross as well as hybrids derived from lines extracted from the two populations.

5.6 Intrapopulation Improvement Methods

Intrapopulation improvement methods include (i) mass selection, (ii) modified mass selection (grid system), (iii) half-sib family testing and selection, (iv) modified half-sib family testing and selection, (v) half-sib family selection using testers, (vi) full-sib family testing and selection, (vii) S_1 family testing and selection, and (viii) S_2 family testing and selection.

5.6.1 Mass Selection

Mass selection is perhaps the oldest selection procedure. It is effective for highly heritable traits (i.e., traits with high heritability). Highly heritable traits are those for which phenotypic differences among plants reflect, to a large extent, the differences in their genetic makeup. Examples of such traits include time to maturity, prolificacy, plant height, and ear placement. Mass selection increases the frequency of desirable alleles and, in effect, desirable/superior plants in the population. In mass selection, the population is advanced from seeds obtained from open-pollinated ears following selection of plants based on traits of interest. No progeny testing is involved in mass selection; this is a major limitation of the mass selection procedure since it does not provide for the separation of genetic from environmental effects on traits compared with procedures that use replicated trials and multilocation trials. To improve the effectiveness of mass selection, inferior plants in the population are rogued out and are not allowed to contribute pollen to the mass of pollen available for pollination of the plants at flowering. In addition to the simplicity of the procedure, another advantage of mass selection is that it makes possible the handling of a larger number of plants; thus it makes a better use of the germplasm pool. One cycle of mass selection is completed in a season, and in locations where two seasons of maize can be grown or when irrigation facilities are available, more than one cycle can be accomplished in one year.

5.6.2 Modified Mass Selection (Grid System)

The modified mass selection method was developed to overcome an important limitation of the simple mass selection method of breeding, which is the lack of control of field variability due to soil and other environmental factors. Between 7500 and 10,000 plants are grown in isolation. All sides of the plot are bordered by four to six rows of the same population. The plot is divided into grids or subplots of 40–60 plants (a procedure known as gridding), depending on selection intensity, which is usually between 5% and 10%. The plants within each grid are evaluated, and an equal number of plants showing the best performance are selected in each grid. The modified mass selection method ensures that selection is not limited to plants in fertile parts of the field or plants that owe their superiority to lower interplant competition due to fewer stands per unit land area. Consequently, well-bordered superior plants in fertile and less fertile portions of the field have an equal chance of being selected.

5.6.3 Half-Sib Family Selection (Ear-to-Row)

About 1000 plants from a source population are established in isolation. Ears from individuals resulting from open pollination are harvested and seeds are processed separately. Seeds from each ear are planted out in single rows for evaluation. Plants within each progeny row are half-sibs because they came from the same ear and have the same female parent. That ear was fertilized by a bulk of pollen from the whole population, so potentially each kernel on the ear had a different male parent.

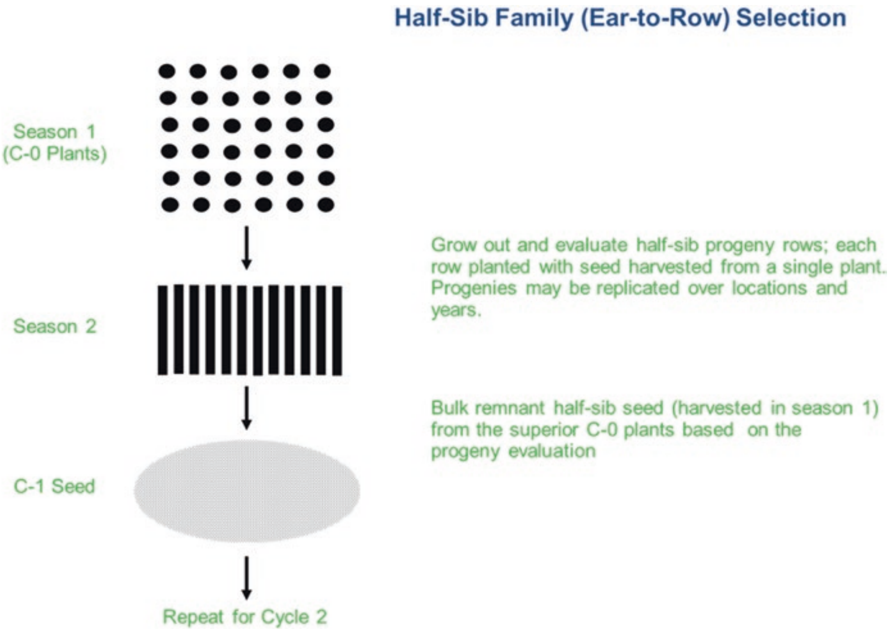

Fig. 5.1 Half-sib family (ear-to-row) selection

This step of progeny evaluation distinguishes half-sib family testing and selection from mass selection. Evaluation of progeny rows allows the separation of genetic variance from variance due to environment. The evaluation of progenies in more than one environment (multiple years or locations or a combination of both) improves the effectiveness of selection. Equal quantities of remnant seeds of superior half-sib families are bulked, and the composite is grown in isolation with open pollination. One cycle of this breeding method takes two growing seasons to complete. It should be noted that in ear-to-row selection, the trial is grown in isolation, and outcrossed ears of selected families become the progeny rows for the next cycle of selection. Consequently, a cycle can be completed in one generation, but the gain from selection per cycle is reduced by one-half compared to classical half-sib selection. A diagram of half-sib family testing and selection is presented in Fig. 5.1.

A variant of this method of breeding is to bulk seeds of superior families obtained from the progeny evaluation in Season 2.

5.6.4 *Modified Ear-to-Row Selection*

In this method, a sample of ears is taken from the population in which improvement is sought. Up to 250 to 400 ears may be sampled. The progenies are grown ear-to-row in an isolation block, preferably in two to three replicates and in one or several

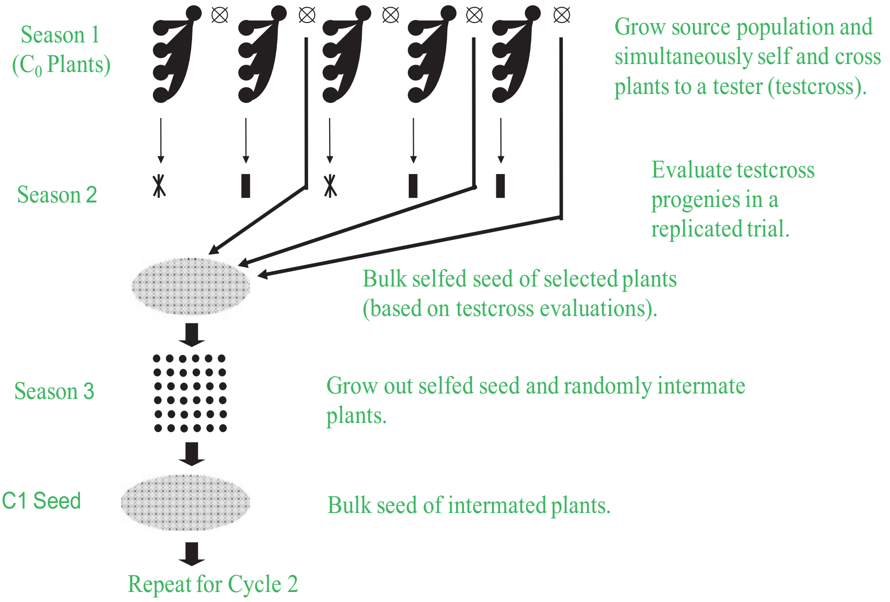

Fig. 5.2 Half-sib family selection using testers

locations. Rows planted to the ears serve as the female rows. Male rows, which are planted at intervals after several female rows, are established from a composite of seeds from all ears (balanced composite). The ratio of female to male rows may be 4:2, 4:1, or 3:1. Female rows are detasselled before pollen shed. Selection is practiced within and among progenies obtained from the female rows only.

5.6.5 *Half-Sib Family Selection Using Testers (Testcross Selection)*

In this half-sib selection scheme, three seasons are required to complete a cycle of improvement. In the first season, the population to be improved is established, and plants of the population are selfed (to produce S_1 plants) and at the same time crossed to a tester (testcross) (Fig. 5.2). In the second season, the testcross progenies are evaluated in a replicated trial at one or several locations. Selection is made based on the performance of the testcrosses. Seeds of the selfed parents of the superior testcrosses are grown out in the third season and intermated. The bulked seed from the intermated plants is the starting material for the next cycle of improvement. It should be noted that for this method, the selection unit that is evaluated (testcross progeny = half-sibs) is not the same as the recombination unit (S_1 families). This difference has implications in the prediction of expected response as well as the actual response to selection, especially if the tester is a different population from that of the progeny being tested. It is worth mentioning at this point a modification of this half-sib family selection using the tester (testcross selection) method that works well in the forest zone of West Africa. This method is referred to as S1/testcross system (personal communication with Professor J.G. Kling, Oregon State University, Corvallis, Oregon, USA). During the first rainy season, many plants are self-pollinated, and S_1 ears from agronomically desirable plants are selected at harvest. In the second rainy season, the S_1 families are evaluated in isolation using an ear-to-row system. Good rows are harvested in bulk to generate testcross families for evaluation in the next rainy season. This permits the screening of many more families and elimination of disease-susceptible ones before going on to multilocational yield trials. Disease pressure is higher in the second season, and S_1s show greater differences in disease response than noninbred families, so it is very effective. Also, plenty of testcross seed is obtained without the need for hand pollinations. Four seasons are utilized, but a cycle can be completed in 2 years, so it doesn't take any longer than the system shown in Fig. 5.2 (testcrosses always have to be evaluated in the main season). This method is particularly effective when breeding for broad adaptation. It also makes it possible to simultaneously carry out recurrent selection and inbred line development (Fakorede et al. 1993).

5.6.6 Full-Sib Family Selection

The full-sib method involves three steps. First, the population is established, and crosses are made randomly between pairs of plants to develop full-sib progenies. The seeds formed on each pair of plants are bulked to generate an adequate quantity of seed to be used in multi-environment trials. Selection is carried out among full-sib families. Remnant seed of superior full-sib families is planted out, and the resulting plants are intermated to obtain the improved population or used to develop improved varieties. Generally new full-sib families are created at the same time that selected families are being intermated, so a cycle can be completed in two generations. Full-sib recurrent selection is illustrated in Fig. 5.3.

5.6.7 S_1 Family Selection

S_0 plants in a heterozygous population are self-pollinated. S_1 families are evaluated for the specific characters under improvement. The evaluation is carried out in replicated trials. About 25% to 30% of the S_1 families evaluated are selected and used to reconstitute the improved population. However, this really depends on the population size. If a large number of S_1 families are screened, the selection can be more stringent. The breeder has to be more careful about maintaining adequate

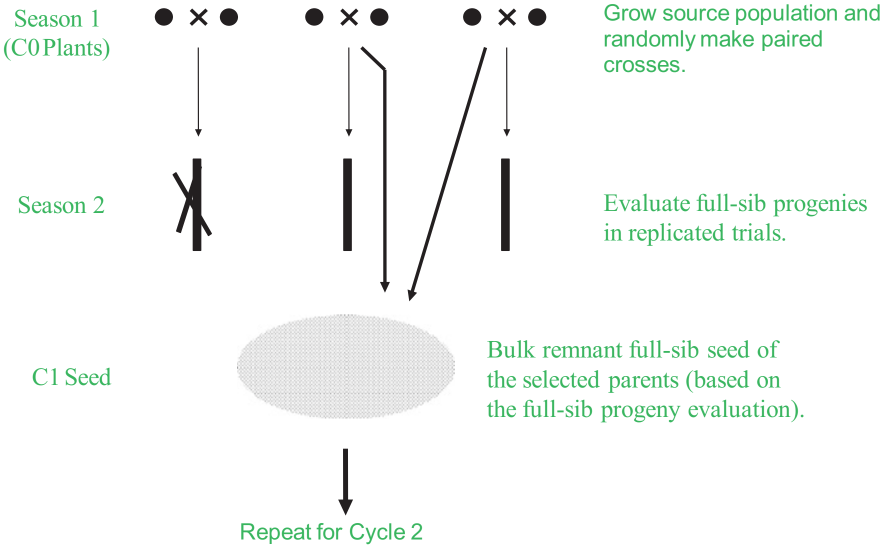

Fig. 5.3 Full-sib family selection

population size and genetic diversity in an S_1 system than in a half-sib selection scheme where half-sib families are recombined. But the situation here is no different than in the half-sib scheme using testers since in both cases, S_1 seeds are used for recombination. Seeds of superior S_1 families are bulked, grown in isolation, and intermated. The seeds are harvested in bulk. A diagram of S_1 family selection is shown in Fig. 5.4.

5.6.8 S_2 Family Selection

The S_2 recurrent selection method is similar to the S_1 family selection except that instead of one generation of inbreeding, inbreeding is carried out for two generations. Individual S_1 plants are selfed to generate S_2 families, which are evaluated in replicated trials. The evaluation of S_2 progenies is carried out in as many environments as seeds and resources permit. Superior S_2 progenies are selected based on yield data across environments (locations and years). Remnant seeds of superior families are recombined, and the improved population is the starting point for the next cycle of improvement.

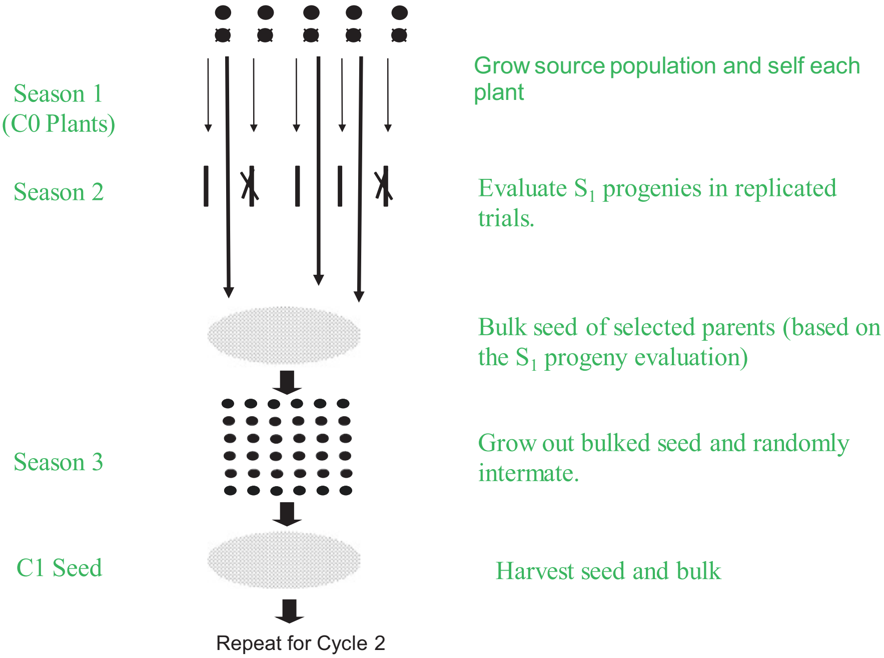

Fig. 5.4 S_1 family selection

5.7 Combined Breeding Methods

The S_1/testcross system is an example of the combined breeding methods. All of the intrapopulation breeding methods may be adapted to local circumstances and modified to meet particular objectives. The evaluation phase always has to be conducted in the target environments. The quantity of seed needed for evaluation of the traits under selection is a very important consideration as well. With the S_2 family selection method, there is only a single ear, compared to two ears for full-sib family selection and several to many ears for a testcross system. In addition, the recurrent selection involving an established inbred line to produce the testcrosses provides an opportunity to identify new inbred lines that combine very well with the tester. Fakorede (1982) proposed this as a rapid method for developing inbred lines to be used in hybrid production in the rainforest agroecology of Southern Nigeria.

5.8 Interpopulation Improvement Methods

5.8.1 Reciprocal Recurrent Selection

This method, which involves simultaneous improvement of two source populations, is effective in the exploitation of general and specific combining ability. It is desirable that the two source populations (A and B) are unrelated and show heterosis in crosses.

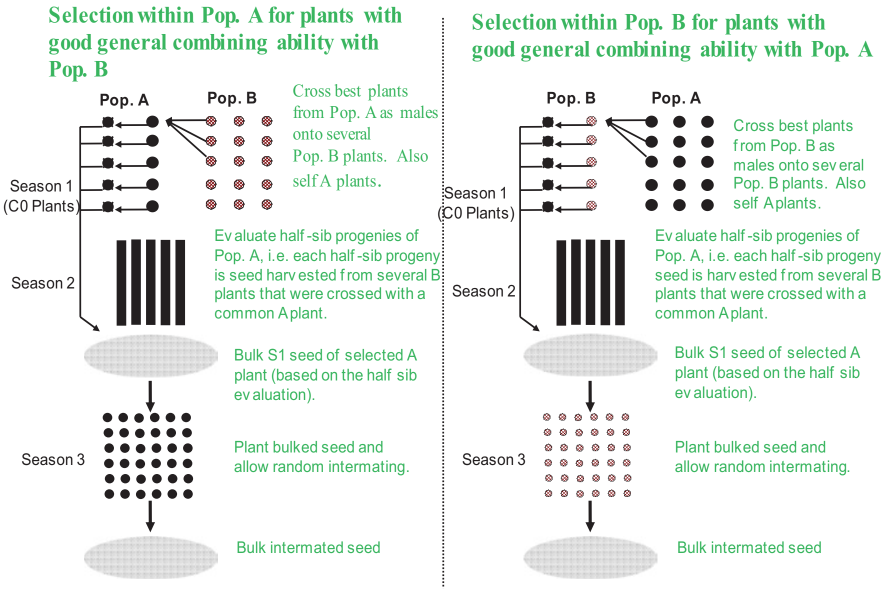

Fig. 5.5 Half-sib reciprocal recurrent selection

The improvement in each of the two populations is achieved using the other population as a tester. The populations developed by reciprocal recurrent selection are utilized for producing commercial hybrids through the development of inbred lines from the improved cycles of the source populations. The inbred lines developed from the improved population (A and B) are expected to be heterotic and, therefore, would serve as parents of new hybrids.

5.8.2 *Half-Sib Reciprocal Recurrent Selection*

A number of plants from source A are self-pollinated and at the same time crossed with a sample of plants from source B (Fig. 5.5). Similarly, a number of plants from source B are selfed and crossed with a sample of plants from source A. In effect, selfed and testcross seeds are produced for each of the two populations. The testcross progenies produced for the two populations, which are half-sibs, are evaluated in replicated yield trials in as many environments as seeds, resources, and logistics permit. Superior testcrosses are selected, and improved cycles of each of the two populations are produced by intermating plants of the S_1 progenies whose testcrosses showed superiority in the evaluation trials. The procedure is repeated for subsequent cycles of selection.

Season	Population improvement program	Breeding program
1	Produce S1 progenies and full-sib crosses: Plant the two populations (C_0) under selection in alternate rows in the breeding nursery. Self-pollinate one ear and cross the other ear. Practice selection among S_0 plants at flowering and at harvest.	___
2	Evaluate full-sib crosses: Grow the full-sib crosses in replicated trials. Pairs of S_1 progenies may be grown in breeding nursery to initiate line hybrid development	Grow S_1 progenies to produce S_2 progenies and full-sib crosses between pairs of S_1 progenies
3	Recombine: Recombine the selected S_1 progenies of the selected full-sib crosses to form C_1 Syn. 1 for each of the two populations.	___
4	Produce S_1 progenies and full-sib crosses: Plant the C_1 Syn. 1 population in alternate rows in the breeding nursery. Self-pollinate one ear and cross the other ear. Practice selection among S_0 plants at flowering and at harvest.	Grow S_2 progenies of selected full-sib crosses in breeding and top cross nurseries for additional selection
	Repeat as in seasons 2 and 3	Grow selected S_3 progenies in breeding nursery and replicated top cross trials.

Fig. 5.6 Full-sib reciprocal recurrent selection

5.8.3 *Full-Sib Reciprocal Recurrent Selection*

In this method, which also requires two populations, the selection units are full-sib families. In maize, this method can be applied when plants of the two populations being improved are prolific, forming two or more ears. The two populations are planted in alternate rows. Pairs of plants of the two populations are selfed and at the same time crossed. S_0 plants are evaluated for important agronomic traits, and superior plants are selected. Kernels obtained from ears resulting from crosses of each pair of superior S_0 plants selected can be bulked to generate adequate seeds for testing in several environments in replicated trials. Full-sib families that show superiority in replicated trials are selected, and S_1 seeds of superior full-sib families of each of the two populations are recombined to form the improved populations that will be the starting point of the next cycle of improvement. The full-sib reciprocal recurrent selection scheme is typified in Fig. 5.6.

5.9 Predicting Response to Recurrent Selection

Recurrent selection consumes a lot of resources, including funds, labor, and time, and requires skills and experiences. Therefore, maize breeders usually prefer to have scientific evidence that they would make progress from selection before making a choice of the population to improve and the recurrent selection method to use. Population parameters are obtained from progeny trials and are used to compute estimates of heritability (H^2 or h^2). Variance components may also be estimated, including genetic (σ_G^2), additive genetic (σ_A^2), genotype × environment interaction (σ_{GE}^2), and phenotypic (σ_P^2) variances, which may be substituted into standard formulae to obtain predicted response to selection. The basic formula for heritability is in two forms—broad sense (H^2) or narrow sense (h^2):

$$H^2 = \sigma_G^2 / \sigma_P^2 \tag{5.1}$$

$$h^2 = \sigma_A^2 / \sigma_P^2 \tag{5.2}$$

The expected gain from selection (ΔG) is then

$$\Delta G = kh^2\sigma_P = kh\sigma_A \tag{5.3}$$

In this formula, k is the standardized selection differential, and genetic variances are defined as in Eqs. 5.1 and 5.2. The basic formulae for heritability and selection response refer to selection among individuals in a population. In practice, plant breeders may prefer to express heritability in terms of the selection units, which are often families. In a normally distributed population, a general formula for the predicted gain from selection (ΔG) may then be expressed as

$$\Delta G = \frac{ck\sigma_a^2}{\sqrt{\sigma_p^2}} = \frac{ck\sigma_a^2}{\sqrt{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e^2}{re}}} \tag{5.4}$$

In the above equation, variance components pertain to the types of families that are evaluated in the recurrent selection program: σ_a^2 = additive genetic variance among families; σ_p^2 = phenotypic variance among families; σ_g^2 = total genetic variance among families; σ_{ge}^2 = genotype × environment interaction variance; σ_e^2 = environmental variance; c = parental control; k = standardized selection differential; r = number of replications per evaluation environment; and e = number of environments in which the progeny trial was conducted. The relationships between genetic variances for families and genetic variances among individuals in a reference population are shown in Table 5.1.

Table 5.1 Genetic variances for different types of families

Selection unit	σ_a^2	σ_g^2
Individual plants	σ_A^2	$\sigma_A^2+\sigma_D^2$
Half-sib families	$\frac{1}{4}\sigma_A^2$	$\frac{1}{4}\sigma_A^2$
Full-sib families	$\frac{1}{2}\sigma_A^2$	$\frac{1}{2}\sigma_A^2+\frac{1}{4}\sigma_D^2$
S_1 families	σ_A^2	$\sigma_A^2+\frac{1}{4}\sigma_D^2$

When the parents used to make the families for recurrent selection are inbred, genetic variances among families may increase. For example, for parents with an inbreeding coefficient of F, additive genetic variance among half-sib families will increase to $\left(1+F\right)\frac{1}{4}\sigma_A^2$.

Heritability is a function of the population from which the progenies are extracted, the sample of environments in which the progenies are evaluated, and the trait under consideration. Similarly, Eq. 5.4 varies depending on the recurrent selection method used, the parental control, and the selection intensity, that is, the proportion of the progenies selected for recombination (see Table 5.2). It must be noted here that some references use i rather than k for the standardized selection differential. Both refer to the same quantity.

There are two important points to note about Table 5.2:

- The selection differential, k, has no unit of measure. It derives directly from a standardized normal distribution.
- The selection differential decreases as selection intensity increases, as presented in Fig. 5.7.

Parental control (c) indicates the relationship between the selection unit and the recombination unit. In general, there are three possible values: 0.5, 1, and 2. The value is 0.5 when the selection unit is the same as the recombination unit and the selected genotypes have been pollinated by both selected and unselected genotypes as in mass selection after flowering. In this case, the breeder has no control over the pollinator genotypes; superior, inferior, and mediocre genes may have been transferred to the selected genotypes. Obviously, this situation will reduce the gain per cycle of selection. Parental control is 1 when the selection unit is the same as the recombination unit, but the selected genotypes have been pollinated by themselves or other selected individuals. Examples are mass selection before pollination, half-sib family selection when remnant half-sib seeds are used for recombination, full-sib family selection, and S_1 family selection. When the selfed seed of selected individuals is used for recombination, as in half-sib family selection using testcrosses

Table 5.2 Selection differential values for different selection intensities[a]

Selection intensity, %	Selection differential, *k*
1	2.66
2	2.42
5	2.06
10	1.75
15	1.55
20	1.40
30	1.16

[a]Values for *k* assume an infinitely large population

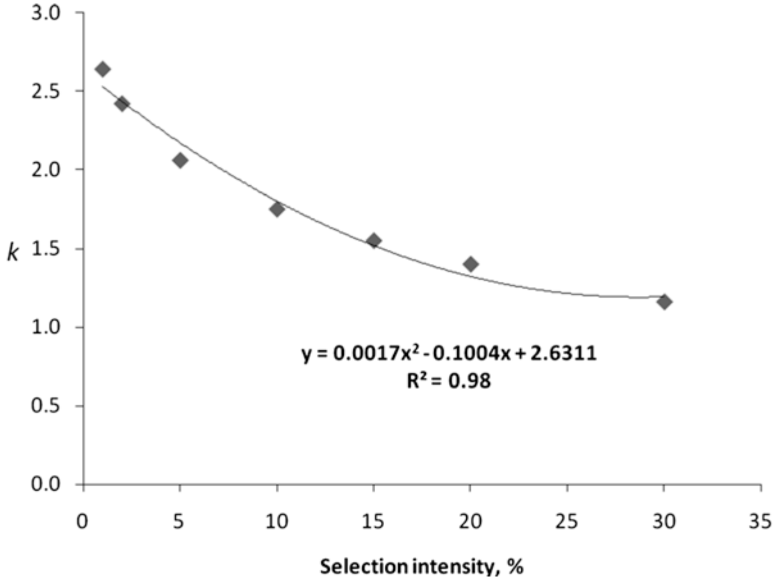

Fig. 5.7 Graphical display of selection differential, *k*, versus selection intensity, %

and the reciprocal selection methods, the parental control is 2. Details of the formulae for predicting response to the different recurrent selection methods may be found in Sprague and Eberhart (1977) and Bernardo (2010).

5.10 Development of Experimental Varieties

Experimental varieties are usually formed based on the performance of families of a population at different locations. About ten families that show the best performance in each location or across the locations used for the testing are selected and intermated to develop experimental varieties. Experimental varieties are expected to show better performance than the mean of the population from which they were extracted since they have been formed from the best fraction of the population. In addition to yield data, consideration is given to other important agronomic traits, such as maturity and plant height, in selecting the best families. It is important to note that experimental varieties may potentially be released to farmers as varieties. Consequently only the most elite families are selected to form the variety. For populations that will continue to be improved through recurrent selection, a greater number of families may be included to maintain the genetic diversity needed for further genetic gains.

Maize breeders run several recurrent selection programs concurrently in their respective institutions. There are also some aspects of such programs that may be executed collaboratively by the international centers and national programs in WCA. An example is the international progeny trials. Annually, IITA maize breeders compose the trials based on progenies from several populations for distribution to collaborators in WCA and many other countries of Africa and beyond. Experimental varieties are developed for some of these locations as well as across locations. Such varieties are given designations that reflect the name of the population from which the progenies were extracted and some or all of the following: the year of the progeny trial, the location of the trial, or the label "ACR" indicating that selections were based on an analysis across locations. The designation "EV" may also be used for an experimental variety. Improved populations resulting from selected and recombined lines/progenies in the recurrent selection program may be named similarly.

Apart from extracting improved varieties as recurrent selection proceeds, an advantage of the scheme is that inbred lines to be used for the development of hybrids may be extracted from the improved cycles of selection. Selected lines are advanced in the inbreeding process while simultaneously testing them in hybrid combinations with selected lines from other sources or the base population serving as testers. The procedure is repeated until the desired level of inbreeding is attained and the best few hybrids are released. According to Fakorede (1982), the advantages of this procedure include (i) simultaneous inbreeding and evaluation trials, (ii) flexibility for concurrent population improvement and inbred line extraction, and (iii) where two natural seasons and off-season irrigation facilities are available, near-homozygous inbred lines can be obtained within 3 calendar years. A summary of procedures for developing open-pollinated maize varieties and hybrids from a recurrent selection program is shown in Fig. 5.8.

5.11 Effectiveness of Recurrent Selection in Maize Improvement: Empirical Results from WCA

Breeders at IITA and some national programs in WA have been using recurrent selection to improve grain yield and resistance/tolerance to abiotic and biotic stresses of maize for about four decades (Efron et al. 1989; Menkir and Kling 1999,

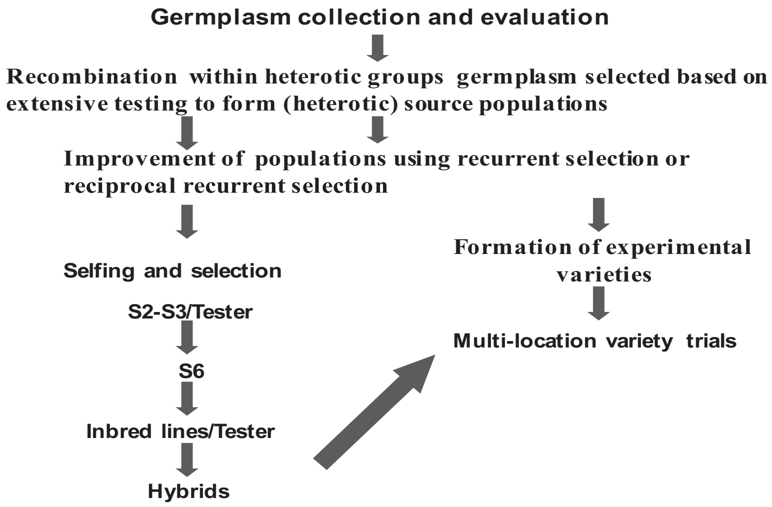

Fig. 5.8 Flexible breeding scheme to develop open-pollinated maize varieties and hybrids from recurrent selection

Table 5.3 CIMMYT International Progeny Testing Trial (IPTT) scheme

Year	Season	Activity
1	1	Formation of full-sib families, usually 250 families
	2	Conduct of IPTT in six locations, two replications per location
2	1	Within-family self-pollination for the improvement of families selected across locations
	2	Half-sib recombination of selected S_1 families to resynthesize the population for the next cycle of selection

2007; Salami et al. 2003; Alabi et al. 2003; Ajala et al. 2002; Badu-Apraku et al. 2007, 2008, 2009). In the 1970s and 1980s, IITA researchers subjected many populations to recurrent selection to improve maize streak virus (MSV) resistance and grain yield. They also screened for resistance to controlled infection by several major diseases, particularly rust, blight, stalk rot, and ear rot. Initially, the breeders adopted the International Progeny Testing Trial (IPTT) approach designed at CIMMYT. This scheme required 2 years per cycle of selection with two seasons per year, as described in Table 5.3 (Efron et al. 1989).

Following each international full-sib evaluation, EVs were produced by recombining the best ten families identified at each testing site. In addition, one EV was created based on performance of families across all the international testing sites. Although the IPTT approach was effective, it was too demanding on resources of national programs, and data obtained from some sites were often highly variable and not useful. Therefore, the number of testing sites was reduced to four that were

Table 5.4 Designation and description of maize streak virus-resistant populations under improvement by recurrent selection at IITA in the 1980s (from Efron et al. 1989)

Population	Maturity	Grain type	Improvement base	Adaptation
TZSR-W-1	Late	White, semi-flint	Ibadan	Lowland forest and savanna
TZSR-Y-1	Late	Yellow, semi-flint	Ibadan	Lowland forest and savanna
TZUT-SR-W	Interm	White, semi-flint	Samaru	Lowland forest and savanna
TZUT-SR-Y	Interm	Yellow, semi-flint	Burkina Faso	Lowland forest and savanna
TZESR-W	Early	White, flint	Ibadan	Lowland forest and savanna
TZESR-Y	Early	Yellow, flint	Burkina Faso	Lowland forest and savanna
Pool-16SR	Early	White, dent	Ibadan	Lowland forest and savanna
DMRLSR-W	Late	White	Owo/Ibadan	Lowland, downy mildew zone
DMRLSR-Y	Late	Yellow	Owo/Ibadan	Lowland, downy mildew zone
DMRESR-W	Early	White	Owo/Ibadan	Lowland, downy mildew zone
DMRESR-Y	Early	Yellow	Owo/Ibadan	Lowland, downy mildew zone
TZMSR-W	Late	White, flint, dent	Jos	Mid-altitude (about 1500 m)
TZEMSR-W	Early	White, flint, dent	Jos	Mid-altitude (about 1500 m)

under the control of IITA, with three replications at each site. By the late 1980s, 13 MSV-resistant populations were undergoing improvement by recurrent selection (Table 5.4). Recurrent selection was effective in improving each of the populations for MSV resistance, grain yield, and some other agronomic traits. Several EVs were also developed from improved selection cycles of the populations and made available to national programs for release or as source material for their breeding programs.

Recently developed populations have also been subjected to recurrent selection for other stress factors. Menkir and Kling (2007) evaluated the genetic gain in a genetically broad-based, late-maturing (about 120 days to physiological maturity) maize composite, TZL COMP1-W, which had undergone six cycles of recurrent selection under *S. hermonthica* infestation. The selection cycles and checks were evaluated with and without *S. hermonthica* infestation at two locations in Nigeria for 2 years. Selection for improved performance under *S. hermonthica* infestation significantly increased grain yield by 24% cycle^{-1} and ears per plant (EPP) by 9% cycle^{-1}. Gains per cycle for other traits were −7% for relative yield loss, −5% for *Striga* host damage rating, −9% for number of emerged *S. hermonthica* plants, −4% for anthesis–silking interval (ASI), and −5% for ear aspect rating. Selection under *S. hermonthica* infestation was accompanied by a concomitant increase in grain yield and improvement in plant aspect and ear aspect in *Striga*-free environments. The observed progress in performance under *S. hermonthica* infestation demonstrates the effectiveness of recurrent selection for increasing polygenic resistance against the parasite in this tropical maize population. Alabi et al. (2003) evaluated the response to three cycles of full-sib recurrent selection for improved low nitrogen tolerance in the low-N-tolerant pool, LNTP-Y (Fig. 5.9). Grain-yield improvement

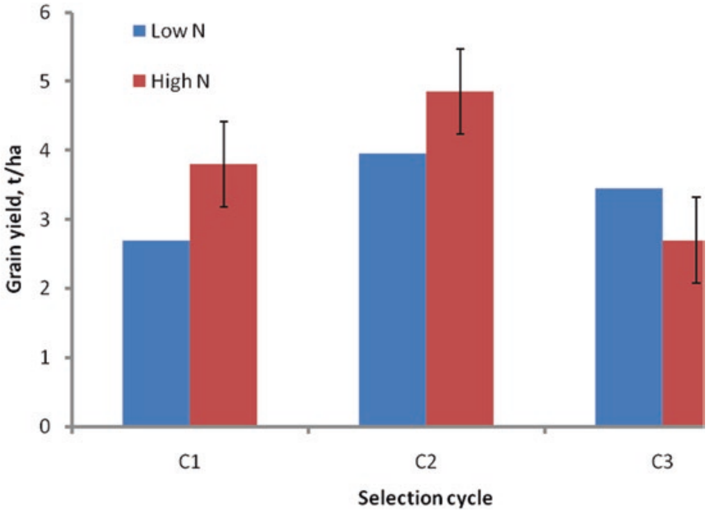

Fig. 5.9 Grain yield of full-sib families extracted from three cycles of recurrent selection and evaluated under low N (20 kg ha^{-1}) and high N (120 kg ha^{-1}) in Samaru, Nigeria, in 1998. *Vertical lines* on the *bars* are standard errors (Adapted from Alabi et al. 2003)

per cycle was 0.15 t ha^{-1} or 5.4% under low N (20 kg ha^{-1}) and 0.13 t ha^{-1} (4.1%) across N levels. Yield performance of C_3 under high N was lower than those of C_1 and C_2 resulting in a nonsignificant gain from selection when the cycles were evaluated under high N (120 kg ha^{-1}).

Recurrent selection has been used to improve early and extra-early maize varieties as well. Salami et al. (2003) evaluated the progress from two cycles of reciprocal recurrent selection in two early maize populations, TZE Comp3 and TZE Comp4. Selection gain in grain yield per cycle was 0.29 ± 0.05 t ha^{-1} (10.4%) for TZE Comp3 and 0.17 ± 0.05 t ha^{-1} (5.7%) for TZE Comp4. Results from an earlier evaluation of the selection program showed mid-parent heterosis of 4% for C_1 and 7% for C_2 relative to the original population cross (Menkir and Kling 1999).

More extensive recurrent selection studies have been carried out in two other early and two extra-early populations by IITA scientists. Presented in the following sections are (i) the methods used for developing the early and extra-early maturing populations that were subjected to recurrent selection, (ii) a description of the recurrent selection methods adopted and development of EVs, (iii) empirical results on the response of the populations to several cycles of recurrent selection, (iv) performance of EVs and other products derived from the recurrent selection programs, (v) inbred–hybrid program from the recurrent selection scheme, and (vi) estimation of residual variances, heritabilities, and predicted responses to further selection, beginning with C_4 of the program.

5.12 Development of Stress-Tolerant Early and Extra-Early Source Populations for Recurrent Selection

The populations that are subjected to recurrent selection are as important as the selection methods used in the program. The breeder may use existing populations or develop new ones. In either case, it is important to ensure that large genetic variation exists in the population for the traits to be improved. This is normally done by estimating the population parameters (genetic, environmental, and genetic × environment variances), heritability, and predicted response to selection. The following is a brief description of the procedures used to develop two early and two extra-early populations subjected to recurrent selection in WCA. More detailed descriptions of the procedures have been presented by Badu-Apraku et al. (2008). These include the strategies adopted for screening for *Striga* resistance/tolerance as well as the water stress management practices that were used for selection for drought tolerance during the development of the populations at the different screening sites.

The development of two *Striga*-resistant and drought-tolerant early-maturing (90–95 days to maturity) populations was initiated in Côte d'Ivoire in 1994. One population has white endosperm (TZE-W Pop DT STR), and the other is yellow (TZE-Y Pop DT STR). The populations were developed from outstanding local and improved maize germplasm with white and yellow endosperm identified as *Striga* resistant and drought tolerant through years of testing in WCA. Following a generation of half-sib recombination of the drought-tolerant white materials, including Pool 16 DT, Pool 16 Sequia C_2, DR-W Pool BC_1F_1, and the inbred line 5012, the resulting early white population was designated as TZE-W Pop. The drought-tolerant yellow sources, DR-Y Pool BC_2F_2, KU 1414, and inbred line 9499, were treated similarly to form the yellow population, TZE-Y Pop. The procedures used for developing the two populations are summarized in Table 5.5. The *Striga*-resistant/*Striga*-tolerant IITA inbred line TZi 3 (1368 STR) was incorporated into TZE-W Pop, and TZi 25 (9450 STR) was introgressed into TZE-Y Pop to upgrade the level of *Striga* resistance/tolerance of each population. This was followed by two backcrosses, generation of S_1 progenies, selection of *Striga*-resistant S_1 lines from each population, and two cycles of random mating under artificial *Striga* infestation and induced moisture stress to form TZE-W Pop DT STR C_0 and TZE-Y Pop DT STR C_0. Selection for drought tolerance was made under controlled conditions at Ferkessédougou (Ferke) (9°30′ N, 5°10′ W; 325 m altitude) and Sinématiali (Siné) (9°37′ N, 3°04′ W; 305 m altitude) in Côte d'Ivoire and Kamboinse (12°28′ N; 1°32′ W) in Burkina Faso. At Ferke and Siné, the crop was grown under irrigation during the dry season. The maize crop was irrigated using an overhead sprinkler irrigation system that applied 12 mm of water per week. Drought stress was achieved by withdrawing irrigation water about 2 weeks before anthesis to the end of the season. At Kamboinse, a Sudan savanna site, varying levels of drought tolerance were achieved using tied and untied ridges. The tied ridge is a water-harvesting technique capable of capturing water and holding it in place to minimize runoff and

Table 5.5 Procedure adopted for the development of the *Striga*-resistant, drought-tolerant, early-maturing, yellow, and white maize populations

Year	Location	Breeding activity	
1990A[a]	Kamboinse	Generation of diallel crosses involving 7 local and improved drought-tolerant selections of white and yellow endosperm maize	
1990B[b]	Kamboinse	Evaluation of diallel crosses using tied and untied ridges	
1991A	Kamboinse	Random mating of selected germplasm without reference to grain color to form a mixed grain population. The population was separated into white and yellow fractions. The white version was designated DR-White Pool and the yellow fraction DR-Y Pool. Thereafter, breeding activities proceeded for the two pools separately	
		TZE-W Pop DT STR	TZE-Y Pop DT STR
1991B	Kamboinse	DR-W Pool crossed to Pop 30 SR to improve MSV[c] resistance	DR-Y Pool crossed to Pop 31 SR to improve MSV resistance
1992B	Kamboinse	DR-W Pool × Pop 30F_1 backcrossed to recurrent parent, DR-W Pool, to obtain DR-W Pool BC_1F_1	DR-Y Pool × Pop 31 F_1 backcrossed to recurrent parent, DR-Y Pool, to obtain DR-Y Pool BC_1F_1
1993A 1993B	Kamboinse Kamboinse	Generation of diallel crosses involving selected outstanding early white maize germplasm (Pool 16 DT, 1368 STR, 5012, Pool 16 Sequia × Pool 16 DT, DR-W Pool BC_1F_1, TZE Comp4)	DR-Y Pool BC_1F_1 advanced to DR-Y Pool BC_1F_2 through selfing under artificial streak virus infestation
1994A	Ferke	Evaluation of diallel crosses involving selected early white maize germplasm and selection of 2–3 ears from each F_1 cross	Selected families from DR-Y Pool BC_1F_2 crossed to KU1414 and 9499 (sources of drought tolerance) and TZi 25 STR (source of *Striga* resistance)

1994B	Ferke	Recombination of 2–3 ears selected from each F_1 cross involving Pool 16 DT, 1368 STR, 5012, Pool 16 Sequia × Pool 16 DT, DR-W Pool BC_1F_1, TZE Comp4 generation of backcrosses TZE-W Pop × (1368 STR × Pool 16 DT), and TZE-W Pop × (Pool 16 Sequia × 1368 STR) in an effort to introgress *Striga* resistance into TZE-W Pop	Generation of backcrosses, DR-Yellow Pool BC_2F_2 × (DR-Y Pool BC_1F_2 × KU1414), (DR-Y Pool BC_1F_2 × 9499) × DR-Y Pool BC_2F_2, and (DR-Y Pool BC_1F_2 × TZi 25 STR) × DR-Y Pool BC_2F_2
1995A	Ferke	Selfing of backcrosses, TZE-W Pop × (1368 STR × Pool 16 DT) and TZE-W Pop × (Pool 16 Sequia × 1368 STR) to produce S_1	Evaluation of selected ears from the backcrosses, DR-Y Pool BC_2F_2 × (DR-Y Pool BC_1F_2 × KU1414), (DR-Y Pool BC_1F_2 × 9499) × DR-Y Pool BC_2F_2 for drought tolerance under induced moisture stress
1996A		Introgression of drought-tolerant and *Striga*-resistant white endosperm selections into TZE-W Pop	
1996B–1998A	Ferke, Siné	Four cycles of random mating of TZE-W Pop under alternate *Striga* infestation and induced moisture stress to form TZE-W Pop DT STR C_0	Four cycles of random mating of TZE-Y Pop under alternate *Striga* infestation and induced moisture stress to form TZE-Y Pop DT STR C_0

Locations are Kamboinse, Burkina Faso, and Ferkessédougou and Sinématiali, Côte d'Ivoire

[a] Main planting season

[b] Off-season

[c] Maize streak virus

improve water infiltration (Boa 1966; Badu-Apraku et al. 2008). At Siné in the southern Guinea savanna, a relatively high plant density of about 80,000 plants ha^{-1} (compared to the standard density of 66,000 plants ha^{-1}) was used to induce stress conditions for selection. The achievements of the program include the development of the two early-maturing populations and several early varieties, synthetics, and inbred lines, with combined *Striga* resistance/tolerance and drought tolerance (Badu-Apraku et al. 2008).

Two broad-based, extra-early (80–85 days to maturity) breeding populations were also developed from diallel crosses involving the most promising materials identified through several years of field evaluations in WCA. Selection of the materials was on the basis of high grain yield, resistance to maize streak virus (MSV), and earliness. The most promising extra-early white varieties selected for use in developing the white population included TZEE-W SR BC$_5$, TZEE-W SR × Gua 314 BC1, Pop 30 × Gua 314 BC1, and Pool 27 × Gua 314 BC1. These were crossed in a diallel fashion, and the progeny was subjected to two cycles of recombination to develop the white population designated TZEE-W Pop. Similarly, the most promising extra-early yellow germplasms were CSP-SR BC5, TZEE-Y SR BC5, CSP × Local Raytiri, and TZEE-Y, which were used to form TZEE-Y Pop. The interrelationship of the different stages of the breeding program is depicted in Fig. 5.10.

Two IITA intermediate-maturing inbred lines TZi 3 and TZi 25 STR were used as sources of resistance for introgression into TZEE-W Pop and TZEE-Y Pop, respectively, in an effort to improve the level of *Striga r*esistance. In addition to *Striga* tolerance, TZi 3 has good levels of resistance to the major diseases in WCA. TZi 25 has low *Striga* seed germination stimulant production. It has also been found to be tolerant to *S. asiatica* in North Carolina (Efron et al. 1989; Ransom et al. 1990). The primary mechanism of resistance in the two inbreds is tolerance, but both inbreds, particularly TZi 25, also support reduced numbers of *Striga* plants. These two *Striga*-tolerant inbred lines were derived from temperate germplasm (Kim et al. 1984), and tolerance is inherited quantitatively by a multigenic system.

The inbreds 1368 STR and TZi 25 STR are later maturing than TZEE-W Pop and TZEE-Y Pop; therefore, the inbreds were planted about 21 days before the populations to ensure synchronization of anthesis and silking. Additional rows of the donor parents were planted again 7 days later. The introgression of *Striga* resistance into each extra-early source population was followed by backcrossing to recover extra-earliness, generation of S_1 progenies, selection of *Striga*-resistant S_1s from each population, and two cycles of recombination under artificial *Striga* infestation. The progenies of the white and yellow extra-early populations were designated as TZEE-W Pop STR C0 and TZEE-Y Pop STR C_0, respectively.

Two additional *Striga*-resistant and drought-tolerant populations, DTE STR-Y Syn Pop and DTE STR-W Syn Pop, were developed in 2008. DTE STR-Y Syn Pop was formed from testcrosses involving selected drought- and *Striga*-resistant yellow inbred lines and TZE-Y Pop DT STR. Similarly, DTE STR-W Syn Pop was developed from white inbred lines and TZE-W Pop DT STR.

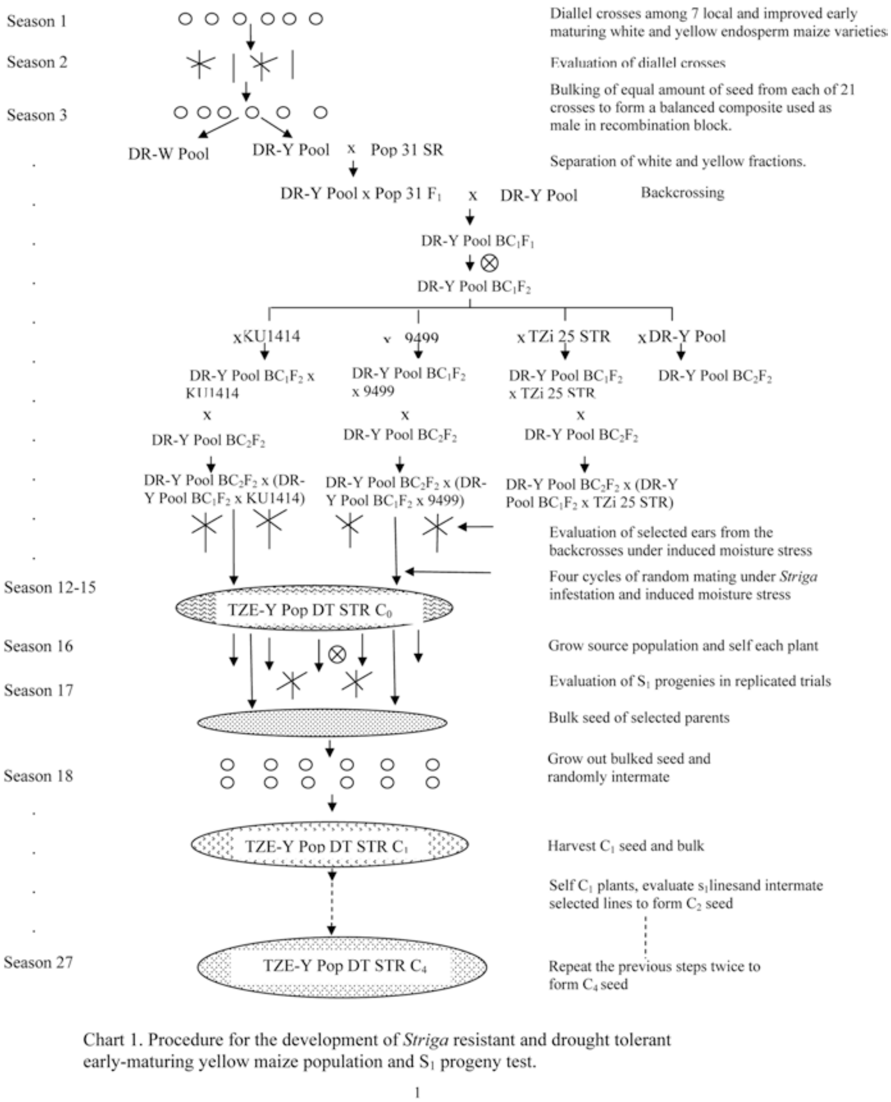

Fig. 5.10 Procedure for the development of *Striga*-resistant and drought-tolerant early-maturing yellow maize population and S_1 progeny test

The four early-maturing breeding populations (TZE-Y Pop DT STR, TZE-W Pop DT STR, DTE STR-Y Syn Pop, and DTE STR-W Syn Pop) are presently under improvement for drought tolerance using the S_1 recurrent selection scheme. A program was initiated in 2009 to introgress drought-tolerant alleles into the populations from drought-tolerant CIMMYT inbreds selected at Ikenne, Nigeria, in 2008. Testcrosses involving each population and the selected CIMMYT inbred lines were evaluated at Ikenne under drought stress during the 2009/2010 dry season and under well-watered conditions during the 2010 growing season. The best 10% of the testcrosses selected from each population were identified and incorporated into the respective populations, and the best ten testcrosses of each population were recombined to form an experimental variety.

5.13 S_1 Recurrent Selection Scheme

Recurrent selection involves the development of progenies from a population, evaluation of the progenies in field trials, and recombination of the selected progenies based on their performance in the field trials. During the rainy season of 1996, recurrent selection, primarily for improved *Striga* resistance, drought tolerance, and grain yield, was initiated in each of the two early populations, TZE-W Pop DT STR C_0 and TZE-Y Pop DT STR C_0, and the two extra-early populations, TZEE-W Pop DT STR and TZEE-Y Pop DT STR. From each population, 167 S_1 lines were generated and evaluated along with two checks under *Striga*-infested, *Striga*-free, and induced drought stress conditions. In 1998, the first cycle of improvement in each population was completed by intercrossing the top 25% or 30% families identified in 1997 through progeny yield trials conducted in Ferkessédougou (Ferke) under artificial *Striga* infestation; Sinématiali (Siné), a high-yield, nonstress environment; and Kamboinse, a drought stress environment. In addition, the top 7−10% families selected in each population were recombined to form an experimental variety. Thereafter, each population was taken through three more cycles of S_1 recurrent selection. S_1 progenies from each of the three cycles of improvement were screened under artificial infestation with *S. hermonthica* at Ferke and under non-infested conditions at Siné. The number of progenies screened in each of the three cycles of improvement ranged from 196 to 256, with a selection intensity of 25−30%. Based on the across-location data for each cycle of selection, 25−30% of the top families of each population were recombined to reconstitute each population for the next cycle of selection. In addition, the top 10% S_1 families of each cycle were intercrossed to form *Striga*-tolerant experimental varieties.

In 2003, 249−355 S_1 progenies (plus 5−7 checks) derived from each of the populations were separately evaluated in Nigeria under artificial infestation with *S. hermonthica* at Abuja and Mokwa. Based on the across-location data, 25–30 best performing progenies of each population were identified using a selection index that integrated grain yield, EPP, days to mid-silk, ASI, plant height, *Striga* damage score, and *Striga* emergence count measured under infested and/or non-infested conditions (Berner et al. 1995). The selected progenies were recombined to reconstitute cycle 4. In addition, the best ten S_1 progenies of each population were intermated to form an experimental variety. Selection was based on the same index of characters used during the formation of the populations. The experimental varieties extracted from the populations as selection progressed were then evaluated in several field trials, and this is described in the following sections.

5.13.1 Evaluation of Progress

The progress from four cycles of selection in the two maturity groups was assessed in separate field trials conducted under artificial *Striga* infestation and non-infested conditions. The study for the early group included a total of 13 entries: the C_0, C_2, C_3, and C_4 from TZE-W Pop DT STR; C_0, C_3, and C_4 from TZE-Y Pop DT STR; two derived *Striga*-resistant varieties of the early white population (2004 TZE-W Pop DT STR C_4 and TZE-W Pop × 1368 S6 F_2) and two varieties from the yellow population (EV DT-Y 2000 STR C_1 and 2004 TZE-Y Pop DT STR C_4); an elite *Striga*-resistant variety (99 Syn WEC) not from the recurrent selection program; and a *Striga*-susceptible check, TZE Comp4. The C_1 from TZE-W Pop DT STR as well as the C_1 and C_2 from TZE-Y Pop DT STR could not be included in the trials because they were lost from the IITA cold room at Bouaké, Côte d'Ivoire, when it was looted during the Ivorian civil war. The trials were planted at Mokwa and Abuja in Nigeria during the growing seasons of 2005 and 2006.

A total of 17 entries were involved in the study for the extra-early group, including the original populations (C_0) along with cycles 2, 3, and 4 of TZEE-W Pop STR and cycles 3 and 4 of TZEE-Y Pop STR, the derived varieties from the cycles of selection of the white source populations (2000 Syn EE-W, 2004 TZEE-W Pop STR C_4) and the yellow populations (99 TZEE-Y STR C0, 2004 TZEE-Y Pop STR C_4), the three elite *Striga*-resistant varieties from other selection programs (Siné TZEE-W STR, Ferke TZEE-W STR, 98 TZEE-W STR), and a *Striga*-susceptible check, TZEE-W SR BC_5. The 17 entries were evaluated in *Striga*-infested conditions at Mokwa and Abuja and *Striga*-free conditions at Mokwa, Abuja, Ikenne, Zaria, and Bagauda, 2005−2007.

A randomized complete block design with four replications was used in the evaluations. The details of the field plot techniques and crop management practices are as described in Chap. 9.

The *Striga* infestation method developed by the IITA Maize Program and presented in more detail in Chap. 9 was adopted to ensure uniform *Striga* infestation with no escapes (Kim 1991a, b; Kim and Winslow 1991).

Data were obtained on grain yield, EPP, plant and ear heights, 50% anthesis and silking, and stalk lodging (percentage of plants broken at or below top ear node) on both infested and non-infested plots. Anthesis–silking interval (ASI) was determined as the difference between 50% silking and anthesis. EPP was determined by dividing the total number of ears/plot by the number of plants harvested. Grain yield adjusted to 15% moisture was estimated from the shelled kernel dry weight. In addition, host plant damage syndrome rating (Kim 1991a; b) and emerged *Striga* counts were made at 8 and 10 WAP (56 and 70 days after planting) in the *Striga*-infested rows. Maize *Striga* damage syndrome was scored per plot on a scale of 1–9 where 1 = no damage, indicating normal plant growth and high resistance/tolerance, and 9 = complete collapse or death of the maize plant, i.e., highly susceptible (sensitive) (Kim 1991a, b).

Analyses of variance (ANOVA), combined over environments, were performed on plot mean basis with PROC GLM in SAS using a RANDOM statement with the TEST option (SAS Institute 2004). *Striga*-infested and *Striga*-non-infested plots were analyzed separately. The variance of *Striga* counts has been found to increase with the mean; therefore a log transformation {log (counts + 1)} was used to reduce the heterogeneity of variance. The cycles of selection of each population across location–year combinations for each growing condition were combined to obtain the entry means. The ANOVA model was

$$Y_{ijk} = m + E_i + R\left(E\right)_{ij} + G_{\mathrm{k}} + \left(GE\right)_{jk} + e_{ijk}$$

In this model, Y_{ijk} is the observed value of a trait; m is the overall mean of the trait; E_i is the effect of the ith environment, and $i = 1, 2, 3, 4$; $R(E)_{ij}$ is the effect of the jth replication within the ith environment, and $j = 1, 2, 3, 4$; G_k is the effect of the kth genotype, and $k = 1, 2,\ldots 0.0.13$, or 17; $(GE)_{jk}$ is the effect of the interaction of the kth genotype with the jth environment; and e_{ijk} is the residual effect.

In the combined ANOVA, the location–year combinations, replicates, and blocks were considered as random factors, while entries were considered as fixed effects. Means were separated using the LSD. Excluding the checks from the data set, entry means of the traits of the cycles across environments were regressed as dependent variables on the cycle numbers (independent variable) to obtain estimates of gain cycle^{-1} of selection for each population. The coefficient of linear regression (b-value) provided an estimate of the gain cycle^{-1} (Fig. 5.11), which was divided by the intercept and multiplied by 100 to obtain percentage response cycle^{-1} of selection. The gains from the different cycles of selection of each population were compared for each trait studied under *Striga* infestation and *Striga*-free conditions, using orthogonal linear contrasts.

5.13.2 Response of the Populations to Recurrent Selection

5.13.2.1 Early Populations

Under *Striga* infestation, combined analysis of variance showed significant genotypic mean squares for grain yield, ears plant^{-1}, and the four *Striga* resistance traits (Table 5.6). Location and year effects were also significant for grain yield and most other traits, but interaction mean squares were significant for only a few of the traits. Under *Striga*-free conditions, genotype, year, and location mean squares were significant for most of the traits, and in many cases, the interaction mean squares were also significant (Table 5.6). Grain-yield response to S_1 recurrent selection in the two early populations in *Striga*-infested environments differed greatly: about 70.6 kg ha^{-1} (6.3%) cycle^{-1} for TZE-Y Pop DT STR and 352.5 kg ha^{-1} (58.0%) cycle^{-1} for TZE-W Pop DT STR (Fig. 5.12). Corresponding values for the two populations under *Striga*-free environments were similar: 194.0 kg ha^{-1} (6.6%) cycle^{-1} and 186.5 kg ha^{-1} (6.0%) cycle^{-1}, respectively.

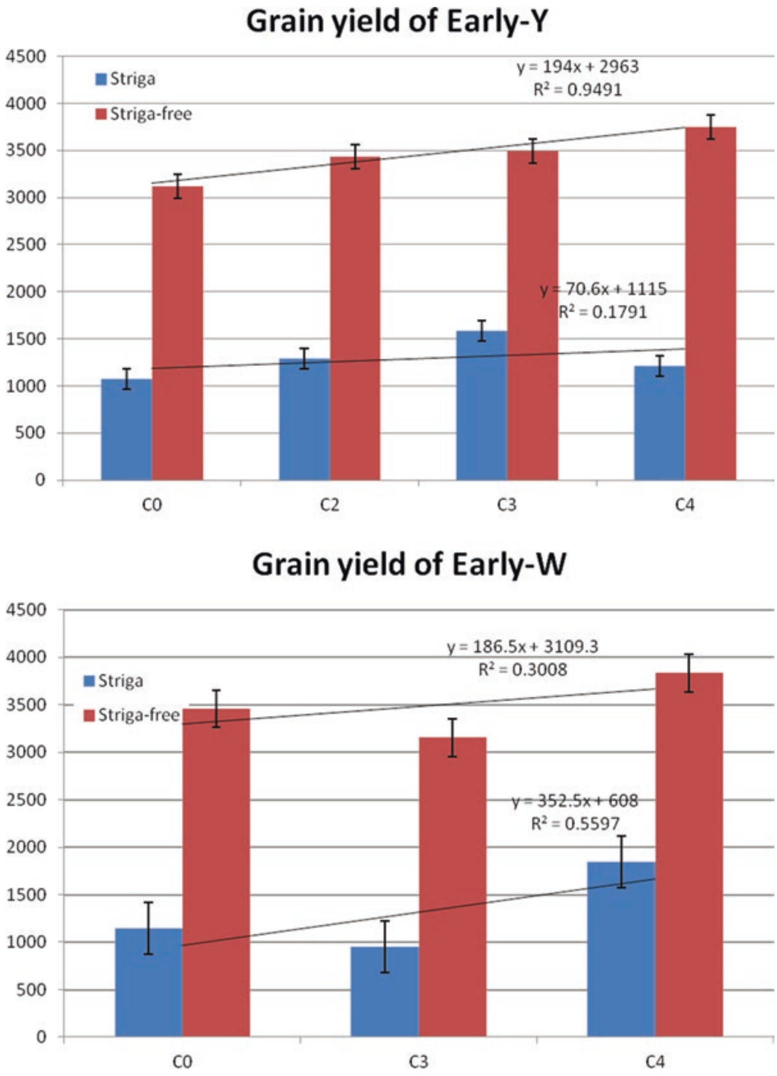

Fig. 5.11 Performance of the cycles of S_1 selection in TZE-Y Pop DT STR (*above*) and TZE-W Pop DT STR (*below*) evaluated in *Striga*-infested and *Striga*-free environments

Table 5.6 S_1 progenies derived from each of the populations evaluated in Nigeria under artificial infestation with *S. hermonthica* at Abuja and Mokwa in 2003

Source population	Number	Experimental varieties
TZE-W Pop DT STR C_0	6	EV DT-W 98, EV DT-W 2000, EV DT-W 99 STR, TZE-W Pop × 1368 S6 F_2, EV DT-W 98 C_2, 2004 TZE-W Pop DT STR C_4
TZE-Y Pop DT STR C_0	4	EV DT-Y 98, EV DT-Y 98 C_2 STR, EV DT-Y 2000 STR, 2004 TZE-Y Pop DT STR C_4
TZEE-W Pop STR	2	EV 98 TZEE-W, 2000 Syn EE-W
TZEE-Y Pop STR	2	EV 98 TZEE-Y, 99 TZEE-Y STR C_1

Striga damage rating at 10 WAP and *Striga* emergence at 8 WAP decreased in the improved cycles of selection in both populations (Table 5.7). In addition, *Striga* damage rating at 8 WAP also decreased in the white population. Apart from ears plant^{-1} that showed 4–7% increase per selection cycle, changes in all agronomic traits in response to selection for yield improvement were not statistically significant under *Striga* infestation. In the *Striga*-free environments, however, stalk lodging of the C_0 was higher than those of the improved cycles in both populations. Similarly in TZE-Y Pop DT STR, ASI decreased in the improved cycles relative to the C_0. Changes in other traits did not show consistent trends.

5.13.2.2 Extra-Early Populations

Genotypes, locations, and years significantly affected grain yield, days to silk, ASI, and ears plant^{-1} under both *Striga*-infested and *Striga*-free conditions (Table 5.8). These sources of variation also significantly affected plant height and stalk lodging under *Striga*-free conditions. Genotype mean squares were also significant for stalk lodging as well as *Striga* damage, but not for the number of emerged *Striga* plants at 8 and 10 WAP. Apart from year × location mean squares that were significant for seven of the ten traits, genotype by environment interaction effects was not significant in *Striga*-infested environments.

In contrast, about 50% of the interaction effects were statistically significant in the *Striga*-free environments, especially genotype × location and year × location sources that were significant for four and five of the six traits, respectively.

Four cycles of S_1 recurrent selection improved grain yield by nearly 90% cycle^{-1} in the yellow extra-early population when evaluated in *Striga*-infested environments (Fig. 5.13). This population was improved at the rate of 18.44% cycle^{-1} when evaluated in *Striga*-free environments. Gains from the selection program were about equal for the white extra-early population under the two *Striga* environments: about 12.66% cycle^{-1} under *Striga* and 12.94% cycle^{-1} without *Striga* (Fig. 5.12). Four cycles of S_1 recurrent selection improved grain yield by nearly 90% cycle^{-1} in the yellow extra-early population when evaluated in *Striga*-infested environments (Fig. 5.12). This population was improved at the rate of 18.44% cycle^{-1} when evaluated in *Striga*-free environments. Gains from the selection program were about equal for the white extra-early population under the two *Striga* environments: about 12.66% cycle^{-1} under *Striga* and 12.94% cycle^{-1} without *Striga* (Fig. 5.12).

Striga counts at 8 and 10 WAP, along with *Striga* rating at 8 but not 10 WAP, were reduced by recurrent selection in TZEE-Y Pop DT STR (Table 5.8). Only the number of emerged *Striga* plants at 8 WAP showed significant reduction in TZEE-W Pop STR. Under *Striga* infestation, selection failed to induce significant changes in the agronomic traits of the two populations, except ears plant^{-1}. In contrast, significant changes occurred in *Striga*-free environments for days to silk, ASI, and plant height in the yellow population and ears plant^{-1} and plant height in the white population (Table 5.9).

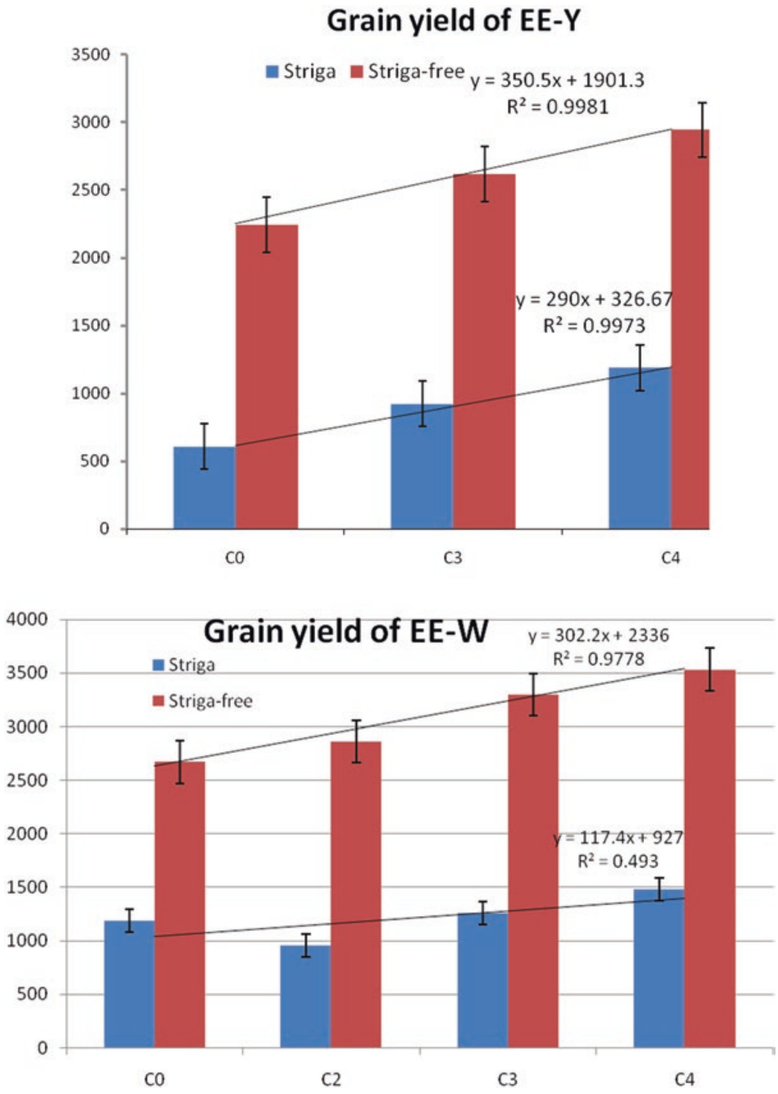

Fig. 5.12 Performance of the cycles of S_1 selection in TZEE-Y Pop DT STR (*above*) and TZEE-W Pop DT STR (*below*) evaluated in *Striga*-infested and *Striga*-free environments

5.13.3 Performance of Derived Cultivars from the Selection Programs

Another objective of the recurrent selection program was to develop cultivars from the different cycles of selection. The performance of the derived cultivars was assessed in several field trials. For the early populations evaluated under *Striga* infestation, ACR 94 TZE Comp5-Y and ACR 94 TZE Comp5-W, which were from

Table 5.7 Level of statistical significance of mean squares from the analysis of variance for agronomic traits associated with four cycles of S_1 recurrent selection in TZE-Y Pop DT STR and TZE-W Pop DT STR maize populations evaluated in *Striga*-infested and *Striga*-free environments in Nigeria in 2005 and 2006

Source of variation	Grain yield	Days to mid-silk	ASI	Ears per plant	Plant height	Stalk lodging, %	*Striga* rating at 8 WAP	*Striga* rating at 10 WAP	*Striga* count at 8 WAP	*Striga* count at 10 WAP
Striga-infested environments										
Genotype	**	ns	ns	**	ns	ns	**	**	*	*
Location	**	*	**	**	**	ns	**	**	**	**
Year	**	**	**	**	ns	**	**	**	**	ns
Genotype × location	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Genotype × year	**	ns	ns	ns	ns	ns	ns	**	ns	ns
Year × location	ns	**	**	ns	**	**	ns	ns	ns	**
Genotype × year × location	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Striga-free environments										
Genotype	**	*	**	**	**	**				
Location	**	ns	**	**	**	**				
Year	**	ns	**	**	ns	**				
Genotype × location	ns	ns	ns	**	ns	**				
Genotype × year	ns	**	**	ns	ns	**				
Year × location	**	**	**	**	**	**				
Genotype × year × location	ns	ns	ns	**	ns	**				

ns not significant
*Significant at $P < 0.05$; **Significant at $P < 0.01$

Table 5.8 Changes in *Striga* resistance traits under *Striga* infestation, along with agronomic traits associated with four cycles of S_1 recurrent selection in TZE-Y Pop DT STR and TZE-W Pop DT STR maize populations evaluated in *Striga*-infested and *Striga*-free environments in Nigeria, 2005–2007

Parameter	Days to mid-silk	ASI	Ears per plant	Plant height, cm	Stalk lodging, %	*Striga* rating at 8 WAP	*Striga* rating at 10 WAP	*Striga* count at 8 WAP	*Striga* count at 10 WAP
Striga-infested environments									
TZE-Y Pop DT STR									
Gain per cycle	0.63	0.36	0.04	0.21	−0.30	−0.09	−0.25	−4.75	−3.04
Percent response per cycle	1.13	0.69	6.60	0.16	−5.48	−1.97	−4.76	−3.68	−1.87
R^2, %	64.3	66.1	86.8	0.7	55.4	52.2	74.3	7.3	10.9
Significance of gain	ns	ns	*	ns	ns	ns	**	*	ns
TZE-W Pop DT STR									
Gain per cycle	0.2	0.65	0.02	1.77	0.11	−0.26	−0.22	−7.22	−1.93
Percent response per cycle	0.35	1.25	4.63	1.40	2.29	−4.70	−3.94	−4.88	−1.16
R^2, %	35.7	53.5	29.4	96.5	7.7	79.4	41.2	23.5	9.7
Significance of gain	ns	ns	*	ns	ns	**	**	*	ns
Striga-free environments									
TZE-Y Pop DT STR									
Gain cycle^{-1}	0.08	−0.11	0.01	1.10	−0.44				
Percent response per cycle	0.13	−3.02	1.56	0.67	−16.01				
R^2, %	3.94	12.29	20.45	12.09	69.89				
Significance of gain	ns	*	*	ns	**				
TZE-W Pop DT STR									
Gain per cycle	0.5	0.04	0.01	−1.60	−0.33				
Percent response per cycle	0.92	1.49	0.66	−1.02	−13.86				
R^2, %	29.67	1.07	89.54	63.26	96.69				
Significance of gain	*	*	ns	*	*				

*Significant at $P < 0.05$; **Significant at $P < 0.01$
ns not significant

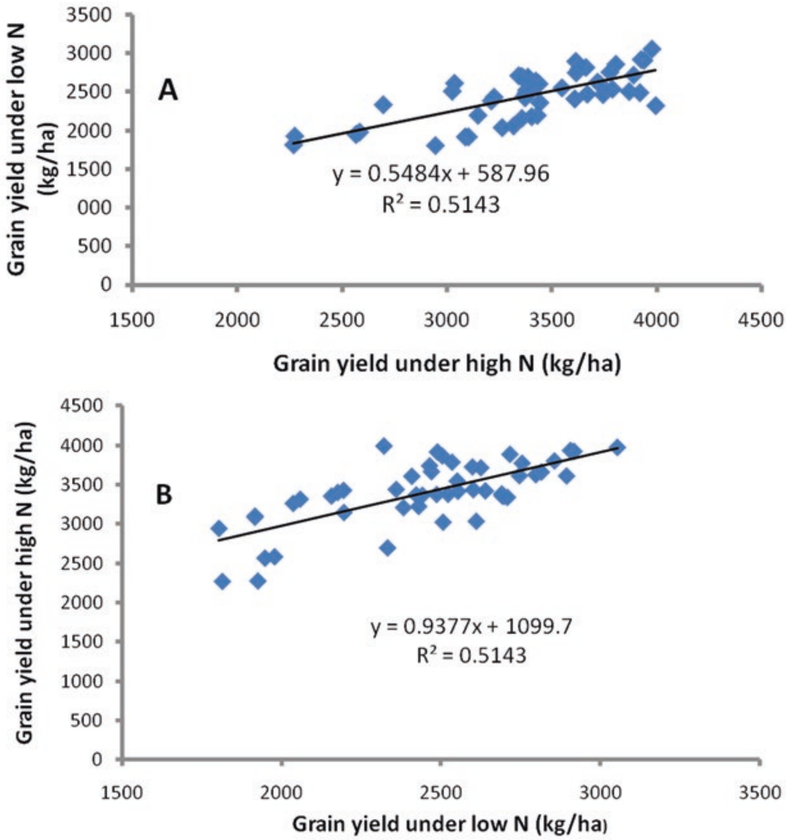

Fig. 5.13 Regression of (**a**) grain yield of low-N environments on grain yield of high-N environments and (**b**) grain yield of high-N environments on grain yield of low-N environments

a different selection program, were the highest-yielding group (2158 and 2124 kg ha^{-1}, respectively, Table 5.10). The second group comprised six products of the selection program, with grain yield ranging from 1806 to 1954 kg ha^{-1}. The third group, with grain yield of 1498 to 1759 kg ha^{-1}, contained mostly *Striga*-susceptible cultivars and the C_0 of the selection program. Under *Striga*-free conditions, the performance of several cultivars from the selection program was equal to or better than ACR 94 TZE Comp5-Y and ACR 94 TZE Comp5-W. The genotype plus genotype × environment interaction biplot analysis demonstrated that EV DT-Y 2000 STR C_1 and TZE-W Pop DT STR C_3 from the selection program, along with ACR 94 TZE Comp5-W, had stable grain yield under *Striga*-infested and *Striga*-non-infested conditions.

Table 5.9 Level of statistical significance of mean squares from the analysis of variance for agronomic traits associated with four cycles of S_1 recurrent selection in TZEE-Y Pop DT STR and TZEE-W Pop DT STR maize populations evaluated in *Striga*-infested and *Striga*-free environments in Nigeria in 2005 and 2006

Source of variation	Grain yield	Days to mid-silk	ASI	Ears per plant	Plant height	Stalk lodging, %	*Striga* rating at 8 WAP	*Striga* rating at 10 WAP	*Striga* count at 8 WAP	*Striga* count at 10 WAP
Striga-infested environments										
Genotype	**	**	*	**	ns	*	**	**	ns	ns
Location	**	**	**	**	**	ns	ns	ns	**	**
Year	**	**	**	**	**	**	ns	*	ns	ns
Genotype × location	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Genotype × year	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Year × location	**	**	**	**	**	**	ns	**	ns	ns
Genotype × year × location	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Striga-free environments										
Genotype	**	**	*	**	**	**				
Location	**	**	**	**	**	**				
Year	**	**	**	**	**	**				
Genotype × location	**	**	**	*	ns	ns				
Genotype × year	ns	**	**	ns	ns	ns				
Year × location	**	**	**	**	**	ns				
Genotype × year × location	ns	ns	**	ns	ns	ns				

ns not significant
*Significant at $P < 0.05$; **Significant at $P < 0.01$

Grain yield of the extra-early genotypes evaluated under *Striga* infestation ranged from 772 kg ha^{-1} for 99 TZEF-Y STR C_0 to 1588 kg ha^{-1} for 99 Syn EE-W (Tables 5.10, 5.11, 5.12).

The susceptible check, TZEE-W SR BC_5, suffered about 66% yield loss under *Striga* infestation compared to *Striga*-free conditions (783 vs 2266 kg ha^{-1}). It also sustained the worst *Striga* damage and was among the genotypes that supported the highest number of emerged *Striga* plants (Table 5.9), indicating that the level of infestation was severe in the evaluation trials. The mean grain yields of the base populations, TZEE-Y Pop STR C_0 and TZEE-Y Pop STR C_0, were not significantly different from that of the susceptible check, TZEE-W SR BC_5, under *Striga* infestation. The most promising white-grained genotypes in terms of grain yield, host damage, and level of *Striga* emergence were 99 Syn EE-W and 98 TZEE-W STR from other selection programs and TZEE-W Pop STR C_4, TZEE-W Pop STR C_3, and 2004 TZEE-W Pop STR from the recurrent selection program. 99 Syn EE-W outyielded the susceptible check by 51% and TZEE-W Pop STR C_4 by 47%. However, there were no significant differences in grain yield among the top-ranking white endosperm genotypes. The highest-yielding yellow-grained genotype was TZEE-Y Pop STR C_4, which was not significantly different in grain-yield performance from the derived cultivars, 99 TZEE-Y STR (derived from TZEE-Y Pop STR C_2) and 2004 TZEE-Y STR C_4 (derived from TZEE-Y Pop STR C_4). TZEE-Y Pop STR C_4 was also comparable in terms of grain yield, *Striga* damage, and *Striga* emergence to the top-ranking white endosperm genotypes. The improved yield production of the derived cultivars from the advanced cycles of selection in TZEE-Y Pop STR was associated with decreases in number of emerged *Striga* plants at 8 and 10 WAP and *Striga* damage at 8 WAP, while that of the white population was accompanied by an increase in days to silking and EPP as well as decrease in number of emerged *Striga* plants at 8 WAP. Changes in all other traits associated with recurrent selection in both populations were not statistically significant (Tables 5.13, 5.14).

The identification of the cultivars DTE-Y STR Syn C_1, EV DT-Y 2000 STR, and 2009 DTE- Y STR Syn as the highest yielding and the most stable across *Striga*-infested environments is not surprising because, apart from the fact that they possess genes for resistance to *Striga*, they also have inherent abilities to tolerate drought, low soil nitrogen, and the maize streak virus. These results suggest that the outstanding cultivars have broad adaptation to the growing environments in WCA. The outstanding cultivars should be extensively tested in on-farm trials in WCA and vigorously promoted for adoption for commercialization in the sub-region.

In the IITA Maize Program, selection for *Striga* resistance is normally conducted under low-N conditions without deliberate selection for low-N tolerance. Selection for *Striga* resistance and drought tolerance started independently in 1988 and 1994, respectively, and has gone through three breeding eras based on the germplasm subjected to improvement and methodologies used. Several comparisons of older and newer hybrids under contrasting N levels have been reported (Castleberry et al. 1984; Tollenaar et al. 1997; Sangoi 2001; O'Neill et al. 2004), but similar studies in

Table 5.10 Changes in *Striga* resistance traits under *Striga* infestation, along with agronomic traits associated with four cycles of S_1 recurrent selection in TZEE-Y Pop DT STR and TZEE-W Pop DT STR maize populations evaluated in *Striga*-infested and *Striga*-free environments in Nigeria, 2005–2007

Parameter	Days to mid-silk	ASI	Ears per plant	Plant height, cm	Stalk lodging%	*Striga* rating at 8 WAP	*Striga* rating at 10 WAP	*Striga* count at 8 WAP	*Striga* count at 10 WAP
Striga-infested environments									
TZEE-Y Pop DT STR									
Gain cycle^{-1}	0.35	−0.27	0.03	−1.00	0.52	−0.11	−0.14	−0.19	−4.12
Percent response cycle^{-1}	0.63	−9.09	7.57	−0.81	11.01	−1.83	−2.15	−0.12	−2.43
R^2, %	52	94	55	25	81	35	48	0.01	0.05
Significance of gain	ns	ns	ns	ns	ns	*	ns	**	**
TZEE-W Pop DT STR									
Gain cycle^{-1}	0.514	−0.46	0.01	−1.51	−0.62	−0.05	−0.09	−11.45	−7.82
Percent response cycle^{-1}	0.91	−7.62	1.52	−1.11	−9.66	−0.80	−1.57	−11.06	−0.42
R^2, %	77	91	2.98	23	98	65	26	0.35	5.61
Significance of gain	ns	ns	**	ns	ns	ns	ns	*	ns
Striga-free environments									
TZEE-Y Pop STR									
Gain per cycle	0.81	−0.27	4.77	0.24	0.014				
Percent response cycle^{-1}	1.55	−9.09	3.23	6.45	1.65				
R^2, %	94	94	96	74	84				
Significance of gain	**	*	ns	**	ns				
TZEE-W Pop STR									
Gain per cycle	1.023	−0.257	0.02	2.257	0.283				
Percent response cycle^{-1}	1.94	−9.08	1.98	1.45	10.14				
R^2, %	0.77	0.77	58.16	0.426	0.464				
Significance of gain	ns	ns	**	**	ns				

ns not significant
*Significant at $P < 0.05$; **Significant at $P < 0.01$

Table 5.11 Grain yield and other agronomic characters of derived cultivars from S_1 recurrent selection in TZE-Y Pop DT STR and TZE-W Pop DT STR maize populations evaluated under *Striga*-free (non-inf.) and *Striga*-infested (inf.) conditions averaged across six locations in West Africa in 2002

	Yield (kg ha^{-1})		Days to silk		Plant ht. (cm)		*Striga* 10 WAP		Ears harvested	
Cultivar	Non-inf.	Inf.	Non-inf.	Inf.	Non-inf.	Inf.	Count	Rating	Non-inf.	Inf.
98 Syn WEC STR C0	2228	1954	52	54	168	143	68	5	25	18
EV DT-Y 2000 STR C1	2203	1831	53	54	171	139	66	5	24	18
EV DT 97 STR C1	2110	1759	53	54	166	136	63	4	22	17
TZE-W POP DT STR C3	2099	1871	53	54	173	140	67	5	24	18
TZE-Y POP DT STR C3	2081	1928	53	55	172	137	64	5	24	16
ACR 94 TZE COMP5-W	2052	2124	52	53	166	144	67	4	24	20
2000 Syn WEC	2048	1826	52	54	169	140	66	5	25	17
ACR 94 TZE COMP5-Y	2033	2158	52	53	163	137	60	4	24	21
TZE-W POP × 1368 STR C1	1950	1689	51	53	162	130	59	5	25	17
Kamboinse 88 Pool 16 DT (RE)	1881	1806	52	54	169	137	65	5	23	17
ACR 94 POOL 16 DT STR	1867	1735	53	55	166	137	68	5	24	15
TZE-W POP × 1368 STR S6 F2	1847	1721	53	55	175	133	58	4	23	16
99 Syn WEC	1811	1541	55	56	171	187	64	5	24	17
EV DT-W 99 STR C0	1803	1806	52	53	159	125	60	5	24	18
EV DT-W 2000 STR C0	1521	1498	53	52	158	135	67	5	24	15
Grand mean	1988	1826	53	54	167	140	64	5	24	173
CV	24	26	5	9	13	42	15	20	15	22
LSD	271	269	2	3	14	37	6	1	2	2
SED	137.8	136.7	0.8	1.5	7.1	18.6	3.0	0.3	1.1	1.1
P stat-test for cultivar	*	*	*	ns	ns	ns	ns	ns	ns	**
P stat-test for env × cultivar	***	**	ns	ns	ns	ns	*	***	ns	**

Products from the S_1 recurrent selection program
ns not significant
*Significant at $P < 0.05$; **Significant at $P < 0.01$

Table 5.12 Grain yield (kg ha^{-1}) and other traits of derived cultivars from four cycles of S_1 recurrent selection in TZEE-Y Pop DT STR and TZEE-W Pop DT STR maize populations evaluated in *Striga*-infested and *Striga*-free environments in Nigeria, 2005–2007

	Grain yield	Days to mid-silk	ASI	Ears per plant	Plant height	Stalk lodging	*Striga* rating		*Striga* count	
Entry	kg ha^{-1}			no.	cm	%	8 WAP	10 WAP	8 WAP	10 WAP
Striga-infested										
99 TZEE-Y STR C_0	772	54	3	0.5	121.2	5.5	5.5	6.0	163	173
Siné TZEE-W STR	1031	57	4	0.6	122.7	4.2	5.3	5.2	118	143
Ferke TZEE-W STR	1106	57	4	0.5	122.7	4.9	5.5	5.2	119	150
98 TZEE-W STR	1345	56	4	0.6	128.5	5.8	5.1	4.6	118	154
99 TZEE-Y STR	1089	52	4	0.5	113.5	3.9	5.6	5.7	120	126
2000 Syn EE-W	1049	56	5	0.5	123.8	5.2	5.6	5.4	120	143
99 Syn EE-W	1588	56	3	0.6	131.2	5.4	4.7	4.6	136	167
TZEE-W SR BC5 (RE)	783	52	5	0.4	115.4	5.1	5.9	6.3	189	182
2004 TZEE-Y Pop STR C_4	956	57	5	0.5	130.0	6.2	5.3	5.4	133	170
2004 TZEE-W Pop STR C_4	1235	57	4	0.5	131.5	5.1	5.4	5.2	111	134
LSD (0.05)	534.9	2.33	1.93	0.2	15.33	1.9	0.8	1.01	69	68
P stat-test for genotypes	**	**	*	**	ns	*	**	**	ns	ns
Striga-free										
99 TZEE-Y STR C_0	2067	54	3	0.8	154	4.8				
Siné TZEE-W STR	2134	56	3	0.8	149	2.8				
Ferke TZEE-W STR	3002	57	2	0.8	163	3.1				

(continued)

Table 5.12 (continued)

Entry	Grain yield kg ha^{-1}	Days to mid-silk	ASI	Ears per plant no.	Plant height cm	Stalk lodging %	*Striga* rating 8 WAP	*Striga* rating 10 WAP	*Striga* count 8 WAP	*Striga* count 10 WAP
98 TZEE-W STR	2861	56	2	0.9	157	2.8				
99 TZEE-Y STR	2366	52	2	0.8	146	3.9				
2000 Syn EE-W	3128	54	2	0.9	156	4.0				
99 Syn EE-W	3254	56	2	0.9	162	3.3				
TZEE-W SR BC5 (RE)	2266	51	2	0.8	152	5.3				
2004 TZEE-Y Pop STR C_4	2934	55	2	0.8	164	5.6				
2004 TZEE-W Pop STR C_4	3366	56	2	0.9	165	3.4				
LSD (0.05)	329.7	0.82	0.54	0.06	7.77	2.00				
P stat-test for genotypes	**	**	*	**	**	**				

Products from the S_1 recurrent selection program
ns not significant
*Significant at $P < 0.05$; **Significant at $P < 0.01$

Table 5.13 Grain yield and other agronomic traits of maize cultivars of three breeding eras evaluated under managed drought stress at Ikenne and natural drought stress at Samaru between 2010 and 2012 and optimum conditions at 24 environments in Nigeria, Benin, and Ghana in 2010 and 2011

Trait	Era	Number of cultivar	Drought stress	Well-watered conditions
Grain yield, kg ha^{-1}	1988–2000	15	1345 ± 52.2	3363 ± 52.5
	2001–2006	16	1305 ± 49.2	3605 ± 46.7
	2007–2010	19	1613 ± 48.8	3956 ± 42.3
Anthesis–silking interval	1988–2000	15	4 ± 0.1	1.8 ± 0.03
	2001–2006	16	4 ± 0.1	1.9 ± 0.03
	2007–2010	19	4 ± 0.1	1.8 ± 0.03
Plant height, cm	1988–2000	15	136 ± 3.0	163 ± 0.8
	2001–2006	16	138 ± 3.0	169 ± 0.7
	2007–2010	19	139 ± 2.7	171 ± 0.7
Plant aspect	1988–2000	15	3.2 ± 0.06	2.6 ± 0.02
	2001–2006	16	3.2 ± 0.06	2.5 ± 0.02
	2007–2010	19	3.0 ± 0.05	2.4 ± 0.03
Ear aspect	1988–2000	15	2.9 ± 0.05	2.7 ± 0.02
	2001–2006	16	2.9 ± 0.05	2.5 ± 0.02
	2007–2010	19	2.8 ± 0.05	2.4 ± 0.02
Ears per plant	1988–2000	15	0.9 ± 0.02	0.9 ± 0.005
	2001–2006	16	0.8 ± 0.02	0.9 ± 0.005
	2007–2010	19	0.8 ± 0.01	0.9 ± 0.004
Stay-green characteristic	1988–2000	15	4.4 ± 0.09	–
	2001–2006	16	4.6 ± 0.09	–
	2007–2010	19	4.4 ± 0.07	–

tropical maize are limited, thus making it difficult to completely ascertain the genetic gain that has been made for grain yield in relationship to N fertility in the numerous varieties that have been released in sub-Saharan Africa. For example, Castleberry et al. (1984) showed that genetic gains for grain yield under low and high soil fertility of 25 open-pollinated and hybrid maize cultivars used between the 1930s and 1980s had been 51 and 87 kg ha–1 year – ^{1}, respectively. Similarly, with four hybrids representing Brazilian maize germplasm released between the 1960s and 1990s, the most recent hybrid produced higher grain yields at all levels of N (Sangoi 2001). Also, a newer hybrid (Pioneer 3902, released in 1988) produced approximately 25% more grain than an older hybrid (Pride 5, released in 1959) at both low N and high N (Tollenaar et al. 1997). In contrast to these studies, O'Neill et al. (2004) showed that a hybrid widely grown in the USA during the 1970s (B73 × Mo17) produced approximately 8% more yield under the deficit N treatment than hybrids released in the early and late 1990s, while the latter had greater yield responses to applied fertilizer N.

Table 5.14 Mean and standard error of grain yield and other agronomic traits of maize cultivars of three breeding eras evaluated under *Striga*-infested and *Striga*-free conditions in Nigeria and Benin between 2010 and 2011

Trait	Era	Number of cultivars	*Striga* infested	*Striga*-free
Grain yield, kg ha^{-1}	1988–2000	15	2537 ± 74.6	3646 ± 98.3
	2001–2006	16	2697 ± 73.9	3770 ± 93.2
	2007–2010	19	3122 ± 65.1	4227 ± 87.5
Striga rating at 8 WAP	1988–2000	15	3.3 ± 0.08	–
	2001–2006	16	3.2 ± 0.07	–
	2007–2010	19	2.9 ± 0.06	–
Striga rating at 10 WAP	1988–2000	15	4.6 ± 0.08	–
	2001–2006	16	4.5 ± 0.07	–
	2007–2010	19	4.1 ± 0.06	–
Striga count at 8 WAP	1988–2000	1	19 ± 1.2	–
	2001–2006	16	20 ± 1.2	–
	2007–2010	19	20 ± 1.2	–
Striga count at 10 WAP	1988–2000	15	27 ± 1.2	–
	2001–2006	16	29 ± 1.3	–
	2007–2010	19	27 ± 1.3	
Ear aspect	1988–2000	15	4.2 ± 0.1	3.4 ± 0.07
	2001–2006	16	4.1 ± 0.1	3.2 ± 0.07
	2007–2010	19	3.8 ± 0.1	3.0 ± 0.06
Ears per plant	1988–2000	15	0.8 ± 0.01	0.9 ± 0.01
	2001–2006	16	0.8 ± 0.01	0.9 ± 0.01
	2007–2010	19	0.9 ± 0.01	0.9 ± 0.01

Table 5.15 Minimum, maximum, and mean ± se of grain yield of maize cultivars of three breeding eras evaluated under low- and high-N conditions at Mokwa and Ile-Ife in 2010 and 2011

Era[a]	No. of varieties	Low N			High N		
		Min	Max	Mean ± se	Min	Max	Mean ± se
1	15	0.8	4.2	2.3 ± 0.056	0.9	3.2	3.2 ± 0.174
2	16	0.3	5.4	2.4 ± 0.063	0.8	5.8	3.3 ± 0.076
3	19	0.7	5.6	2.5 ± 0.055	1.0	5.5	3.7 ± 0.068

[a] Era 1, 1988–2000; era 2, 2001–2006; and era 3, 2007–2011

In the third study, the hypothesis that tolerance to low N had been significantly improved while selecting for *Striga* resistance during the three breeding eras was tested. The 50 early-maturing cultivars used for the drought and *Striga* studies were also evaluated in replicated field trials in 2010 and 2011 at Mokwa, in the southern Guinea savanna and Ile-Ife, and in the rainforest agroecology under both low-N (30 kg N ha^{-1}) and high-N (90 kg N ha^{-1}) levels. The data were subjected to ANOVA and regression analysis. Under both low and high N, grain yield increased significantly from the first to the third breeding era (Table 5.15). Similarly for both low and high N, plant and ear heights increased slightly, while ear aspect decreased from era 1 to era 3 (data not shown). Breeding era did not alter the number of days to flowering as well as stalk and root lodging. Rather, under low but not high N, plant aspect and the stay-green character improved in era 3 relative to era 1. In the ANOVA, variety-within-era source of variation was highly significant for both low- and high-N environments. The highest-yielding cultivars under both N environments, such as TZE-W DT C2 STR, EV DT-W 2008 STR, 2009 DTE-Y STR Syn, and TZE-W DT C1 STR, were mainly from breeding era 3. For the 50 varieties, yield performance in the low-N environments predicted grain yield under high N fairly accurately with an R^2 value of about 0.54 (data not shown). Analysis on individual era basis, however, showed that grain yield in low-N environments for eras 2 and 3 cultivars predicted grain yield in high-N environments than era 1 cultivars (Fig. 5.13). Based on the results of this study, it may be concluded that selection for *Striga* resistance and drought tolerance in early-maturing maize populations enhanced low-N tolerance in the maize cultivars derived from the populations. The improvement was higher in later than earlier breeding eras in WA.

No direct comparisons of grain-yield potential and other agronomic traits have been made across multiple stresses for the early-maturing, drought-tolerant, and *Striga*-resistant maize cultivars developed during the three breeding eras. Since drought, *Striga* infestation, and low N do not occur singly but occur together under field conditions, a holistic evaluation of the gains from the efforts over the three eras seems warranted at this time to serve as basis for the direction to pursue in future breeding efforts in the sub-region. Therefore, the fourth study was conducted at 16 locations in WCA for 2 years to determine genetic improvement in grain yield of maize cultivars developed during three breeding periods, across drought, *Striga* infestation, low soil nitrogen, and optimal growing environments. The objective was to evaluate the genetic yield gain that has been made in breeding stress-tolerant early-maturing maize during the three breeding eras across multiple stresses (managed and natural drought stress, *Striga* infestation, low N) and optimal growing environments.

Grain yield had annual genetic gain of 1.52% and 1.24% under multiple stresses and optimum growing environments, respectively (Table 5.16). The average annual rate of increase in grain yield was 30 kg ha^{-1} year^{-1} across stresses and 37 kg ha^{-1} year^{-1} across optimum growing environments. The annual genetic gains in grain yield were 0.56% for the period 1 cultivars, 1.52% for the period 2 cultivars, and 1.62% for the period 3 cultivars. Among the agronomic traits under stress, only ears per plant (0.32% year^{-1}), ear aspect (−0.51% year^{-1}), plant aspect (−0.24% year^{-1}), and days to anthesis (0.11% year^{-1}) changed significantly ($P < 0.05$ or <0.01) during the three eras. The increase in grain yield from the first- to the third-generation cultivars across stress environments was associated with significant improvement in plant and ear aspects, increased ears per plant, and stay-green characteristic. Under optimal growing environments, the increase in grain yield from the first- to the third-generation cultivars was 1.24% per annum, and the gain was associated with significant improvement in plant and ear heights, plant and ear aspects, husk cover, and increased ears per plant. It was concluded that substantial

Table 5.16 Mean grain yield (kg ha^{-1}) ± SE for three breeding eras, regression parameters, and percent genetic gain era^{-1} for early-maturing maize cultivars evaluated in two groups of environments in Benin, Ghana, and Nigeria, 2010 and 2011

Environment	Era			Regression parameters			% genetic gain era^{-1}
	1 (1988–200) 15 cvs	2 (2001–2006) 16 cvs	3 (2007–2010) 19 cvs	R^2	Intercept	*b*-value	
Multi-stress (16 env)	2176 ± 54.20	2286 ± 49.20	2606 ± 49.00	0.93	1926.0	215.0	11.16
Nonstress (35 env)	3398 ± 52.50	3615 ± 46.70	3957 ± 42.30	0.98	3097.7	279.5	9.02
Mean	2760.25	2908.5	3206.5	0.96	2512.2	223.1	8.88

improvement in the yield potential of maize has been made in this sub-region by breeding for stress tolerance during the past three decades. The varieties EV DT-W 2008 STR, 2009 DTE-Y STR Syn, and TZE-W DT C2 STR (cultivars 22, 28, and 29, respectively), all from the latest era of improvement, were identified as the highest-yielding and most stable cultivars across stress environments and should be promoted to contribute to food security in this sub-region.

5.14 Conclusions

Recurrent selection has been effective in improving early and extra-early maize populations in WCA for tolerance/resistance to *Striga hermonthica* infestation, drought, and low soil N. Based on the results of the evaluation of the 50 early-maturing cultivars of the three breeding eras, it may be concluded that substantial progress has been made in breeding for high-yielding, *Striga*-resistant/*Striga*-tolerant, and drought- and low-N-tolerant cultivars during the past three decades. The outstanding cultivars should be extensively tested in WCA and vigorously promoted for commercialization to contribute to food security in the sub-region.

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Chapter 6
Inbred and Hybrid Maize Development: Experiences in Sub-Saharan Africa

6.1 Introduction

Hybrid varieties are the first-generation offspring of a cross between inbred line parents, open-pollinated varieties, and other populations. The greatest exploitation of hybrids has been based on the use of inbred lines. Such inbred lines are developed through many generations of inbreeding and are near-homozygous individuals. Inbred lines that produce outstanding hybrids are usually dissimilar for specific traits. Among the different types of varieties and methods known, hybrid varieties make the best use of heterosis or hybrid vigor. Heterosis describes the superior performance (yield, vigor, etc.) of an F_1 hybrid over the mean of its parents (known as mid-parent heterosis) or the better-performing parent (high-parent heterosis or *heterobeltiosis*). Heterosis can also manifest in greater resistance to diseases and insect pests. Maize is unique for hybrid production because of the separation of the staminate and pistillate inflorescences on the plant, making selfing and crossing easier than in many other crops with perfect flowers. In addition, many seeds can be produced in one pollination, thereby making available enough seeds for field trials.

6.2 Brief History of Hybrid Breeding and Importance in Sub-Saharan Africa

In 1880, W. J. Beal in Michigan, USA, provided evidence for the greater productivity of maize hybrids over open-pollinated varieties. By the 1940s, hybrid maize varieties were commercially exploited on considerable acreage in the USA, and acreage under maize hybrids continued to increase in subsequent years, completely replacing open-pollinated varieties. The increase in acreage under hybrid maize in the USA was associated with yield increase. Hybrid maize cultivation thereafter

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spread to Europe, Asia, and Africa. Hybrid maize production in East and Southern Africa started in the 1960s, increasing considerably in the 1970s. Although open-pollinated varieties are more popular among farmers in West and Central Africa, there is a growing demand for hybrids to take advantage of heterosis. The Nigerian government provided seed money to the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, for initiating inbred–hybrid breeding development program in 1979. Since then, there has been considerable effort directed to inbred–hybrid breeding in the sub-region. The benefits of hybrid maize varieties in sub-Saharan Africa, particularly West and Central Africa (WCA), are, however, yet to be fully exploited.

Plants of a hybrid variety are heterozygous, though derived from homozygous parents. However, the population of hybrid cultivar is homogeneous because every plant is exactly alike in genetic constitution. Differences among plants of a hybrid cultivar are due to differences in the environment of the plants. Since the inbred parents of hybrids are homozygous, the genetic constitution of the latter is maintained exactly the same year after year unless mutation occurs, which, fortunately, is a rare event. The hybrid seed technology (HST) started a revolution in agricultural productivity characterized by uniformity with respect to many traits. The genetic mechanism of hybrid technology enabled the creation of a specialized seed business.

6.3 Types of Hybrids

Hybrids can be classified into two broad groups: conventional and nonconventional. Conventional hybrids are formed from only inbred lines which include single-cross, three-way cross, and double-cross hybrids. Variants of single-cross and three-way cross hybrids are modified single cross and modified three-way cross, respectively. Nonconventional hybrids include topcross hybrids, double topcross hybrids, varietal cross hybrids, and family hybrids. Nonconventional hybrids are less uniform and lower yielding than their conventional hybrid counterparts. Seeds of the former are produced with greater ease due to the fact that none or only one component of nonconventional hybrid is an inbred.

6.4 Conventional Hybrids

6.4.1 Single-Cross Hybrid

A single-cross (*SC*) hybrid is one that is formed by crossing two genotypes, usually unrelated inbred lines. Single-cross hybrids have higher yield potentials than other types of hybrids due to the exploitation of the greatest amount of heterosis. Single-cross hybrids provide the highest level of uniformity for different traits. The parents of single-cross hybrids are easier to produce and maintain than the parents of other types of hybrids. A major disadvantage of SC is the low yield of the female parent resulting in relatively high cost of SC hybrid seed. To overcome this limitation, modified single-cross (*MSC*) hybrid can be produced. MSC hybrid is formed by crossing an F_1 hybrid between two related inbred lines (A and A′) as female parent to an unrelated inbred line, B, as a male parent [(A × A′) × B)]. The increased seed yield obtained from the female parent reduces the cost of seed, making it affordable to many more farmers than the conventional SC hybrid seed. However, it has the disadvantage that it requires (i) the production and maintenance of the three parental lines and (ii) two seasons to produce the MSC hybrid, that is, one season to cross A × A′ and another season to cross (A × A′) with B. A third disadvantage is that A′ may not be a true isoline of A, thereby making the hybrid (A × A′) × B different from the original SC A × B. This may have grave consequences for seed companies marketing the seed and farmers growing the hybrid.

6.4.2 Three-Way Cross

A three-way cross (*TWC*) is a hybrid formed from three inbred lines; a single-cross hybrid formed from two unrelated inbred lines (A × B) is crossed to another unrelated inbred line (C). Seed yield of TWC is higher than seed yield obtained from single crosses. This results in lower cost of production and price of the hybrid. However, the hybrid is less uniform in height and other traits compared to SC hybrids. As with MSC, TWC hybrids require the production and maintenance of three inbred parents. The modified three-way cross (*MTWC*) hybrid is formed by crossing two unrelated inbred lines, A × B, as a female parent to an F_1 hybrid between two related lines, C × C′, as a male parent. The cross is denoted as [(A × B) × (C × C′)]. The use of an F_1 hybrid between related lines as a male parent ensures the production of large quantity of pollen which contributes to good seed set. In addition to this, good seed set is ensured by the highly productive F_1 used as female parent. As would be expected, MTWC hybrids are less uniform than TWC hybrids. MTWC hybrids require the production and maintenance of four parental inbred lines.

6.4.3 Double-Cross Hybrid

Double-cross (*DC*) hybrids are produced from the crossing of two single-cross hybrids, each of which is produced from two inbred lines. All the four inbred lines used to form DC hybrids are unrelated. The F_1 hybrids used as both male and female parents produce abundant pollen and seed, respectively. Due to the high seed yield, the cost of DC hybrids is lower but is less uniform than TWC hybrids. In general, uniformity of resulting hybrids is inversely proportional to the number of inbred parents used to produce the hybrid; the more the number of inbred parents, the lower the uniformity. Hence, DC hybrids require the production and maintenance of four parental inbred lines. A major disadvantage of double-cross hybrids is that their production requires seven separate production fields, including four blocks to maintain and produce the inbred lines, two fields to produce the single-cross hybrids, and one production field for the double-cross hybrid seed.

6.5 Nonconventional Hybrids

Topcross Hybrid Topcross (*TC*) hybrids are produced by crossing a number of inbred lines to a common tester, the tester being an open-pollinated variety, synthetic, population, family, or a single-cross hybrid. Topcrosses are easy to produce and often useful in the early stages of a hybrid breeding program. For evaluation purposes, it is more convenient to make the noninbred parent (NIP) the male. In the latter, pollen is collected from many plants of the NIP to ensure that gene frequencies for the various traits truly reflect those of the NIP. For commercial exploitation, however, the NIP is used as the female parent to ensure the production of a large quantity of seed, thus reducing the cost of production and price of seed. Since a NIP is heterogeneous, the resulting topcross is not uniform.

Double Topcross Hybrid A double topcross (*DTC*) hybrid is formed by crossing a single cross with a variety, synthetic, family, or population.

Varietal Cross Hybrid Varietal cross (*VC*) hybrids are produced by crossing two unrelated OPVs (OPV × OPV). One advantage of varietal crosses is the abundant pollen and seed production of the male and female parents. The latter reduces the cost of seed of VC hybrids. VC hybrids are the least productive and least uniform among all types of hybrids.

Family Hybrid Family hybrids are produced from two full-sib or half-sib families derived from the same or different populations.

Synthetic Variety This is an advanced generation of a mixture of hybrids that is maintained by open pollination for a certain number of generations before being reconstituted. Each of the components of a synthetic variety must exhibit high combining ability with all the other components.

The types of hybrids to be produced would depend on (i) the yield potential of the hybrids; (ii) level of uniformity desired in the hybrid; (iii) productivity of the parental lines; (iv) stage of development of the seed industry; (v) cost of seed production and affordability of seed to growers; (vi) ease of seed production, processing, and marketing; and (vii) ease of maintaining parents of the hybrids.

6.6 Steps in Producing Hybrids

Three main steps are involved in the development of hybrids, and they are as follows:

(i) Selection of desirable plants in a natural or segregating population of a cross-pollinated crop and selfing of the plants through many generations to develop inbred lines.
(ii) Crossing the developed inbred lines and evaluating the crosses to determine the best pair in terms of productivity. This is referred to as the test of the combining ability of the lines.
(iii) Production of seeds of the hybrids identified in (ii) above for commercial production.

6.7 Development and Evaluation of Inbred Lines: Experiences in Sub-Saharan Africa

An inbred line is a homozygous genotype produced through many generations of inbreeding and can be maintained indefinitely without major genetic changes. Inbred line development process is considered under the following subheadings:

- Sources of inbred lines
- Inbreeding and its consequences
- Methods of inbred line development
- Testing inbred lines in hybrid combinations

6.8 Sources of Inbred Lines

Inbred lines can be developed from:

(i) Open-pollinated varieties with desirable traits and proven agronomic performance
(ii) Selected lines of families from improved cycles of selection of a broad-based population
(iii) Narrow-based populations containing desirable traits
(iv) F_2 populations of crosses of elite inbred lines with complementary desirable traits
(v) Doubled haploid technique
(vi) Backcross populations

Open-Pollinated Varieties At the initial stages of a hybrid program, inbred lines are extracted mainly from the best available open-pollinated varieties, especially those with desirable traits and proven agronomic performance. At the initial stage of the hybrid program at IITA, outstanding inbred lines were extracted from Tuxpeño dent; Caribbean flint; material from other parts of the tropics and subtropics, especially through CIMMYT in Mexico; temperate material from the US Corn Belt; lowland germplasm; mid-altitude germplasm; and a host of other sources (Kim 1997). Similarly, at the initial stages of the hybrid maize program at the University of Ife (now Obafemi Awolowo University), Nigeria, inbred lines were extracted from improved, popularly grown OPVs such as TZSR-W, TZSR-W-1, TZPB (FARZ 27), TZB (FARZ 34), Western Yellow (FARZ 7), 096EP6 (FARZ 23), and TZSR-Y-1 (Fakorede et al. 1993). Lines were also extracted from some local varieties, the improved cycles of modified ear-to-row selection in FARZ 7, and early-maturing populations such as TZE4 and TZESR-W. Hybrid maize programs in Ghana and Cameroon also extracted their initial inbred lines from the best available OPVs. The strategy at the initial stages of a hybrid maize breeding program is to develop inbred lines from as many source populations as possible. This is to ensure genetic variability that would forestall genetic vulnerability and maximize the chances of identifying good inbred lines for the production of hybrids that would make a dramatic, positive impact on maize yield. Breeders working on hybrid maize in different institutions should be careful not to duplicate source populations for inbred line extraction. One way to avoid duplication of efforts is to have interinstitutional collaboration in the developing and testing of inbred lines, as recommended by Fakorede et al. (1978).

6.9 Selected Lines of Families from Improved Cycles of Selection of a Broad-Based Population

Plant breeders subject maize populations to recurrent selection, a procedure that involves the development and evaluation of some type of progenies in field trials. The best performers of the progenies are selected and recombined genetically to form an improved population on which the process can be repeated. The progenies selected for recombination from each cycle may also be subjected to inbreeding to develop inbred lines for hybrid production. Recurrent selection involving simultaneous improvement of two populations is of great advantage in inbred–hybrid development, particularly when the two populations being improved are heterotic. The lines from one population serve as testers for those from the other population and vice versa. This procedure has been used extensively to develop hybrids for SSA. Also, IITA maize breeders have used the best 7–10 of the selected progenies to develop experimental varieties, which are actually synthetic varieties developed from noninbred or early generation inbred lines. However, some of the experimental varieties have been subjected to inbreeding for inbred line extraction.

6.10 Narrow-Based Populations Containing Desirable Traits

As population improvement progresses, the synthetic or experimental varieties developed from each cycle are likely to be higher yielding than the original broad-based population used to initiate the program. They are also likely to manifest desirable traits, especially if some type of index selection has been applied in the program. Although the new varieties are likely to have narrower genetic base than the original population, the genetic base may still be sufficiently broad for the extraction of good inbred lines for hybrid production. One reason for evaluating residual genetic variation after some cycles of recurrent selection is to ensure that good combining inbred lines can be extracted from the improved, though narrower, genetic-based populations. One white (TZE-W Pop DT STR) and one yellow (TZE-Y Pop DT STR) endosperm early populations, along with one white (TZEE-W Pop DT STR) and one yellow (TZEE-Y Pop DT STR) endosperm extra-early populations, have been subjected to five cycles of S1 recurrent selection for drought tolerance and *Striga* resistance at IITA. In addition, one white (DTE STR-W) and one yellow (DTE STR-Y) endosperm populations have undergone four cycles of recurrent selection for the two stresses. The early and extra-early populations and several of the derived varieties have shown superior performance under both *Striga*-infested and *Striga*-non-infested conditions and have proved to be invaluable sources of *Striga*-resistant synthetics and inbred lines. Several *Striga*-resistant and/or drought-tolerant varieties and inbred lines from the four early and two extra-early source populations have been made available to the national maize programs and farmers of WCA (Badu-Apraku et al. 2006c; Badu-Apraku and Lum 2007). Also, inbred lines have been extracted from each population and used to develop *Striga*-, drought-, and low-N-resistant/low-N-tolerant synthetics and hybrids. In addition, several normal endosperm early and extra-early *Striga*-resistant populations, inbred lines and OPVs, and hybrids have been converted to QPM and provitamin A in an effort to raise the lysine and tryptophan levels, and these are presently being evaluated in on-farm trials and promoted for adoption in WCA. Results of evaluations of the four normal endosperm maize source populations and the varieties derived from them under artificial *Striga* infestation, induced moisture stress, and stress-free conditions across locations in the WCA sub-region have confirmed the outstanding performance of the populations and the derived inbred lines and varieties.

6.11 F_2 Populations of Crosses of Elite Inbred Lines with Complementary Desirable Traits

Elite x elite crosses, or recycling of inbred lines, have been extensively utilized in the IITA early and extra-early program. In one set of studies, four early-maturing elite inbred lines (TZEI 1, TZEI 2, TZEI 11, and TZEI 17) with contrasting reactions to drought but with complementary agronomic traits and resistance to *S. hermonthica* were selected based on the available field data and intercrossed in 2007 to form two biparental crosses, namely, TZEI 1 × TZEI 2 and TZEI 17 × TZEI 11. The objective of the program was to generate superior early-maturing DT inbred lines with combined resistance to *Striga* and higher levels of tolerance to drought. The two biparental crosses, TZEI 1 × TZEI 2 (BBA4) and TZEI 17 × TZEI 11 (BBA2), were selected for marker-assisted recurrent selection. A total of 270 S_2 lines derived from TZEI 1 × TZEI 2 were crossed to the tester, TZEI 19, in 2008. The resulting 270 testcrosses were evaluated at Mokwa and Abuja under artificial *Striga* infestation and under optimal conditions in 2009 at Ikenne. Similarly, 382 S_2 lines of the second cross involved in the marker-assisted selection program, TZEI 17 × TZEI 11, were crossed to the tester, TZEI 23, in the 2009/2010 dry season nursery at Ibadan for the continuation of the MAS as described in detail in the chapter on MAS. In addition, inbred line development was initiated with the S_2 lines using repeated self-pollination and evaluation under artificial *Striga* infestation and managed drought stress to develop inbred lines with combined tolerance to the two stresses.

6.12 Doubled Haploid Technique

The doubled haploid (DH) technique, which involves routine in vivo induction of maternal haploids in maize, is presently an important source of inbred line development in the CIMMYT program. Major advantages of DH lines compared to selfed lines include (i) maximum genetic variance between lines for per se and testcross performance from the first generation, (ii) reduced length of the breeding cycle, (iii) perfect fulfillment of DUS (distinctness, uniformity, stability) criteria for variety protection, (iv) reduced expenses for selfing and maintenance breeding, (v) simplified logistics, and (vi) increased efficiency in marker-assisted selection, gene introgression, and stacking genes in lines (Geiger and Gordillo 2009). To induce maternal haploids, the donor plant is pollinated by a specific maize stock (line, single cross, or population) called inducer. Besides regular F_1 kernels, the pollination results in a certain proportion of kernels with a haploid maternal embryo and a regular triploid endosperm. Such kernels display a normal germination rate and lead to viable haploid seedlings (Röber et al. 2005; Geiger 2009). After artificial chromosome doubling the successfully treated seedlings are self-pollinated, resulting in completely homozygous and homogeneous progenies (DH lines). Artificial chromosome doubling used to be a serious constraint in producing doubled haploids on a commercial scale. Spontaneous doubling was observed only in very few germplasm sources (Chase 1964; Shatskaya et al. 1994). A breakthrough was accomplished by Gayen et al. (1994) who cut off the tip of the haploid coleoptiles and immersed the seedlings into a 0.06% colchicine solution plus 0.5% DMSO (dimethyl sulfoxide) for 12 h at 18 °C. Deimling et al. (1997) further increased the efficacy of the method by reducing the roots to 20–30 mm and placing the immersed seedlings in the dark. After the colchicine treatment, the seedlings are carefully washed in water and subsequently grown in the greenhouse to the five- to six-leaf stage (during the first days under high humidity). Thereafter, the treated plants are transferred to the field. Eder and Chalyk (2002) applied the method to a broad range of donor genotypes and achieved an average doubling rate of 49%. About 50–60% of the successfully treated plants shed pollen and could be selfed. Thus, about one out of three colchicinized seedlings produced seeds. The number of viable seeds per ear varies from less than 5 to more than 20. Since colchicine is highly toxic to humans, most breeding companies meanwhile are applying less hazardous proprietary substances for chromosome doubling. Generally, the latter are sprayed onto the haploid seedlings at the three- to five-leaf stage, while the plants are still in a greenhouse (personal communications from various breeders). Artificial chromosome doubling procedures have successfully been adapted to large-scale commercial applications. The induction rate is under polygenic control.

The key challenge with the application of the in vivo haploid induction approach is an efficient screening system that will allow the breeder to differentiate between kernels or seedlings obtained from haploid induction and those derived from regular fertilization.

One cycle of DH-line development with two stages of testcross evaluation takes about 4 years if off-season nurseries are available. Cycle length can be shortened to 3 years if the first three breeding steps (recombination, haploid induction, and DH plant production) are completed in a year. Genome-wide marker-assisted selection can effectively be incorporated into DH-line-based breeding schemes. Because of the genetic, methodological, and logistic advantages, further progress in maize breeding is expected to increase considerably with the development of DH lines. However, the success of employing DH lines is dependent on a robust and efficient haploid induction technology as well as on breeding strategies that make best use of the genetic, technical, and financial resources of the breeder (Gordillo and Geiger 2008).

6.13 Backcrossing

Backcrossing involves mating the F_1 repeatedly to one of the two parents. One of the two parents is referred to as the recurrent parent, while the other is the donor parent. The parent used several times in the breeding method is the recurrent parent, whereas the one involved only once is the donor parent. The line to be considered for use as a recurrent parent must have distinguished itself in the area of intended use of the new line. The backcross method is used to increase in the progeny the frequency of alleles of the recurrent parent while maintaining the desirable alleles of the donor parent by selection. This method is used to modify elite inbred lines for specific traits of interest by correcting their weaknesses. In effect, new traits can be incorporated into elite inbred lines using the backcross method. One major advantage of the backcross method is that improvement is in a stepwise fashion, thus ensuring that previous gains are not lost. The newly developed inbred lines are expected to exhibit the characteristics of the elite recurrent inbred parent but now also possessing the desirable trait of the donor inbred line. An inbred line developed by the pedigree method of breeding can further be improved by the backcross method.

Table 6.1 Levels of heterozygosity and homozygosity at different generations of inbreeding

Generation	Percent heterozygosity	Percent homozygosity
0	100	0
S_1	50	50
S_2	25	75
S_3	12.5	87.5
S_4	6.25	93.75
S_5	3.125	96.875
S_6	1.5625	98.4375
S_7	0.78125	99.21875

Source: Allard (1960)

6.14 Inbreeding and Its Consequences

Inbred lines are developed by manual self-pollination. Selfing is the most dramatic form of inbreeding involving the mating of a plant to itself (silks of the ear of a plant are fertilized with pollen from the same plant). Sib-mating is a mild form of inbreeding. In a naturally cross-pollinated crop like maize, selfing causes a reduction in vigor and fecundity. The former is evidenced by a reduction in height and robustness, while the latter manifests as a reduction in ear size and number of kernels produced. Inbreeding also results in delayed flowering and it affects the levels of heterozygosity and homozygosity. For every generation of inbreeding, the level of heterozygosity reduces by half of the level of the previous generation with a corresponding increase in the level of homozygosity. After seven generations of inbreeding, percentage homozygosity attained is over 99%. On average, inbreeding to homozygosity results in about 25% reduction in height compared to the mean height of the parent population. Yield reduction is about 68%, while delay in days to tasseling is about 6.8 days. The theoretical levels of heterozygosity and homozygosity for each generation of inbreeding are presented in Table 6.1. Homozygosity is also referred to as inbreeding coefficient (F), which is expressed on a 0–1 scale.

At the early stages of the hybrid program in WCA, several studies were conducted on inbreeding (Fakorede et al. 1993). Five generations of inbreeding in TZSR-W were compared with the noninbred population for yield and agronomic traits. Inbreeding increased the number of days from planting to flowering (delayed maturity) but decreased the expression of all other traits (Table 6.2). For example, at complete inbreeding ($F = 1$), grain yield of this population would be reduced to about 1.35 t/ha, a reduction of about 80% relative to the noninbred population. Coefficients from the regression of mean values of the traits on the inbreeding coefficient (F) were essentially linear for grain yield, ear number, ear length, and kernel moisture at harvest (Table 6.2). In contrast, quadratic models made a large contribution to the total variance of flowering traits (tasseling, anthesis, silking) and, to a lesser extent, plant and ear heights. Grain yield and yield components were the most sensitive to inbreeding. On the other hand, several traits had little or no inbreeding

Table 6.2 Parameters from the regression of mean values of grain yield and agronomic traits at different generations of inbreeding on the coefficient of inbreeding in the TZSR-W maize population (Fakorede et al. 1993)

Trait	Model type	μ	β_1	β_q	R^2	ΔR^2
Days to tasseling	Linear	53.98	3.92	–	0.34	
	Quadratic	55.26	−10.23	14.54	0.65	0.31
Days to anthesis	Linear	57.46	3.06	–	0.30	
	Quadratic	58.36	−6.86	10.19	0.53	0.23
Days to silking	Linear	59.16	4.97	–	0.50	
	Quadratic	60.14	−5.87	11.14	0.67	0.17
Plant height, cm	Linear	212.14	−35.08	–	0.85	
	Quadratic	207.76	13.35	−49.76	0.97	0.12
Ear height, cm	Linear	108.18	−24.70	–	0.65	
	Quadratic	105.91	0.45	−25.84	0.69	0.04
Grain yield, t/ha	Linear	5.06	−3.71	–	0.98	
	Quadratic	5.17	−4.94	1.27	0.99	0.01
Ear number/plot	Linear	20.08	−10.36	–	0.97	
	Quadratic	19.91	−8.58	−1.83	0.98	0.01
Ear length, cm	Linear	17.02	−6.03	–	0.96	
	Quadratic	17.11	−7.08	1.12	0.97	0.01
Grain moisture, %	Linear	22.34	−4.46	–	0.92	
	Quadratic	22.39	−6.44	2.19	0.93	0.01

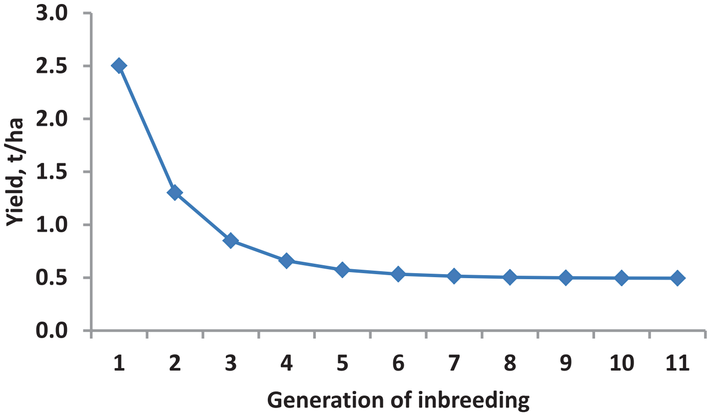


Fig. 6.1 Response of grain yield of TZSR-W-1 maize population to 11 generations of inbreeding (Adapted from Fakorede et al. 1993)

depression even after five generations of inbreeding. For example, at $F = 1$ plant and ear heights were only about 17% and 22% lower than the original population. An example is illustrated in Fig. 6.1, in which yield reduces in a quadratic manner as the generation of inbreeding increases.

Table 6.3 Parameters from the regression of mean values of grain yield at different generations of inbreeding on the coefficient of inbreeding for five lines derived from TZSR-W maize population (Fakorede et al. 1993)

Line	Model type	M	β_l	β_q	R^2	ΔR^2
11	Linear	4.94	−5.10	–	0.94	
	Quadratic	5.11	12.21	7.82	1.00	0.06
13	Linear	5.02	−2.89	–	0.81	
	Quadratic	5.12	−6.88	4.40	0.86	0.05
21	Linear	5.13	−4.09	–	0.99	
	Quadratic	5.11	−3.34	−0.83	1.00	0.01
36	Linear	5.05	−3.77	–	0.96	
	Quadratic	5.12	−6.32	2.81	0.98	0.02
41	Linear	5.06	−2.74	–	0.64	
	Quadratic	5.13	−5.70	3.26	0.67	0.03

Hallauer and Sears (1973) conducted one of the most extensive studies on changes associated with inbreeding in maize. In their study, linear model accounted for more than 92% of the variation in grain yield, plant height, and ear height, whereas quadratic model was significant for some other traits, including kernel row number, ear diameter, and kernel depth. To a large extent, the results from studies conducted in WCA corroborate those obtained by Hallauer and Sears (1973) on US Corn Belt maize germplasm.

Results from these studies also showed that response to inbreeding differs among lines and populations. Inbreeding depression associated with the S_0 to S_5 generations of individual lines developed from TZSR-W was evaluated in field trials conducted at Ile-Ife. The rate of attainment of homozygosity for grain yield varied considerably among the lines (Table 6.3). The coefficient of linear regression, β_l, an indicator of the rate of inbreeding depression, varied from −5.10 t/ha for line 11 to −2.74 t/ha for line 41.

For quantitatively inherited traits in a population at linkage equilibrium, theoretical expectation after one generation of inbreeding by self-pollination (S_1) is a 50% reduction in the performance relative to the noninbred population (S_0) and about 94% after four generations of inbreeding (S_4). Data summarized in Table 6.4 showed that on average, inbreeding depression for grain yield at the S_1 generation of three maize populations was 41% and about 76% at the S_4 generation. All other traits had smaller inbreeding depressions. In this study also, the performance of several traits changed very little with inbreeding, for example, silking date. The three populations differed substantially in their response to inbreeding (Table 6.4). TZSR-W-1 appeared to be the most sensitive to inbreeding.

Results of these inbreeding studies have several practical implications for maize breeding programs in sub-Saharan Africa. First, inbred lines extracted from the populations are not likely to be homozygous at most loci until many generations of inbreeding have been completed. Second, because inbreeding depression associated with plant and ear heights is small, hybrids produced from the inbred lines emanating

Table 6.4 Inbreeding depression (%) at the S_1 and S_4 generations of lines derived from TZSR-W-1, TZPB (FARZ 27), and TZB (FARZ 34) maize populations

	TZSR-W-1		FARZ 27		FARZ 34		Across pop.[a]	
Trait	S_1	S_4	S_1	S_4	S_1	S_4	S_1	S_4
Grain yield, t/ha	−42.3	−82.1	−35.0	−70.6	−45.3	−74.1	−40.9	−75.6
Ear number	−9.9	−45.8	−2.8	−30.4	−24.9	−35.9	−12.5	−37.4
Ear length, cm	−12.9	−29.4	−11.2	−27.0	−6.9	−16.8	−10.3	−24.4
Ear diam, cm	−11.6	−19.8	−2.2	−20.4	−4.9	−20.8	−5.9	−20.3
Stand count	−7.2	−34.5	−4.6	−11.2	−7.1	−42.7	−6.3	−29.5
Plant ht., cm	−14.6	−28.1	−8.3	−12.4	−1.7	−7.8	−8.2	−16.1
Silking date	+2.5	+3.4	+2.8	+7.9	+4.6	+7.0	+3.3	+6.1

[a] *Across pop* Across population

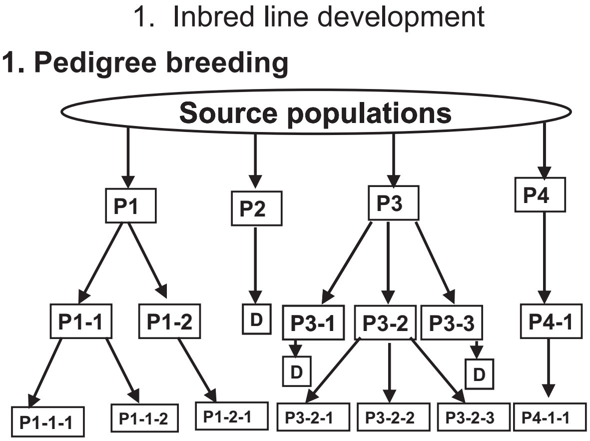
from these populations are likely to have undesirable heights. Third, inbreeding has little effect on flowering, an indication that the maturity classes of the lines are likely to remain more or less the same as that of the source populations. Fourth, undesirable linkage blocks are likely to remain unbroken in the many inbred lines, thus making such lines inherently low yielding in hybrid combinations. In other words, it will take quite a bit of effort to isolate outstanding inbred lines from these populations. If the populations used in these studies typify WCA maize germplasm, the breeders will need extra effort to produce inbred lines that will be high yielding and have desirable heights in hybrid combinations.

On the basis of these results, the following principles for inbred line development in SSA were established, and breeders have applied them over the years:

(i) A large number of plants (close to 1000) should be sampled from the source population for self-pollination.
(ii) Breeding methodology that includes intense selection during the inbreeding process would produce better inbred lines.
(iii) There should be deliberate selection against plant and/or ear heights during inbreeding.
(iv) Although hybrid performance of inbred lines may be evaluated in the relatively early stages of inbreeding, uniform, high-yielding inbred lines would be obtained only after several generations of inbreeding, perhaps S_6 or later.

High level of homozygosity implies fixation of genes and the traits they condition. In addition, selfing exposes deleterious recessive traits, allowing the plant breeder to practice selection against them. Since vigor loss of S_1 lines developed from populations improved by half-sib and full-sib recurrent selection is considerably less than those derived directly from the original population, it is recommended that germplasm for the development of inbred lines should preferably be those that have been exposed to some form of self-pollination such as the S_1 or S_2 family recurrent selection methods. In addition, if inbred lines are to be used to develop source populations, they should be those with the minimum number of undesirable traits.

Fig. 6.2 Diagrammatic scheme of the pedigree breeding method for inbred line development



Plants to be selfed are selected for vigor, freedom from diseases, and other agronomically desirable traits. Selection is also practiced at harvest since many attributes of importance cannot be ascertained at the time of pollination. Only selected ears are advanced for selfing. Kernels from selected ears are planted ear-to-row the following season. Selection of the best plants is practiced within and between progenies. During inbreeding, many progenies are lost due to gross deficiencies, while others are discarded because they lack appeal. Outstanding progenies are advanced further.

6.15 Methods for Inbred Line Development

Inbred line development methods used in maize breeding are pedigree, backcrossing, single-seed descent, gamete selection, and monoploids (homozygote diploids, maternal; androgenesis, paternal; gametophyte factor; and pollen culture). The first three are most commonly used in SSA and these will be presented here. The others require some level of sophisticated equipment and have not been used in our program. Some detailed description of the three methods may be found in Hallauer et al. (2010).

Pedigree

The pedigree method is the most common approach for developing inbred lines. Individuals in segregating generations are selected based on desirable agronomic traits; pollen shed-silking synchrony; resistance to diseases, pests, and lodging; and desirable plant type while maintaining records on parent–progeny relationships and agronomic characteristics of selected lines. A diagrammatic scheme of the pedigree method is shown in Fig. 6.2.

Backcross

For the transfer of a one-gene trait from one parent to another, backcross selection has an advantage over pedigree selection because 50% of the plants for backcross selection would be homozygous for the trait compared to only 25% of the plants for pedigree selection in the first selfing generation. Backcrossing also may be used for traits that are not controlled by one or two genes, e.g., incorporation of exotic germplasm into adapted populations. The backcross method has been used successfully in the IITA maize breeding program in developing several BC_2 populations from elite early × late/intermediate crosses to increase drought tolerance and/or *Striga* resistance in extra-early and early-maturing populations; early and extra-early stress-tolerant hybrids have been developed using the pedigree method. Furthermore, extra-early × intermediate crosses have been used successfully to develop earlier versions of intermediate and later-maturing populations in the IITA program. It is important in these instances to ensure that larger plant numbers are used to sample the array of genotypes in the recurrent and nonrecurrent parental populations. For example, novel *Striga*-resistant genes from the IITA intermediate-maturing yellow-grained inbred lines derived from *Zea diploperennis*, TZSTRI 108, were crossed to the extra-early yellow population, TZEE-Y Pop STR C4, in 2008 to improve the level of resistance to *S. hermonthica*. This was followed by two generations of backcrossing to the yellow population during the growing seasons of 2009 and 2010 to recover earliness. The BC_2S_1 families were evaluated under *Striga* infestation at Abuja and Mokwa in Nigeria in 2010, and the best families were introgressed into the respective populations. Also, the BC_2S_1 involving each population was planted in the 2010 major season nursery for advancement through selfing to the BC_2S_2 stage. Subsequently, the BC_2S_2 families of each population were planted in September 2010 and advanced by selfing to the BC_2S_3 stage. At the S_4 stage, 250 lines per se were evaluated at Mokwa under artificial infestation with *S. hermonthica* seeds collected from sorghum [*Sorghum bicolor* (L.) Moench] fields near Mokwa. About 5000 germinable *Striga* seeds per maize hill were used for the artificial infestation. The yield performance of the S_4 lines per se, *Striga* damage rating, number of emerged *Striga* plants, ear number, and other desirable agronomic characters were used as criteria for selecting 90 S_4 lines, which were also advanced to the BC_2S_5 in 2011. The BC_2S_5 inbreds were advanced to the BC_2S_6 stage during the dry season of 2012. The BC_2S_6 inbreds were evaluated under drought at Ikenne in 2010. The BC_2S_6 inbreds were evaluated under *Striga* infestation during the growing season of 2012 and also screened for drought tolerance under drought stress at Ikenne during the 2012/2013 dry season and heat stress at Kadawa during the dry season of 2013. Results showed that the set of yellow inbreds possessed wide variability for grain yield and other adaptive traits under each stress and across multiple stresses. Fourteen yellow inbreds were identified as multiple stress tolerant based on the IITA multiple stress tolerance base index (MI). Inbreds TZdEI 24, TZdEI 14, and TZdEI 17 were identified as the best in terms of grain yield across stresses. The three inbreds outyielded significantly the tolerant checks under multiple stresses (Table 6.5). The inbreds have been used for the development of several outstanding hybrids for commercialization in WCA.

Table 6.5 Mean values of grain yield and agronomic traits of 25 early yellow inbred lines evaluated under multiple stresses (drought, low N, and *Striga* infestation) at 6 environments in Nigeria between 2012 and 2014

Inbred	Grain yield, kg/ha				Days to silk	Days to anthesis	ASI	Plant height, cm	Husk cover	Plant aspect	Ear aspect	Ear rot	Ears per plant	Stay-green characteristics	*Striga* damage rating at 10 WAP	Emerged *Striga* count at 10 WAP	MI
	ACROSS	DT	LN	STR	ACR	ACR	ACR	ACR	ACR	ACR	ACR	ACR	ACR	DT&LN	STR	STR	
TZdEI 24	2116	1647	2503	1810	56	55	2	111	2.7	3.0	3.4	2.7	0.8	3.3	4.5	29	10.5
TZdEI 14	1796	471	2295	2124	57	55	1	114	2.2	3.1	3.4	2.0	1.0	3.8	3.5	29	9.8
TZdEI 17	1718	706	1986	2194	59	58	1	131	2.4	2.8	3.4	3.3	0.9	4.0	4.0	27	9.0
TZdEI 21	1344	471	1706	1492	57	57	1	121	2.5	2.8	3.4	1.7	1.0	3.8	4.5	36	6.9
TZdEI 1	1425	784	1909	1098	58	56	2	97	3.0	3.0	3.8	2.3	0.8	3.5	5.0	36	4.6
TZdEI 23	1392	941	1922	784	59	59	1	134	2.9	3.1	3.6	0.3	0.7	4.3	6.0	25	2.9
TZdEI 28	1173	471	1093	2037	56	56	1	104	2.7	3.8	3.9	2.2	1.0	4.3	4.0	18	2.9
Check 1-TZEI 17	1109	784	989	1674	54	53	1	89	2.8	3.3	3.8	1.0	0.8	3.8	4.5	20	2.9
TZdEI 29	1029	784	696	1941	55	55	0	91	2.5	3.4	3.8	2.3	1.0	5.0	4.0	21	2.3
TZdEI 16	1325	596	1959	784	61	60	1	131	2.7	3.1	3.9	1.3	0.7	4.0	5.5	29	2.2
TZdEI 22	1013	627	1006	1412	57	57	1	111	3.1	3.5	3.9	3.0	1.0	4.8	4.5	31	1.0
TZdEI 38	1071	361	1649	627	61	60	1	127	2.8	2.9	3.9	1.7	0.6	3.7	5.5	36	0.7
TZdEI 27	980	471	1097	1255	57	57	0	98	2.4	3.4	3.8	2.3	0.8	5.2	3.5	25	0.6
TZdEI 15	925	784	1145	627	57	55	2	106	3.0	3.1	4.1	1.3	0.8	3.5	6.0	36	0.6
TZdEI 5	971	596	963	1363	57	58	0	85	2.6	3.7	4.4	3.2	1.0	5.0	5.0	14	0.1
Check 2-TZEI 23	772	627	761	941	64	59	5	97	2.5	3.3	4.1	0.8	0.6	4.3	4.5	15	−1.4
TZdEI 34	986	784	763	1634	57	57	1	111	2.8	3.7	3.8	3.3	0.9	5.8	4.5	36	−1.6
TZdEI 26	807	1123	660	784	57	57	1	119	3.1	3.5	3.8	1.5	0.8	5.2	5.5	22	−1.9
TZdEI 12	807	941	594	1098	59	59	1	102	3.1	3.8	4.1	2.8	0.8	5.3	4.5	20	−2.7

TZdEI 9	938	627	1249	627	56	57	1	114	3.1	3.4	4.0	1.8	0.7	5.5	6.5	18	−3.0
TZdEI 39	1070	1397	1205	471	58	56	2	118	3.0	3.4	4.2	1.5	0.7	5.0	7.0	32	−3.2
TZdEI 2	750	235	913	941	60	59	1	117	2.9	3.6	4.1	3.0	0.8	5.2	6.0	23	−3.7
TZdEI 37	854	471	1002	941	60	58	3	124	2.7	3.7	4.1	1.7	0.7	5.3	5.5	30	−4.2
TZdEI 18	856	784	1084	471	57	55	3	112	4.5	3.5	4.2	1.0	0.7	5.3	8.0	16	−4.9
TZdEI 19	791	627	876	784	61	60	1	107	3.2	4.1	4.5	2.0	0.8	5.5	6.0	27	−6.3
TZdEI 8	542	314	613	627	60	58	2	108	3.0	3.7	4.6	2.7	0.5	5.3	8.0	45	−11.1
TZdEI 40	911	627	1195	627	59	58	2	107	3.0	4.5	5.1	0.2	0.5	5.3	9.0	49	−13.3
MEAN	**1092**	**706**	**1253**	**1154**	**58**	**57**	**1**	**111**	**2.9**	**3.4**	**4.0**	**2.0**	**0.8**	**4.6**	**5.4**	**27**	
LSD	**518.9**	**1040**	**738**	**810**	**2.0**	**1.6**	**1.1**	**15.6**	**1.2**	**0.6**	**0.6**	**1.7**	**0.2**	**1.2**	**1.7**	**24**	
P stat for Genotype	**	**Ns**	**	**	**	**	**	**	**ns**	**	**	**	**	**	**	**ns**	
P stat for Stress	**	–	–	–	**	**	**	**	**	**	**	**	**	**	–	–	
P stat for G × S	**	–	–	–	**	**	**	**ns**	**ns**	**	**	**	**	**	–	–	

*, **Significant at 0.05 and 0.01 levels of probability, respectively

ns not significant, *ACR* across multiple stresses, *DT* drought stress, *LN* low soil nitrogen, *STR* artificial *Striga* infestation, *MI* multiple stress tolerance base index

Backcrossing has also been an effective and convenient method for the introgression or the improvement of specific traits into elite inbred lines. Furthermore, backcross breeding method has also been used for the conversion of normal endosperm maize to quality protein maize (QPM) and the yellow endosperm populations into provitamin A populations from which outstanding inbred lines have been developed. Also, the backcross method has been used for the adjustment of morphological characters, color characteristics, and simply inherited traits such as earliness, plant height, seed size, and shape. The major consideration in the use of backcross method is that the character under transfer needs to be of moderate to high heritability. A character governed by several genes is more easily transferred by backcrossing than a character of low heritability governed by one or two genes. For characters of low heritability and governed by one or two genes, it is important to use a large population size for successful transfer of the genes.

Single-Seed Descent

The single-seed method involves growing a large sample of seeds from a source population and self-pollinating each plant. At the maturity stage, only one seed is picked from each selfed ear and bulked. The bulked single seeds are then planted in the next generation of inbreeding, and the procedure is repeated. This method has several advantages: (i) a large number of inbred lines can be developed economically in terms of smaller nursery space, labor, and expenses; (ii) one seed is saved from each genotype in successive generations of inbreeding until approximate homozygosity is reached; (iii) seeds from the same ear can be used for different methods of inbreeding; and (iv) wide genetic diversity is maintained from generation to generation. Because there is little or no selection pressure applied by using this method, there is a tendency of carrying mediocre lines during the process of inbreeding. This is a major disadvantage of this method. Also, because there are no pedigree records, any line lost due to external factors cannot be replaced. Therefore, in spite of its advantages, the single-seed descent method is not used extensively in maize breeding. One way to reduce the negative impact of the disadvantage is to harvest each ear into labeled envelope, plant a three- or four-plant hill per ear, and store the remnant seed in case of the need to supply the missing hills. This modification is more expensive than the original method and has also not been used to any great extent in maize breeding. If and when used, seed supplies of the progenies obtained by single-seed descent are increased for evaluation in replicated tests at the desired level of homozygosity.

The pedigree and backcross methods use the principles of the single-seed descent method because selected plants in selected progenies are propagated to the next generation. The distinction is that artificial selection is maximized in the pedigree and backcross methods and minimized in single-seed descent. The single-seed descent method has been used in studies to estimate genetic parameters in Iowa Stiff Stalk Synthetic (BSSS) maize population in Iowa, USA (Hallauer and Sears 1973), and inbreeding depression of inbred lines from TZSR-W at Ile-Ife, Nigeria, after five generations of inbreeding (Fakorede and Ajala 1986). In the latter study, appreciable inbreeding depression had occurred at the S_2 generation with little additional

Table 6.6 Inbreeding depression (%) for agronomic traits and grain yield of TZSR-W maize population at two levels of inbreeding using single-seed descent and pedigree selection methods

	S_2		S_5	
	Single-seed descent	Pedigree selection	Single-seed descent	Pedigree selection
Silking	5.0	6.5	6.6	7.4
Plant height	−21.3	−29.6	−26.4	−28.1
Ear length	−27.5	−28.9	−29.4	−29.4
Ear diameter	−14.4	−15.6	−16.7	−19.8
Ear number	−43.8	−49.9	−49.8	−45.8
Grain yield	−73.6	−75.3	−79.0	−84.1

changes from S_2 to S_5 (Table 6.6). For example, yield decreased by 73% from S_0 to S_2 but by an additional 5% from S_2 to S_5. Similar trends were obtained for other traits, thus providing further evidence that most traits were near fixation as from S_2. Values of inbreeding depression obtained using single-seed descent and those obtained through pedigree selection for the same population were quite similar (Table 6.6). Fakorede and Ajala (1986) concluded that inbred lines from TZSR-W may be tested for combining ability at the S_2 generation to identify high-performing lines and continued inbreeding to S_5 or later generations would only be necessary to ensure precise repeatability of the lines or for specific genetic studies. In the SSA national programs where human and financial resources are limited, the modified single-seed descent method used by Fakorede and Ajala (1986) may be preferred over other inbred line development methods.

6.16 Testing Inbred Lines in Hybrid Combinations

Following the development of inbred lines, the next task is to identify pairs of inbred lines that produce high-yielding hybrids. While it is desirable to evaluate the developed lines for per se performance, the latter does not provide information on those that are capable of giving high yield in hybrid combinations. Consequently, the developed inbred lines need to be crossed in all possible combinations, and the crosses should be evaluated in replicated trials in several locations to identify the pair with the highest yielding potential. Crossing in all possible combinations is known as diallel. The number of inbred lines and F_1 hybrids produced from them is related by the formula $F_1 = n(n - 1)/2$, where n is the number of inbred lines. This formula does not make provision for reciprocals. In effect, progenies obtained from the seeds of the cross between A and B, when A is male and B is female and vice versa, are considered similar and could, therefore, be bulked. The number of single-cross hybrids increases geometrically with the number of inbred lines. Table 6.7 shows the number of single-cross hybrids obtained with different numbers of inbred lines.

Table 6.7 Number of hybrids obtainable when inbred lines are crossed in all possible combinations

No. of inbred lines (*n*)	No. of hybrids
10	45
20	190
100	4950
500	124,750

Table 6.7 shows that while the development of inbred lines can be demanding, the greater challenge is in producing and testing the resulting hybrids. Plant breeders have devised strategies to overcome this problem. The strategy aims to identify fewer inbred lines for all possible crosses to be evaluated in hybrid trials.

6.17 Testcross or Topcross Evaluation

At a certain stage of inbreeding, lines with good agronomic characteristics are crossed to a common parent that is referred to as tester. This approach, known as testcross or topcross evaluation, has the advantage of yielding fewer hybrids for evaluation. The number of hybrids to be evaluated is the same as the number of lines. With a common tester, the differences in performance of resulting hybrids are attributed to the differences in the combining ability of the lines. Two concepts of combining ability are useful in the testing of lines. These are general combining ability (GCA) and specific combining ability (SCA). The use of GCA is applicable when the tester is an open-pollinated variety. Test for GCA usually commences at S_3 or S_4 stage when the level of homozygosity is between 87.5% and 93.75%. Studies have shown that the average yield obtained from a wide array of cross combinations is correlated to GCA. It is, thus, advantageous to use a heterogeneous tester like an open-pollinated variety at the preliminary stage of inbred–hybrid development. Evaluation of topcrosses is done in two replications in few locations. After this stage, only inbred lines with high GCA are advanced to the next stage of inbreeding. Specific combining ability (SCA) refers to the contribution of an inbred line to superior yield in specific combinations. When inbred line A shows high yield only in combination with inbred line B but does not show high yield with inbred lines C, D, E, and F, it could then be inferred that inbred line A owes it superior performance in the cross with B more to SCA and less to GCA.

The topcross test helps to reduce developed inbred lines to a number that can be handled in a diallel. After five or six generations of inbreeding, every plant of a line is similar in appearance (since homozygosity at S_5 is greater than 95%), but differences among lines are large. At this time selfing is discontinued and plants of a line may be sib-mated. Diallel crosses help to identify the best pair of inbred lines for the production of single crosses and also provide estimates of GCA and SCA of the inbred lines used. In instances where superior inbred lines already exist, it may be advantageous to use the latter as testers. The usefulness of a tester lies in its ability to help the plant breeder identify lines with good GCA and SCA. The inbred line with good pollen production is used as the male parent, while that with the best ear, seed characteristics, and standability is used as the female parent. The few inbred lines in the final stage of the hybrid development can also be used to develop three-way and double crosses.

The number of three-way crosses and double crosses that can be produced from n number of inbred lines may be determined as follows:

$$\text{No. of three-way crosses} = \left[n(n-1)\times(n-2)\right]/2$$

$$\text{No. of double-crosses} = \left[n(n-1)\times(n-2)\times(n-3)\right]/8$$

For example, 25 inbred lines will produce 300 single crosses, 6900 three-way crosses, and 37,950 double crosses. As with single crosses, when the numbers of inbred lines are large, the number of three-way and double crosses is too large to be produced and evaluated. Jenkins (1934) proposed a formula for predicting the performances of three-way and double crosses from the performance of single crosses derived from their inbred parents. Yields of single crosses are nowadays routinely used to predict the yields of double crosses. The yield of a double cross can be predicted from the mean yield of the four non-parental single crosses as follows:

$$\text{Yield of}\left[P_1\times P_2\right]\left[P_3\times P_4\right] = 0.25\left[(P_1\times P_3)+(P_1\times P_4)+(P_2\times P_3)+(P_2\times P_4)\right]$$

Evaluation in one season or 1 year is inadequate for the purpose of selection. Selection of hybrids is done after evaluation in multiple locations for 2–3 years. Broadly adapted and superior hybrids are thereafter identified and released. Arrangements are made with private seed companies for the multiplication of the parental lines as well as production of seeds of the hybrids for sale to farmers.

6.18 Inbred–Hybrid Development Program at IITA

Although inbred line development at IITA started in the early 1970s, the objective was to use the lines for the production of synthetic varieties. Beginning from 1979, greater attention was focused on the development of inbred lines for the production of experimental hybrids (Kim et al. 1993; Kim 1997). One important principle of hybrid maize research is that the highest-yielding hybrid combinations adapted to the tropical environments are produced from crosses of lines developed from different races of maize (Wellhausen 1977). Wellhausen had identified four outstanding racial complexes for the improvement of maize production in the tropics, namely, Tuxpeño, a purely dent type that originated from the Gulf of Mexico, and its related Caribbean and US dents; Cuban flints; Coastal Tropical Flints; and ETO. The latter three races are all flint and are more closely related to one another than to Tuxpeño. Although crosses involving pairs of the three races exhibit considerable heterosis, crosses involving Tuxpeño and the three flints are more strikingly vigorous and higher yielding and exhibit exceptionally strong heterosis. IITA identified outstanding inbred lines from Tuxpeño dent; Caribbean flint; material from other parts of the tropics and subtropics, especially through CIMMYT in Mexico; temperate material from the US Corn Belt; lowland germplasm; mid-altitude germplasm; and a host of other sources (Kim 1997). Emphasis was on intermediate/late maturity germplasm.

In 1982, the Federal Government of Nigeria provided a special hybrid maize research grant to IITA to develop within 3 years, hybrid maize varieties for Nigeria (Kim et al. 1985). At that time, IITA had already developed over 2000 lines at different levels of inbreeding up to the S_4. In collaboration with their counterparts from several national institutions, which together constitute the national agricultural research and extension system (NARES) of Nigeria, scientists from IITA took the challenge and provided the much-needed coordination and leadership for hybrid maize production in Nigeria and, later, in other countries of the WCA sub-region. Progress toward the development of hybrids was rapid, and in 1984, experimental hybrids were tested in a total of about 150 ha of farmers' fields located all over Nigeria. On average, hybrids were 25% higher yielding than the best OPVs in the forest and 43% in the savanna zones. The best farmers recorded hybrid yields of 9.4 and 11.8 t/ha in the forest and savanna agroecology, respectively. In 1985, Nigerian farmers planted about 6000 ha of hybrid maize (Kim et al. 1997; Fakorede et al. 2001). Since that time, inbred–hybrid maize development has become an integral part of the IITA Maize Improvement Program, and this has extended to the national maize programs of several countries in the sub-region.

One important impact of hybrid maize in Nigeria is the dramatic shift in extensive production from the rainforest and forest–savanna transition zones (that used to be the "maize belt" of Nigeria) to the northern Guinea savanna (NGS) and mid-altitude savanna (MAS) zones. The demand for maize increased tremendously in the savannas, and it became necessary to develop varieties adapted to the relatively short season in much of this agroecology. Therefore, the development of early and extra-early varieties, which had been initiated on a relatively small scale at IITA, was devolved to the regional maize network of the Semi-Arid Food Grain Research and Development (SAFGRAD) project. The network later became autonomous and was named West and Central Africa Collaborative Maize Research Network (WECAMAN) with IITA as the executing agency. The coordinating office located in the facilities of the West Africa Rice Development Association (WARDA) in Côte d'Ivoire. WECAMAN/IITA developed many populations and varieties in the two maturity groups and eventually started an inbred–hybrid development program as well.

Early and extra-early inbred line development program was initiated in 1994 by WECAMAN/IITA from several broad-based *Striga*- and MSV-resistant extra-early populations (TZEE-W Pop STR C_0 and TZEE-Y Pop STR C_0), crosses (TZEE-W SR BC_5 × 1368 STR, TZEE-W Pop STR × LD, and TZEF-Y SR BC_1 × 9450 STR), and early inbreds from four diverse germplasm sources with resistance to *Striga* and MSV and tolerance to drought (TZE-W Pop DT STR C_0, TZE-Y Pop DT STR C_0, TZE Comp 5-Y C_6, and TZE-W Pop × 1368 STR) (Badu-Apraku et al. 2006b, c). Selected S_1 lines extracted from each population were evaluated at Ferkessédougou (9°3°, 5°10′W, mean annual rainfall of 1400 mm) and Sinématiali (9°37′N, 3°04′W, mean annual rainfall of 1200 mm), Côte d'Ivoire, during the rainy season of 1997. At Ferkessédougou, the lines were evaluated under artificial *Striga* infestation [about 5000 germinable *Striga* seeds per maize hill (Kling et al. 2000)], and outstanding S_1 lines selected from each population were taken through 6 cycles of pedigree inbreeding and selection under artificial *Striga* infestation. At the S_4 stage, 250–300 lines derived from each population were crossed to the corresponding base population as the tester. The S_4 lines per se and the testcrosses were evaluated at Sinématiali under *Striga*-free conditions and at Ferkessédougou under artificial infestation with *S. hermonthica* seeds collected from sorghum [*Sorghum bicolor* (L.) Moench] fields near each testing site. The yield performance of the lines per se, their combining abilities for grain yield, *Striga* damage rating, *Striga* emergence count, ear number, and other desirable agronomic characters across the two locations were used as criteria for selecting 90–100 S_4 lines, which were advanced to S_6. Eighty-one lines selected from all source populations were evaluated during the dry and rainy seasons of 2001 under artificial infestation with *S. hermonthica* and under non-infested conditions at Ferkessédougou. In the dry season trial, the maize inbred lines were irrigated up to physiological maturity using an overhead sprinkler irrigation system, which applied 12 mm of water per week. Irrigation water was withdrawn based on the results of the progeny yield trials of 1997 rainy season. The selected S_1's from each population had undergone six cycles of pedigree inbreeding and selection under artificial *Striga* infestation. At the S_4 stage of inbreeding and selection, 250–300 lines derived from each population were evaluated per se and in testcrosses at Ferke and Sinématiali (9°37′N, 3°04′), Côte d'Ivoire, for general combining ability, with the same population as the tester. Each source population which is broad-based and adapted to the growing environments in WCA served as the tester for general combining ability for the lines derived from it. According to Hallauer and Miranda (1988), in selection for GCA, a broad-based heterogeneous population is used as a tester. It can be the parental population or any broad genetic base (synthetic or open-pollinated variety), unrelated population. Apart from that, it is common practice in maize breeding to use the parental population as a tester when proven broad-based testers are not available as in the case of WCA. Based on the combining ability for grain yield, desirable agronomic characters, *Striga* resistance, tolerance to drought, and the yield performance of the lines per se across the two locations, 8–10 S_4 lines from each population were selected and separately randomly mated to form synthetic varieties. Furthermore, 90–100 S_4 lines were selected based on the test performance and advanced to the S_6 stage using pedigree selection under artificial *Striga* infestation and induced moisture stress. Selection for high grain yield under *Striga* infestation was based on an index of characters including *Striga* damage rating, *Striga* emergence count, ear number, grain yield under artificial *Striga* infestation, and grain yield and ear rot ratings under non-infested conditions. On the other hand, under drought stress, a base index integrating high grain yield, anthesis–silking interval, number of ears per plant, and plant and ear aspects was adopted. Through this program, several S_6 inbred lines and synthetic varieties were developed from each population (Badu-Apraku et al. 2006a, b, c). The grain yield and characteristics of some of the released early and extra-early inbreds are presented in Tables 6.7 and 6.8.

Table 6.8 Mean characters of 17 extra-early inbred lines evaluated under *Striga* infestation and *Striga*-free conditions at Abuja, Mokwa, in 2004 and Ferkessédougou in 2001 and 2002

Inbred line	Parentage	Grain yield[a] (kg/ha)		Days to silking	Plant height (cm)	*Striga* emergence count (10 weeks)	*Striga* rating[b] 10 weeks	Grain texture	Grain color
		Non-inf	Inf	Inf	Inf				
TZEEI 1	TZEE-W SR BC$_5$ × 1368 STR S$_7$ INB 35	1906	1524	57	106	31	5	Flint	White
TZEEI 2	TZEE-W SR BC$_5$ × 1368 STR S$_7$ INB 40	845	743	55	116	34	4	Flint	White
TZEEI 3	TZEE-W SR BC$_5$ × 1368 STR S$_7$ INB 76	562	433	54	84	43	5	Flint/Dent	White
TZEEI 4	TZEE-W SR BC$_5$ × 1368 STR S$_7$ INB 85	627	535	52	114	45	5	Flint	White
TZEEI 5	TZEE-W SR BC$_5$ × 1368 STR S$_7$ INB 91	520	254	55	109	26	5	Flint	White
TZEEI 6	TZEE-W SR BC$_5$ × 1368 STR S$_7$ INB 100	650	413	58	110	27	5	Flint	White
TZEEI 7	TZEE-W SR BC$_5$ × 1368 STR S$_6$ INB 55A −1-2	647	568	57	112	55	4	Flint	White
TZEEI 8	TZEE-W SR BC$_5$ × 1368 STR S$_6$ INB 55B −1-2	715	681	56	111	56	4	Flint	White
TZEEI 9	TZEF-Y SR BC$_1$ × 9450 STR S$_6$ INB 8A	2498	2486	60	96	10	4	Flint	Yellow
TZEEI 10	TZEE-W Pop × LDS$_6$ (Set A) INB 21	3966	3070	62	116	17	4	Flint/Dent	White
TZEEI 11	TZEE-W Pop × LDS$_6$ (Set A) INB 37	2682	1716	63	98	6	4	Flint	White
TZEEI 12	TZEE-W Pop × LDS$_6$ (Set A) INB 26	3528	2163	62	118	29	5	Flint	White

TZEEI 13	TZEE-W Pop × LDS$_6$ (Set A) INB 27	2098	1933	63	111	16	4	Flint	White
TZEEI14	TZEE-W Pop × LDS$_6$ (Set A) INB 41	2349	1711	62	120	5	4	Flint	White
TZEEI 15	TZEE-W Pop × LDS$_6$ (Set B) INB 44	2180	1862	64	130	1	5	Flint	White
TZEEI 16	TZEE-W Pop × LDS$_6$ (Set A) INB 44	3236	3112	64	123	6	4	Flint	White
TZEEI 17	TZEE-W pop STR C0 S$_6$ INB 35 2-3	2260	1506	62	113	3	5	Flint	White
	TZEE-W SR BC$_5$ × 1368 STR S$_7$ INB 91 (Susceptible check)	1109	544	50	93	141	7	Flint	White
	Means	2358	1999	55	99	49	4		
	SE	330	380	3	10	4.7	0.7		

[a] Averaged across two to three locations and years

[b] Rating for host plant damage syndrome where 1 is little or no damage and 9 is severe damage due to *S. hermonthica*

PI nos PI numbers

6.19 Conclusions

Based on the experience with inbreeding in tropical germplasm, a number of principles for inbred line development in SSA have been established, and breeders have applied them over the years. These are (i) a large number of plants (about 1000) should be sampled from the source population for self-pollination; (ii) breeding methodology that includes intense selection during the inbreeding process would produce better inbred lines; (iii) there should be deliberate selection against plant and/or ear heights during inbreeding; and (iv) although hybrid performance of inbred lines may be evaluated in the relatively early stages of inbreeding, uniform, high-yielding inbred lines would be obtained only after several generations of inbreeding, perhaps S_6 or later stage. In order to continue to make gains in performance and diversity in maize germplasm in SSA, there is the need to broaden the tropical germplasm base through germplasm enhancement and introgression of local accessions to increase diversity as well as identifying exotic maize germplasm and improving adaptation through crosses with adapted elite germplasm. There is also a need for the establishment of a DH facility in IITA so that the maize programs in the WCA sub-region could take advantage of the DH facility to enhance inbred line development.

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Chapter 7
Genetic Diversity, Heterotic Grouping, and Testers in Hybrid Maize Production

7.1 Introduction

Heterosis is the genetic expression of the superiority of a hybrid in relation to its parents (Falconer and Mackay 1996; Miranda Filho 1999). Heterosis is important in maize breeding and is dependent on the genetic divergence of parental lines (Moll et al. 1965; Hallauer and Miranda 1988). The phenomenon is also influenced by the gene frequencies and the nonadditive gene action in the parental lines in a population cross (Falconer 1989). In maize, hybrid breeding remains the method of choice for attaining maximum genetic gains from heterosis. Van Oosterom et al. (1996) indicated that the nonadditive genetic effects responsible for heterosis can exert its influence under stress conditions. In contrast, Blum (1997) postulated that heterosis is a constitutive trait and does not require stress in order to be expressed. This appears to suggest that the expression of heterosis depends on genes that are expressed in genotypes irrespective of the stress conditions.

Two types of heterosis may be described: mid-parent or average heterosis, which is the increased vigor of the F_1 over the mean of the two parents, and high-parent or better-parent heterosis, also termed heterobeltiosis, which is the increased vigor of the F_1 over the better parent (Sinha and Khanna-Chopra 1975; Jinks 1983). Heterosis, usually considered to be synonymous with "hybrid vigor," is one of the primary reasons for the success of the commercial maize industry (Stuber 1994*)*. Although several economically important crops benefit from the manifestation of heterosis, both the genetic and physiological mechanisms underlying this phenomenon are still not fully explained (Hallauer and Miranda 1988; Tollenaar et al. 2004). Three major theories, including dominance, overdominance, and epistatic effects, have been proposed as the main theories to explain mechanisms underlying the phenomenon of heterosis (Hallauer and Miranda 1988; Singh 2005). However, it is generally accepted that heterosis, to a large extent, is due to dominance gene action

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(Singh 2005). To overcome many of the difficulties that are encountered in the interpretation of heterosis for complex traits, component analysis approaches have been used to study the effects of heterosis on grain yield (Sinha and Khanna-Chopra 1975). Grain yield has been partitioned, for instance, into ear number, kernel number, and kernel weight in an attempt to understand how heterosis influences grain yield (Sinha and Khanna-Chopra 1975).

The manifestation of heterosis depends on genetic divergence of the two parental varieties (Moll et al. 1965; Hallauer and Miranda 1988). Low heterosis for grain yield is observed for crosses among genetically similar germplasm and in crosses among broad genetic base germplasm (Beck et al. 1990, 1991; Crossa et al. 1990; Vasal et al. 1992). Higher levels of heterosis have been observed with increased divergence within a certain range, but such heterosis tended to decline in extremely divergent crosses (Moll et al. 1965; Prasads and Sikh 1986). The extent of genetic divergence of the parents is inferred from the heterotic patterns manifested in series of crosses (Moll et al. 1965; Hallauer and Miranda 1988; Miranda Filho 1999).

Heterosis in maize has been extensively studied. Hallauer and Miranda (1988) reported that mid-parent heterosis ranged from −3.6% to 72.0%, while better-parent heterosis ranged from −9% to 43.0%. The magnitude of heterosis has not changed during the hybrid period (Duvick 1999), even though the mean commercial maize grain yield has substantially increased during the period (Troyer 1990; Tollenaar and Wu 1999). Crossa et al. (1987) reported heterosis of 0% to 47.7%, in the better parent of a maize population. Beck et al. (1991) observed better-parent heterosis for grain yield ranging from −14.8 to 9.9% in crosses among CIMMYT's subtropical and temperate maize germplasm. Vasal et al. (1992) reported a maximum better-parent heterosis of 13% in diallel crosses among seven CIMMYT subtropical and temperate early-maturing maize inbred lines. Glover et al. (2005) reported better-parent heterosis of 46% in crosses among ten Chinese and US lines. In another study, an average heterosis of 167% for grain yield, 109% for 42 kernels weight per plant, and 12% for thousand kernel weight in maize were observed (Tollenaar et al. 2004).

Classification of maize inbreds into distinct heterotic groups is crucial to the development of superior hybrids, synthetics, pools, and breeding populations for tolerance to stresses such as drought, low N, and *Striga hermonthica*. Furthermore, an understanding of the genetic relationship among inbreds is invaluable in planning crosses, assigning lines to specific heterotic groups for the purpose of developing high-yielding synthetics and hybrids and for precise identification with respect to plant varietal protection (Hallauer and Miranda 1988).

7.2 Predicting Inbred–Hybrid Relationships

Identifying parental inbreds that produce superior hybrids is the most expensive and time-consuming stage in maize hybrid development program. This is because per se performance of maize inbreds for grain yield is not a good predictor of the performance of a single-cross hybrid. Precise prediction of single-cross hybrid value or heterosis between parental inbreds could, therefore, increase the efficiency of breeding programs. Therefore, accurate assessment of inbred lines in hybrid combinations under appropriate contrasting environments is crucial to the success of a hybrid program and the selection of parents for the development of synthetic varieties or introgression into elite source populations. Consequently, the IITA maize improvement program has spent considerable efforts and resources in the identification of inbred testers for single-cross hybrid development and production as well as the identification of single-cross testers as they facilitate the development of three-way and double-cross hybrids during the process of early generation testing. In the development of stress-tolerant hybrids, maize breeders need to consider inbred and hybrid relationships under stress and non-stress conditions. However, there have been contradictory reports on inbred–hybrid relationships under stress conditions. For example, Oyekunle and Badu-Apraku (2013) reported the absence of correlation between inbred line per se and hybrid performance under drought and optimal growing conditions, indicating that the performance of inbred lines cannot be used to predict their performance in hybrid combinations under the research conditions. These results are consistent with the findings of Lafitte and Edmeades (1995), but contrary to those reported by Betrán et al. (2003a, b). This implies the need to evaluate hybrids under stress conditions to identify superior hybrids for stress environments.

7.3 Genetic Diversity and Hybrid Performance

Information on the genetic diversity and heterosis of inbred lines is of great interest to maize breeders because it facilitates the identification of inbreds that would produce crosses exhibiting high levels of heterosis. The information makes it possible to develop productive hybrids without testing all possible hybrid combinations among the potential parents available in a hybrid program. Molecular markers are also useful in assessing the extent of genetic diversity within breeding materials (Semagn et al. 2012) because they are DNA based and are thus not affected by the environment or developmental stage of the species. Several studies have been conducted to examine the relationship between genetic distance and hybrid performance in maize using molecular markers (Smith et al. 1990; Betrán et al. 2003a, b; Menkir et al. 2010). The authors reported that marker-based genetic distance (GD) estimates can be used to reduce the cost of testing by avoiding the testing of crosses between related lines and discarding crosses with inferior performance based on prediction (Melchinger 1999). Information on the reliability of molecular markers in placing inbreds into heterotic groups is contradictory. For example, several workers have reported no significant correlation between genetic distance and hybrid yield (Shieh and Thseng 2006; Benchimol et al. 2008; Menkir et al. 2010). In contrast, positive relationship between mid-parent heterosis (MH) of F_1 grain yield and parental genetic divergence has been reported by Moll et al. (1965) and Paterniani and Lonnquist (1963). Similarly, Lanza et al. (1997) and Balestre et al. (2008)

reported a significant positive correlation between hybrid yield and molecular markers. It was concluded that the molecular markers used were very efficient in placing the inbred lines into heterotic groups. Furthermore, the relationship between GD and hybrid performance has been studied in maize using molecular markers (Lee et al. 1989; Godshalk et al. 1990; Smith et al. 1990; Betrán et al. 2003a; Makumbi et al. 2011). In a situation where heterotic groups are not well established, marker-based GD estimates could be invaluable in avoiding the production and testing of crosses between related lines, and crosses with low MH could be discarded based on prediction (Melchinger 1999). Akaogu et al. (2012) used 22 yellow-grained extra-early inbred lines selected from the panel of 43 extra-early inbreds of the IITA Maize Program based on their resistance to *Striga hermonthica* and/or drought tolerance to determine the effect of genetic diversity based on simple sequence repeat (SSR) of the extra-early inbreds on hybrid performance. Results showed that the correlation between the SSR-based GD estimates of parental lines and the means observed in F_1 hybrid under *Striga* infestation and optimal growing conditions were not significant for grain yield and other traits except ASI under optimal conditions. Grain yield of inbreds was not significantly correlated with that of F_1 hybrid. However, a significant correlation existed between F_1 hybrid grain yield and heterosis under *Striga* infestation. The absence of correlation between inbred line and hybrid performance indicated that the per se performance of inbred lines cannot be used to predict the performance of inbred lines in hybrid combinations. These results are consistent with the findings of Lafitte and Edmeades (1995) who reported no significant correlation between S_2 line grain yield and topcross grain yield under low N. In contrast, Betran et al. (1997, 2003b) reported significant correlations between inbred line and hybrid grain yield under drought stress and optimal conditions. The low correlation observed in this study could be due to the degree of inbreeding as suggested by Betrán et al. (2003b). The inbred lines used in this study are fixed (S_6) generations, and this may explain the low correlation observed. The lack of any definitive correlation between yields of parent inbred lines and their crosses indicated that selection for combining ability should be based on the performance of the lines in crosses rather than on the performance of inbred lines (Hallauer and Miranda 1988). The low correlations observed in this study emphasized the need to evaluate hybrids under stresses to identify superior hybrids for contrasting environments.

For assessment of genetic diversity, molecular markers have been generally superior to morphological, pedigree, heterosis, and biochemical data (Melchinger et al. 1991; Melchinger 1993). Molecular markers are a powerful complement to help define heterotic groups and to examine the relationships among inbred lines at the DNA level (Smith et al. 1997; Senior et al. 1998; Melchinger 1999). Genetic diversity studies using DNA fingerprinting techniques have become simple and efficient to detect sufficient polymorphisms in various crop species including maize (Smith and Smith 1992; Pejic et al. 1998). Molecular markers are not influenced by environmental factors and are also fast, efficient, and more sensitive than field testing to detect large numbers of distinct differences between genotypes at the DNA level (Smith and Smith 1992; Westman and Kresovich 1997; Melchinger 1999).

Various molecular marker types have been used to investigate relationships among maize inbred lines from different heterotic groups (Smith et al. 1997; Xia et al. 2004, 2005). The most commonly used marker methods in maize are restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNA (RAPD), simple sequence repeats (SSRs), and single nucleotide polymorphisms (SNPs). However, with the development of many DNA marker technologies, there is the need to determine the most suitable for various applications in plant genetics and breeding. Molecular markers differ in efficiency, complexity, and cost-effectiveness (Yang et al. 1996; Pejic et al. 1998). Polymerase chain reaction (PCR)-based markers are designed to amplify fragments that contain a microsatellite using primers complementary to unique sequences surrounding the repeat motif (Weber and May 1989).

Among the markers used in genetic diversity studies, SSR markers are superior to other marker types in terms of reliability, reproducibility, discrimination, standardization, and cost-effectiveness (Smith et al. 1997; Melchinger 1999). The microsatellite markers or SSRs are DNA markers with short stretches of tandemly repeated di-, tri, or tetranucleotide motif (Weber 1990). They are also known as short tandem repeats (STRs) or simple sequence length polymorphisms (SSLPs) (Tanya et al. 2001). Microsatellite markers are characterized by great abundance (Matsuoka et al. 2002), high variability (Schug et al. 1998), and even distribution throughout a wide range of genomic regions (Liu et al. 1996; Senior et al. 1996). These markers are codominant, highly polymorphic, and multiallelic and have become the markers of choice for genetic analysis in crops (Gupta and Varshney 2000).

In maize, microsatellites have proved to be invaluable tool for genome mapping (Taramino and Tingey 1996), population and conservation genetics studies (Powell et al. 1996), property rights protection (Kubik et al. 2001), marker-assisted selection (Weising et al. 1998), and diversity measurements (Warburton et al. 2002; Xia et al. 2004, 2005; Legesse et al. 2007). SSRs can provide greater power of discrimination than RFLP markers and can reveal genetic associations that reflect the pedigree of the inbred lines (Smith et al. 1997; Pejic et al. 1998). SSR markers also have the power of distinguishing between closely related inbred lines (Smith et al. 1997; Legesse et al. 2007).

The differences in the number of repeat motif are readily assayed by measuring the molecular weight of the resulting PCR fragments. As the differences may be as small as two base pairs, the fragments are separated by electrophoresis on polyacrylamide gels or using capillary DNA sequencers that provide sufficient resolution. Microsatellites have also proved useful for classification of lines into heterotic groups (Enoki et al. 2002).

Genetic diversity in relation to hybrid performance and heterosis has been studied extensively in maize. Moll et al. (1965) reported positive correlations between morphological markers-based genetic diversities of the parents with heterosis in maize hybrids. However, morphological markers have shortcomings in detecting differences among closely related genotypes and are influenced by prevailing environmental conditions (Smith and Smith 1992). Genetic distance based on molecular markers has been suggested as a tool for grouping of similar germplasm as a first step in identifying promising heterotic patterns (Melchinger 1999). Several reports have demonstrated the high correlation between genetic distance and hybrid performance in maize (Lee et al. 1989; Smith et al. 1990; Betrán et al. 2003a; Xu et al. 2004; Makumbi 2005; Kiula et al. 2008). However, contrary to these reports, other workers have reported that genetic distance measures are of limited use in predicting hybrid performance, heterosis, and SCA of single crosses (Melchinger et al. 1990; Makumbi 2005; Legesse et al. 2007). Drinic et al. (2002) reported that SSR markers provide an effective method for predicting hybrid performance and heterosis. In general, genetic distance estimate is more efficient for the prediction of hybrid performance between closely related inbred lines than in crosses between distantly related inbred lines (Melchinger 1999).

Molecular genetic markers constitute a powerful tool to delimit heterotic groups (Melchinger 1999). Estimates of genetic diversity and distance among tropical maize lines as well as correlation between genetic distance and hybrid performance would be useful for determining breeding strategies, classifying inbred lines, defining heterotic groups, and predicting future hybrid performance (Betrán et al. 2003a). Molecular analyses in conjunction with morphological and agronomic evaluation of germplasm are recommended because these provide complementary information and increase the resolving power of genetic diversity analyses (Singh et al. 1991).

Accurate assessment of the levels and patterns of genetic diversity is very important in crop breeding for (i) an analysis of genetic variability in cultivars (Smith 1984; Cox et al. 1986), (ii) the identification of diverse parental combinations to create segregating progenies with maximum genetic variability for further selection (Barrett and Kidwell 1998), and (iii) the introgression of desirable genes from diverse germplasm into available genetic base (Thompson et al. 1998). Knowledge and understanding of grouping of inbred lines on the basis of phenotypic values of genetic traits are highly desirable in maize breeding for designing guidelines for use in developing heterotic populations and synthetic varieties (Hallauer and Miranda 1988; Badu-Apraku et al. 2006). Badu-Apraku and Lum (2007) reported the use of multivariate analysis for morphological traits to assess the genetic diversity among early-maturing inbred lines in order to develop heterotic patterns, design mating schemes, and provide guidelines for managing the diversity of the inbred lines of the IITA-West and Central Africa Maize Collaborative Research Network (WECAMAN) breeding program.

Molecular genetic techniques can be applied for the evaluation of genetic diversity and as a complementary strategy to traditional approaches in the conservation and utilization of plant genetic resources (Gauthier et al. 2002; Ghebru et al. 2002). For example, microsatellite markers are highly informative and are easily detectable with PCR. They occur frequently in plant genomes, showing an extensive variation in different individuals and accessions (Akkaya et al. 1992; Senior and Heun 1993). Owing to their multiallelic and highly polymorphic nature, they have been widely used for assessing maize genetic diversity (Smith and Smith, 1991; Smith et al. 1997; Messmer et al. 1993). The markers have high potential for use in characterizing inbred lines, particularly for classifying inbred lines for which records of ancestry are not readily available and for exploiting the heterosis known for tropical by temperate crosses (Adetimirin et al. 2008). Hoxha et al. (2004) reported that SSR markers constitute a powerful tool for detection of genetic diversity in maize populations and indicated that they can be used for devising strategies for conserving and managing maize germplasm.

7.4 Genetic Diversity and Hybrid Performance: Empirical Results from West and Central Africa

7.4.1 Genetic Diversity Assessment of Extra-Early Maturing Yellow Maize Inbreds and Hybrid Performance in Striga-*Infested and* Striga-*Free Environments*

Akaogu et al. (2012) evaluated 120 extra-early hybrids and an open-pollinated variety (OPV) check 2008 Syn EE-Y DT STR at two locations each under *Striga*-infested (Mokwa and Abuja) and *Striga*-free (Ikenne and Mokwa) conditions between 2010 and 2011 in Nigeria. The objective of the study was to determine the effect of genetic diversity based on simple sequence repeat (SSR) of the extra-early inbreds on hybrid performance. The *Striga*-resistant hybrids were characterized by higher grain yield, shorter ASI, better ear aspect, higher EPP, lower *Striga* damage rating, and lower number of emerged *Striga* plants at 8 and 10 WAP compared with the susceptible inbreds. Under *Striga* infestation, mean grain yield ranged from 711 to 3176 kg ha^{-1} and 1194 to 3940 kg ha^{-1} under *Striga*-free conditions. The highest yielding hybrid TZEEI 83 x TZEEI 79 outyielded the OPV check by 157% under *Striga* infestation. The hybrids TZEEI 83 x TZEEI 79 and TZEEI 67 x TZEEI 63 were the highest yielding under *Striga*-infested and *Striga*-free conditions. The GGE biplot identified TZEEI 88 X TZEEI 79 and TZEEI 81 X TZEEI 95 as the ideal hybrids across research environments. Twenty-three pairs of SSR markers were used to assess the genetic diversity among the inbred lines. The correlation between the SSR-based genetic distance estimates of parental lines and the means observed in F_1 hybrid under *Striga* infestation and optimal growing conditions were not significant for grain yield and other traits except ASI under optimal conditions. Grain yield of inbreds was not significantly correlated with that of F_1 hybrids. However, a significant correlation existed between F_1 hybrid grain yield and heterosis under *Striga* infestation ($r = 0.72$, $p < 0.01$). These hybrids have the potential for increasing maize production in *Striga* endemic areas in WCA.

7.4.2 Genetic Analysis and Molecular Characterization of Early-Maturing Maize Inbred Lines for Drought Tolerance

Drought is an important abiotic constraint to crop production in West Africa. Knowledge and understanding of the inheritance and genetic diversity of breeding lines with drought tolerance would guide breeding strategies. A study was conducted

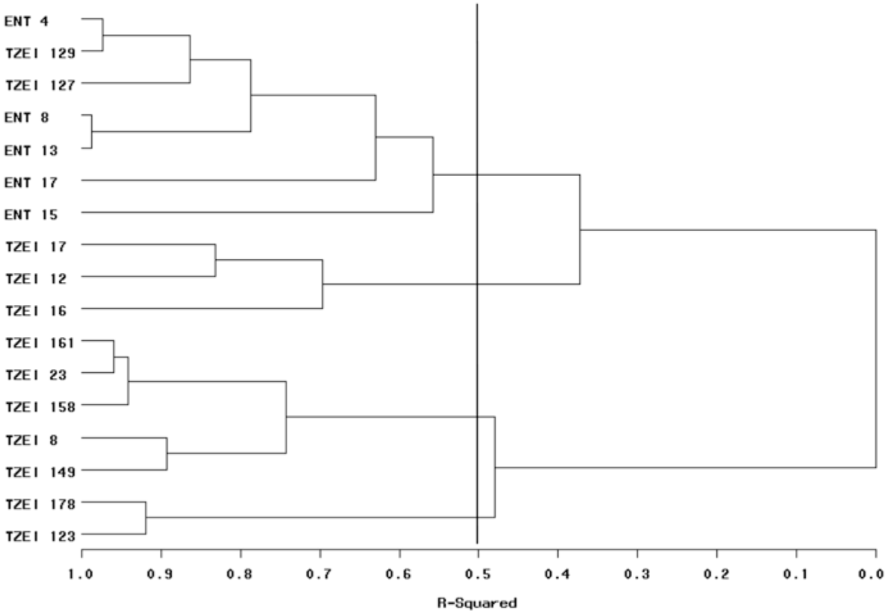

Fig. 7.1 Dendrogram of 17 early-maturing yellow maize inbred lines based on HSGCA values using Ward's minimum variance cluster analysis across drought, low N, and optimal conditions

between 2007 and 2010 to determine the levels of drought tolerance in some early-maturing maize inbred lines and the performance of hybrids among them, the genetic control of drought tolerance, and the genetic diversity among selected inbred lines in order to classify them into heterotic groups.

A total of 156 early-maturing inbred lines; 110 hybrids comprising 20 single, 60 three-way, and 30 double crosses, derived from 10 drought-tolerant inbred lines along with 11 checks; and 150 hybrids generated by crossing 30 inbred lines in sets using the North Carolina Design II along with 6 checks were evaluated in separate experiments under drought and well-watered conditions at 3 locations in Nigeria, between 2007 and 2010. Also, 42 inbred lines were genotyped using 23 microsatellite markers.

Results showed that inbred lines differed significantly ($P < 0.01$) in grain yield and other measured traits under drought and well-watered conditions. Grain yield of inbreds was significantly ($P < 0.01$) correlated with ears per plant ($r = 0.50$), anthesis–silking interval (ASI) ($r = -0.55$), plant aspect ($r = -0.57$), ear aspect ($r = -0.35$), and leaf death score ($r = -0.28$) under drought. Forty-eight percent of the lines were drought tolerant with tolerance indices ranging from 0.17 (low) to 15.31 (high). A total of 130 microsatellite alleles were detected in 42 lines with a range of 2–9 alleles per locus and an average of 5.7 alleles per marker. Polymorphic information content ranged from 0.17 in *phi308707* to 0.77 in *phi084*, with an average of 0.54. Five heterotic groups were obtained with microsatellite markers (Fig. 7.1).

Inbreds TZEI 31 and TZEI 17 were identified as the best testers. The identification of TZEI 17 as the best tester in this study confirmed the findings of Badu-Apraku et al. (2011). Hybrids were significantly different for measured traits under drought and well-watered conditions; however, means of single-, three-way, and double-cross hybrids were not significantly different for grain yield under drought. These results indicated the importance of dosage effects in the parental inbred lines. Ordinarily, single-cross hybrid is expected to outyield three-way and double-cross hybrids under optimal growing conditions, but the dosage effects of drought tolerance genes in the parental lines might have given the latter comparative advantages under drought. The rankings of genotypes under induced drought were found to be associated with those under well-watered conditions. However, the variation in grain yield under well-watered conditions accounted for 39% for single-, 4% for three-way, and 2% for double-cross hybrids and 9% for improved open-pollinated varieties of the total variation in grain yield under induced drought. It appears that the association observed in the ranking of genotypes under the two research conditions was mainly from single-cross hybrids. These results indicate that little progress will be made in the development of drought-tolerant hybrids by selecting superior performance under well-watered conditions. Therefore, selection of superior three-way and double-cross hybrids under induced drought is crucial for identification and development of drought-tolerant hybrids. Under drought, the general combining ability (GCA) and specific combining ability were significant ($P < 0.01$), with GCA accounting for over 50% of the total variation for all traits except ASI and plant and ear height, indicating that additive genetic effects largely controlled grain yield of the hybrids. Mid-parent and better-parent heterosis for grain yield averaged 45.2% and 18.4% under drought and 112% and 103% under well-watered conditions, respectively. Grain-yield reduction under drought ranged from 39% to 90%, averaging 61%. The best single-cross hybrids TZEI 31 x TZEI 18 outyielded the best open-pollinated varieties by 19%.

The results indicated that there is genetic variation for drought tolerance among early-maturing inbred lines and hybrids, with grain yield under drought and optimal conditions largely controlled by additive genetic effects. These results indicated that selection for drought-tolerant inbred lines can enhance the development of drought-tolerant hybrids and synthetic varieties for the drought-prone areas, while the inbred lines per se could be used to introgress drought tolerance genes into breeding populations. Yield improvement in drought-tolerant maize was associated with the level of drought tolerance in parental lines. The broad genetic diversity revealed by microsatellite markers indicated the latter's usefulness in resolving the heterotic groups of inbred lines that are yet to be field-tested in hybrid combinations. The information generated could be used for better understanding of the genetic relationships among the early-maturing inbred lines, more effective utilization of the inbred lines in the breeding programs for the development of synthetic varieties and hybrids, and formation of heterotic populations used to derive promising inbred lines.

7.4.3 Genetic Diversity Among IITA and CIMMYT Early-Maturing Maize Inbred Lines Using SSR and SNP

Ifie et al. (2014, unpublished) used 31 SSR and 261 SNP markers to assess the genetic diversity available among 85 IITA and 9 CIMMYT early-maturing inbred lines from the DTMA panel of inbreds with combined resistance and/or tolerance to *Striga*, low N, and drought. The SSR markers produced 114 alleles with a mean of 3.68 alleles per locus. The polymorphic information content (PIC) of SSR and SNP was 0.58 and 0.25, respectively. There was a close correspondence between SSR and SNP markers in assigning the inbred lines into the different clusters. The CIMMYT inbred lines were clustered into five different groups together with some IITA inbred lines. The model-based structure analysis grouped the CIMMYT lines into one cluster together with the IITA lines derived from Pool 16 DT. Both SSR and SNP markers showed a relatively high level of genetic diversity among the IITA and CIMMYT early-maturing maize inbred lines that could be exploited for population improvement, hybrid production, and development of new lines with combined *Striga* resistance, drought, and low-N tolerance.

7.4.4 Identification of Heterotic Patterns of Maize Inbreds and Efficiency of Heterotic Grouping Methods

Information on the heterotic groupings of the parental lines is of utmost importance to the success of a hybrid program. The classification of inbreds into appropriate heterotic groups determines the potential usefulness of inbred lines in the program since it allows a better understanding of the genetic relationships among the inbred lines and facilitates effective utilization of the inbreds in the breeding programs for the development of synthetic varieties, hybrids, and formation of heterotic populations. Subsequently, inbred lines could be extracted from such populations for the production of superior hybrids and synthetics. It is expected that inbreds extracted from complementary populations developed from the inbred lines of the opposite heterotic groups would show high combining ability with lines from the complementary population.

Several methods including the use of phenotypic values of genetic traits, specific combining ability (SCA) effects of grain yield, general combing ability (GCA), and SCA effects of yield and molecular markers have been proposed and used in grouping inbred lines into heterotic groups. Heterotic grouping of maize inbred lines on the basis of phenotypic values of genetic traits is highly desirable in maize breeding in designing guidelines for use in developing heterotic populations, synthetic varieties, and hybrids. Researchers have therefore used multivariate analysis of morphological and agronomic traits to assess the genetic diversity among maize inbred lines. Also, molecular markers have been found to be a powerful tool for defining heterotic groups and examining the relationships among inbred lines at the

DNA level and have therefore been used to complement existing approaches. Combined use of molecular markers that allow direct comparison of the similarity of inbreds at the DNA level with testcross evaluation in the field has facilitated the separation of inbred lines into well-defined heterotic groups. Another commonly used method for classifying maize inbreds into heterotic groups is the SCA effects of grain yield. However, there may be difficulty in classifying tropical inbred lines into distinct heterotic groups based only on the results of combining ability studies. For example, Agbaje and co-workers (Agbaje et al. 2008) used the line x tester analysis to study the heterotic patterns among selected *Striga*-resistant early yellow maize inbreds. The testers were unable to discriminate efficiently among the lines, and they could therefore not be separated into definite heterotic groups. Furthermore, there has been difficulty in classifying tropical lines into heterotic groups based on only the results of combining ability studies because the SCA effect of grain yield of inbred lines has often been found to be influenced by the interaction between two inbred lines and between hybrids and environment. This often leads to the classification of the same inbred to different heterotic groups in different studies. Several methods have therefore been proposed to overcome this problem. One such method is the heterotic groups' specific and general combining ability (HSGCA) method that combines both SCA and GCA effects as a more appropriate method for assigning inbred lines into heterotic groups. Studies conducted by researchers have so far proved this method to be more effective than the use of SCA effects of grain yield alone or molecular markers for classifying inbred lines into distinct heterotic groups. For example, Akinwale et al. (2014) evaluated 378 hybrids derived from diallel crosses of 28 early inbreds along with two checks in *Striga*-infested and *Striga*-free environments for 2 years at two locations in Nigeria. The objective of the study was to determine the combining ability of 28 early-maturing inbreds, classify them into heterotic groups, identify suitable testers under *Striga*-infested and *Striga*-free environments, and assess the efficiency of the three heterotic grouping methods. Twenty-seven of the 28 inbreds were genotyped with 46 polymorphic simple sequence repeat (SSR) markers previously mapped on the 10 maize chromosomes. Analysis of variance revealed highly significant ($P < 0.01$) general combining ability (GCA) and specific combining ability (SCA) mean squares for most traits under test conditions. Based on the SCA effects and heterotic group's specific and general combining ability (HSGCA) for grain yield, four and five heterotic groups were identified under *Striga*-infested and *Striga*-free environments, respectively. Two inbreds could not be classified into any of the four groups under *Striga* infestation. The SSR markers revealed a wide genetic variability among the inbred lines as the genetic distance ranged between 0.21 and 0.68. Four heterotic groups were identified based on genetic distance (GD) derived from the SSR analysis. The authors reported low but significant and positive correlation coefficients between GD and other grouping methods and attributed this to the large number of observations used in their study. Simple sequence repeat-based genetic distance had a higher correlation with SCA effects in *Striga*-free environments than under *Striga* infestation. This result is similar to the findings of Betrán et al. (2003b) who reported a higher correlation between SCA and GD under optimal growing conditions than under drought stress.

The higher correlation was attributed to the effect of the mild stress of the *Striga*-free environment on the full expression of genetic potential of the inbreds in crosses as compared to when under artificial *Striga* infestation. The higher correlation between GD estimate and SCA than between GD and HSGCA under *Striga*-free conditions indicated that the GD was a better measure of the nonadditive component of the genotypic composition of the inbred lines. George et al. (2010) observed that the highest correlation between GD and SCA obtained for crosses between lines within a cluster was reasonably stable even when the environment had a severe effect on grain yield. There was nonsignificant correlation between GD and MP of the inbreds indicating that GD could not be used to predict the per se performance of the inbreds. This result is in agreement with the findings of Betrán et al. (2003b) who found nonsignificant correlation between GD and MP under severe drought stress and low-N stress. However, these authors reported significant and positive correlation between the two methods under well-watered and high-N conditions. This discrepancy could imply that inbreds exhibited varied genetic response to different types and levels of stress.

An efficient heterotic grouping method is expected to identify groups which allow inter-heterotic group crosses to be more vigorous than within-group crosses (Fan et al. 2009). In the study of Akinwale et al. (2014), correlation analyses showed that grouping using GD was more consistent with grouping based on SCA under *Striga*-free than under *Striga*-infested environments. On the basis of the mean values of intra- and inter-heterotic groups, HSGCA proved to be the most efficient method because it identified distinct heterotic groups in which intragroup mean yields were significantly lower than all intergroup environments. For example, two of the three intergroup crosses had significantly higher grain yield ($P < 0.05$) than the intragroup crosses of Groups 1, 2, and 4, while all the three intergroup crosses had higher yields than intragroup crosses in Group 3 (Table 7.1). Using SCA and SSR-based GD methods, however, most of the intergroup crosses were not significantly higher than intragroup crosses. Using SCA method, the two inbreds that could not be classified into the four groups had significantly higher grain yield for intragroup crosses than intergroup crosses. Under *Striga*-free conditions, all the intergroup crosses had significantly higher yield ($P < 0.05$) than intragroup crosses using HSGCA and for most intergroup crosses using SCA and SSR-based GD. Across both research conditions, intergroup crosses had significantly higher yield ($P < 0.05$) than intragroup crosses for all the grouping methods (Table 7.1). This finding is in agreement with Fan et al. (2009) who reported that HSGCA method increased breeding efficiency by 16.7–23.6%. This indicates that this heterotic grouping method is highly efficient in the grouping of inbreds.

The grouping methods based on SCA were generally inefficient in identifying clear heterotic groups. However, it should be noted that no heterotic group classification method is perfect due to unlimited genetic combinations between any two inbred lines which may result in the development of superior hybrids from crosses made within a heterotic group. The grouping of the 48 inbred lines by SSR markers was closely related to their pedigree data and their combining ability. This result is in agreement with those of several previous studies (Messmer et al. 1992; Senior

Table 7.1 Mean values (±s.e) for grain yield of hybrids within and between heterotic groups based on SCA, HSGCA, and SSR-based genetic distance methods under each and across *Striga* infestation and *Striga*-free conditions

Group/group combination	*Striga*-infested environments			*Striga*-free environment			Combined across environments		
	HSGCA	SCA	SSR markers	HSGCA	SCA	SSR markers	HSGCA	SCA	SSR markers
1 × 1	1156 ± 173.0	1409 ± 90.7	1328 ± 125.2	3953 ± 54.4	3747 ± 106.5	4729 ± 133.7	3107 ± 108.0	2761 ± 116.6	3492 ± 146.6
1 × 2	2639 ± 134.0	1774 ± 68.4	1466 ± 86.0	5104 ± 84.2	5214 ± 145.2	4667 ± 90.0	4294 ± 149.1	4294 ± 149.2	3503 ± 92.6
1 × 3	1155 ± 69.1	1174 ± 96.6	1979 ± 72.7	5277 ± 139.2	4358 ± 83.5	5036 ± 63.0	3375 ± 132.3	3772 ± 100.3	3925 ± 67.0
1 × 4	1679 ± 66.5	1524 ± 74.9	1273 ± 60.5	4729 ± 117.3	4671 ± 147.3	4841 ± 69.3	3390 ± 182.2	3390 ± 182.2	3543 ± 76.0
1 × 5				4642 ± 50.4	5054 ± 85.4		3715 ± 78.2	3456 ± 86.5	
2 × 2	2606 ± 148.2	1732 ± 90.4	1405 ± 121.6	2949 ± 166.1	2949 ± 166.1	4244 ± 133.4	2671 ± 141.2	2671 ± 141.6	3212 ± 132.9
2 × 1	1667 ± 341.2	1770 ± 135.1	1566 ± 66.1	5224 ± 163.2	5224 ± 163.1	4667 ± 90.0	4336 ± 144.5	4168 ± 118.2	3601 ± 52.6
2 × 3	2551 ± 81.3	1630 ± 161.7	2085 ± 77.9	5235 ± 347.2	4957 ± 183.6	4950 ± 63.7	3914 ± 157.5	4185 ± 139.0	3908 ± 65.4
2 × 4	2475 ± 123.3	1614 ± 90.4	1243 ± 55.4	4902 ± 268.1	4902 ± 268.4	4496 ± 62.6	3893 ± 249.2	3893 ± 249.1	3313 ± 68.1
2 × 5				5020 ± 110.5	5108 ± 136.8		4193 ± 108.2	4359 ± 141.3	
3 × 3	906 ± 65.0	1300 ± 154.5	2473 ± 89.9	4560 ± 251.3	4101 ± 74.5	4626 ± 80.6	3008 ± 103.0	3617 ± 84.0	3842 ± 71.1
3 × 1	1102 ± 175.1	1192 ± 109.5	1979 ± 72.7	5453 ± 171.2	4200 ± 85.2	5036 ± 63.0	3382 ± 91.9	3812 ± 122.2	3995 ± 51.0
3 × 2	1818 ± 75.5	1428 ± 84.3	2285 ± 77.9	5653 ± 317.1	5110 ± 98.1	4950 ± 63.7	4195 ± 112.3	4104 ± 117.4	3908 ± 65.4
3 × 4	1249 ± 43.5	1425 ± 99.0	1869 ± 56.3	5239 ± 354.3	4760 ± 166.6	4980 ± 52.7	3530 ± 189.0	3535 ± 199.3	3849 ± 55.0
3 × 5				5220 ± 109.6	4743 ± 70.2		3549 ± 69.3	3716 ± 78.1	
4 × 4	1650 ± 56.2	2014 ± 101.7	1004 ± 62.7	2017 ± 293.3	2017 ± 293.1	4464 ± 84.6	1487 ± 245.0	1487 ± 245.2	3206 ± 89.0
4 × 1	1807 ± 151.1	1626 ± 114.8	1273 ± 60.5	4685 ± 160.2	4937 ± 240.9	4841 ± 69.3	3685 ± 213.1	3464 ± 263.2	3543 ± 76.0
4 × 2	2675 ± 123.3	1888 ± 93.8	1243 ± 55.4	5012 ± 238.2	5012 ± 238.2	4496 ± 62.6	3993 ± 241.7	3993 ± 241.0	3313 ± 68.1
4 × 3	1329 ± 107.3	1445 ± 100.7	1889 ± 76.3	4876 ± 278.1	4319 ± 131.3	4995 ± 62.5	3200 ± 211.5	3457 ± 155.3	3849 ± 55.0
4 × 5				4609 ± 125.3	4908 ± 120.1		3352 ± 121.3	3352 ± 135.2	
5 × 5				*4719 ± 58.6*	*5073 ± 70.6*		*3678 ± 58.1*	*3394 ± 61.0*	

(continued)

Table 7.1 (continued)

Group/group combination	*Striga*-infested environments			*Striga*-free environment			Combined across environments		
	HSGCA	SCA	SSR markers	HSGCA	SCA	SSR markers	HSGCA	SCA	SSR markers
5 × 1				4849 ± 63.2	5185 ± 88.5		3800 ± 80.4	3425 ± 86.3	
5 × 2				5215 ± 108.2	5245 ± 110.1		4140 ± 100.3	4205 ± 97.1	
5 × 3				5302 ± 154.3	4730 ± 66.4		3441 ± 95.2	3661 ± 71.9	
5 × 4				4972 ± 168.1	5035 ± 157.2		3608 ± 164.3	3613 ± 158.2	
0 ×0		*2132 ± 255.4*							
1 × 0		2460 ± 177.2							
2 × 0		2419 ± 216.9							
3 × 0		1843 ± 173.4							
4 × 0		2484 ± 327.7							

Source: Akinwale et al. (2014)

et al. 1998; Reif et al. 2003a, b; Fan et al. 2004). Generally, results obtained from all the different analyses carried out in this study revealed four heterotic groups under *Striga* infestation and five under *Striga*-free conditions. The HSGCA method was identified as the most effective in classifying the early-maturing maize inbreds under *Striga*-infested and *Striga*-free environments.

A major drawback of heterotic grouping either by SCA or HSGCA is that it is based primarily on grain yield. However, grain yield is a complex trait controlled by polygenes and has low heritability especially under stress environments. For example, selection for grain yield under severe drought stress has often been considered inefficient because the estimate of heritability of grain yield has been observed to decline with reduced yield levels. Therefore, improvement in yield is difficult through direct selection under stressed environments, and it is more effective to use component traits that have a strong correlation with grain yield for indirect selection for improved yield. It has, therefore, become a routine practice to gather data on multiple traits associated with grain yield and to use this in a base index to select for improved yield in stressed environments.

It was therefore hypothesized that a classification based on GCA effects of multiple traits should give a better, more predictable, and usable heterotic grouping of the lines since GCA measures additive gene effects for each trait. A grouping method based on the GCA of multiple traits designated HGCAMT was therefore proposed by Badu-Apraku et al. (2013). The HGCAMT approach was compared with the SCA effects of yield, the HSGCA, and molecular markers of the SSR (simple sequence repeat) type to determine their effectiveness in classifying selected extra-early yellow inbreds into contrasting heterotic groups in a study by Badu-Apraku et al. (2013). One hundred and ninety hybrids derived from the diallel cross of 20 extra-early yellow endosperm inbreds plus 6 open-pollinated check varieties were used in the 3 field studies conducted under *Striga* infestation, low soil nitrogen, and optimal growing environments in 2011 at 4 locations in Nigeria. In addition, the 20 yellow endosperm extra-early inbreds used for the field studies were used for a genetic diversity assessment study. The inbred lines were grown in the IITA screenhouse in Ibadan, and young leaves were harvested at 6 leaf stages from 15 to 20 seedlings of each inbred line 10 days after planting and stored at −80 °C. Genomic DNA extraction was carried out using the miniprep extraction protocol described in Dellaporta et al. 1983 by Dellaporta and co-workers. The purified DNA was quantified on a nanodrop spectrophotometer. Sixty mapped SSR markers were randomly selected from maize GDB database (www.maizegdb.org), with six markers per chromosome and three markers per chromosome arm. The 60 primer pairs were tested on four selected inbreds to identify the polymorphic markers which were used for the genotyping of the 20 inbred lines. The SSR analyses were conducted according to the method developed by Vroh Bi et al. (2006). Molecular marker analysis was carried out using PowerMarker V3.25 software.

GCA effects of the parents and SCA of the crosses, as well as their mean squares across all ten environments for grain yield, days to silking (DS), days to anthesis (DA), anthesis–silking interval (ASI), plant height (PLHT), ear aspect (EASP), number of ears per plant (EPP), and plant aspect (PASP); four test environments for stay-green characteristic; and two test environments for *Striga* damage and number of emerged *Striga* plants at 8 and 10 weeks after planting, were estimated in the 14 x 14 diallel crosses following Griffing's method 4 model 1 (fixed model). Effects of GCA and SCA for the traits were computed from the mean values adjusted for the block effects for each environment and across environments.

Heterotic grouping based on GCA of multiple traits proposed by Badu-Apraku et al. (2013, 2015a) was used to group the inbred lines. This was achieved by standardizing the GCA effects of 12 traits that had significant mean squares across test environments to minimize the effects of different scales of the traits.

The statistical model used for the HGCAMT method to assign the inbreds into the heterotic groups is as follows:

$$Y = \sum_{n}^{i=1}\left(\left(Y_i - \overline{Y_i}\right)/\,s\right) + \varepsilon_{ij}$$

where *Y* is the HGCAMT, which is the genetic value measuring relationship among genotypes based on the GCA of multiple traits *i* to *n:*

Y_i is the individual GCA effect of genotypes for trait *i*.
μ is the mean of GCA effects across Y genotypes for trait *i*.
s_i is the standard deviation of the GCA effects of trait *i*.
ε_{ij} is the residual of the model associated with the combination of inbred *i* and trait *j*.

The selected traits included grain yield, DS and DA, ASI, PL HT and ear E HT, *Striga* damage at 8 and 10 WAP, number of emerged *Striga* plants at 10 WAP, ear aspect, number of ears per plant (EPP), and the stay-green characteristic. The standardized GCA effects were subsequently subjected to Ward's minimum variance cluster analysis to construct the groupings. The HSGCA method proposed by Fan and co-workers in Fan et al. 2008 was used to assign inbred lines into heterotic groups. The HSGCA estimates were subjected to Ward's minimum variance cluster analysis using SAS software version 9.3 (SAS Institute Inc. 2011). Similarly, the standardized GCA effects were subjected to Ward's minimum variance cluster analysis. Dendrograms were also constructed for the groupings based on molecular markers. The inbred lines were classified into four heterotic groups based on SCA effects and three groups based on heterotic groups' specific and GCA, the GCA effects of multiple traits of inbred lines and molecular markers. It is striking that the classification of the seven extra-early yellow inbreds in an earlier study by Badu-Apraku and Oyekunle in Badu-Apraku and Oyekunle (2012) using the SCA method showed a close correspondence with the classification by the HGCAMT and HSGCA methods used in that study. Of the seven inbreds used in the 2011 study, the six which were common to the 2012 study were classified similarly by the HGCAMT and HSGCA methods, indicating the effectiveness of HSGCA classification method and thus confirming the findings of the 2008 studies of Fan and co-workers and Akinwale and co-workers in Akinwale et al. (2014). It is also striking that the SCA method could classify only 16 of the 20 inbreds (80%) compared to the HGCAMT, SSR marker, and the HSGCA methods which classified all the extra-early inbreds into heterotic groups. Furthermore, the classification of inbreds based on the HGCAMT method was consistent with the classification based on SSR markers indicating that the HGCAMT method is effective in classifying inbred lines into appropriate heterotic groups. These results indicated that the grouping of the inbreds was based largely on the pedigree of the inbreds and to a small extent on the reaction of the inbreds to the stress environments. These results further suggested that molecular markers could be used in classifying other inbreds that are yet to be field-tested in hybrid combinations.

Based on the classification of the extra-early inbreds into contrasting heterotic groups, *Striga*-resistant and low-N-tolerant breeding populations could be developed for the national maize breeding programs in WA. The inbreds in each heterotic group may be recombined to form heterotic populations which could be improved through recurrent selection. Subsequently, inbred lines could be extracted from each population for the production of superior hybrids and synthetics. It is expected that inbred lines extracted from complementary populations developed from the inbred lines of the opposite heterotic groups would show high combining ability with lines from the complementary population.

Recurrent drought and low levels of soil nitrogen (low N) constitute major constraints to maize production in the savannas of West Africa (WA). Presently, only a few early-maturing maize hybrids have been commercialized in WA despite the availability of numerous early inbreds in the IITA Maize Program and the increasing demand for hybrid seed. Hybrid combinations between the IITA inbreds and selected elite exotic CIMMYT inbreds from environments similar to WA could produce outstanding hybrids. One hundred and thirty-six single-cross hybrids derived from a diallel cross of 11 IITA and 6 CIMMYT early yellow inbreds plus 4 hybrid checks were evaluated under drought, low N, and optimum conditions at 4 locations in Nigeria between 2010 and 2012. The objectives were to examine the combining ability of the inbreds for grain yield and other traits, group the inbreds, and identify the best testers under the contrasting environments. Results revealed that the general combining ability (GCA) effects for all traits were greater than specific combining ability (SCA) effects under drought, low N, and optimum and across environments suggesting that additive gene action was more important than the nonadditive in the set of inbred lines. The inbred lines were classified into four heterotic groups each across environments based on the HSGCA (Fig. 7.1) and the SNP-based genetic distance methods (Fig. 7.2), while the HGCAMT placed them into three groups (Fig. 7.3). There was a close correspondence between the classifications based on the three grouping methods, indicating that they were all effective in classifying the inbreds into heterotic groups. However, the HGCMAT was the most efficient method followed by the HSGCA and then the SNP-based genetic distance methods across research environments because it was the only method that had significant linear contrasts for all possible group comparisons (Table 7.2). HGCAMT identified CIMMYT inbreds ENT 17, ENT 15, and ENT 8 as the best testers for heterotic Groups 1, 2, and 3, respectively, across research environments. ENT 13 had

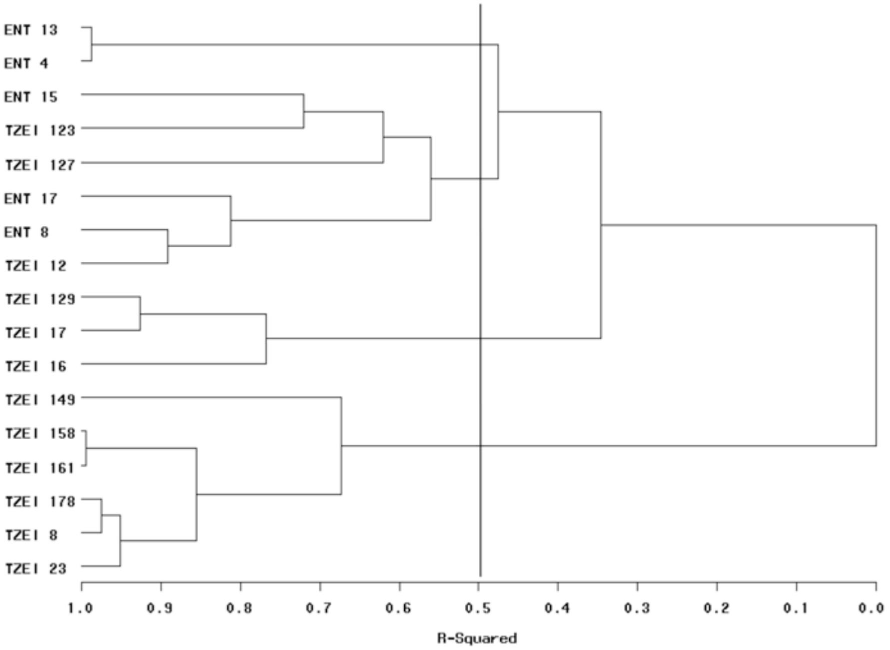

Fig. 7.2 Consensus UPGMA dendrogram constructed using Ward's minimum variance cluster analysis of modified Roger's distance coefficients for 17 early-maturing yellow maize inbred lines

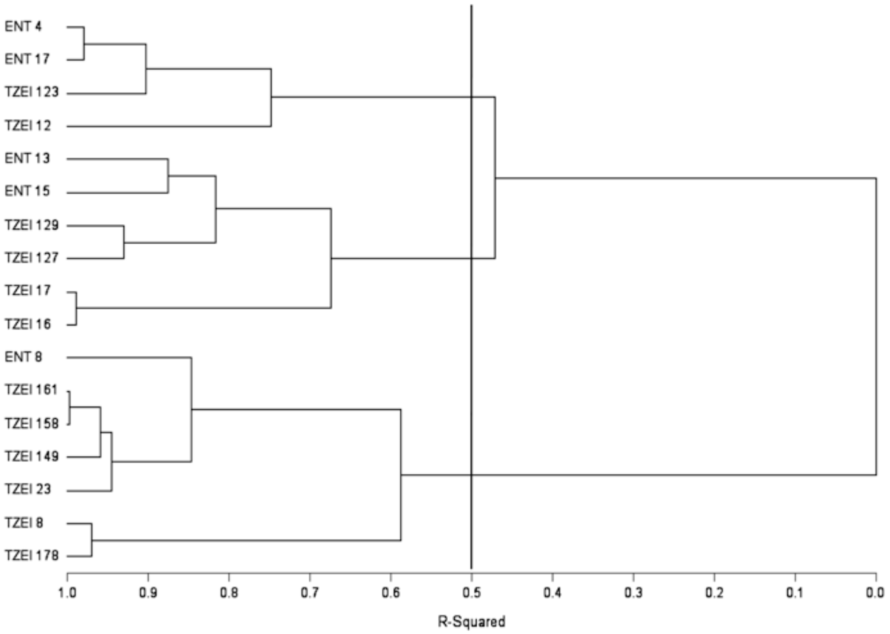

Fig. 7.3 Dendrogram of 17 early-maturing yellow maize inbred lines constructed from GCA effects of grain yield and other traits (HGCAMT) using Ward's minimum variance cluster analysis across drought, low N, and optimum conditions

Table 7.2 Sum of squares from the linear contrasts of heterotic groups based on HSGCA, HGCAMT, and SNP-based genetic distance of grain yield under drought, low N, and optimum and across research conditions

Contrast	df	Drought			Low N			Optimum			Across		
		HSGCA	HGCAMT	GD	HSGCA	HGCAMT	GD	HSGCA	HGCAMT	GD	HSGCA	HGCAMT	GD
Group 1 vs Group 2	1	512678.9	7675360.2**	343388.3**	29430.6	1632960.5	173322.7	4724806.6*	8920655.3**	97544.4	27836135.5**	28821725.60**	61619.8
Group 1 vs Group 3	1	2294263.3**	434972	7180897.0**	41353441.7*	57530554.2**	79672651.8**	49169274.1**	155051116.9**	145357600.70**	128704165.3**	66132581.40**	185390525.4**
Group 2 vs Group 3	1	232104.5	740569.1	3894212.7**	27367242.4**	41456696.3**	33785882.6**	89244576.2**	128742322.9**	56305811.00**	47137762.5**	136104009.40*	69267555.9**
Group 1 vs Group 4	1		5638489.6**		3944499.1*						11722929.8**		49.9
Group 2 vs Group 4	1		5638489.6**		3944499.1*						11722929.8**		49.9
Group 3 vs Group 4	1		4123804.6**		18866751.98**						4146.6		30861468.2**

*,**Significant at 0.05 and 0.01 probability levels, respectively

significant and high positive GCA effects for grain yield and EPP under all environments except EPP under drought, suggesting that the inbred could be an invaluable source of favorable alleles for the traits for improving IITA germplasm. Similarly, the IITA inbreds TZEI 17 and TZEI 16 had positive and significant GCA effects for grain yield under low N and optimum and across research environments. Furthermore, TZEI 16 had significant and positive GCA effects for ASI under drought, low N, and optimum environments and negative and significant GCA effects for stay-green characteristic under drought and could be used to improve the CIMMYT germplasm for drought tolerance and the stay-green characteristic. Hybrids TZEI 17 x ENT 15 and TZEI 149 x ENT 15 were the highest yielding and most stable across test environments and should be promoted for commercialization in WA.

In another study, diallel crosses involving 11 IITA and 6 CIMMYT early yellow inbreds plus 4 hybrid checks were evaluated under drought and low N and in optimal conditions and across environments at 4 locations in Nigeria for 2 years. The objectives were to examine the combining ability of the inbreds for grain yield and other traits, group them, and identify the best testers under the contrasting environments. General combining ability (GCA) effects for all traits were greater than specific combining ability (SCA) effects in the contrasting research environments. The inbreds were classified into four heterotic groups each across environments based on the heterotic groups' SCA and GCA (HSGCA) and the SNP-based genetic distance methods; the GCA effects of multiple traits of the inbred line (HGCAMT) method placed them into three groups. There was a close correspondence between the classifications based on the three methods. However, HGCAMT was the most efficient followed by HSGCA and then SNP-based genetic distance method across environments. The HGCAMT identified CIMMYT inbreds ENT 17, ENT 15, and ENT 8 as best testers for heterotic Groups 1, 2, and 3, respectively, across environments. Two hybrids, TZEI 17 x ENT 15 and TZEI 149 x ENT 15, were the most outstanding across environments.

Two major constraints militating against the achievement of food security in West Africa (WA) are recurrent drought and poor soil fertility. Seventeen early-maturing maize inbreds from IITA and CIMMYT were used as parents to produce 136 diallel crosses which were evaluated along with 4 checks in contrasting environments at 4 locations for 2 years in Nigeria. The objectives of the study were to (i) examine the combining ability of the lines under drought, low soil nitrogen (low N), and optimal and across environments; (ii) classify the inbreds into heterotic groups using the SCA effects of grain yield, HSGCA, the HGCAMT, and the molecular-based GD methods; (iii) compare the efficiencies of the four heterotic grouping methods in classifying the inbreds and identifying the best testers; and (iv) examine the performance of the inbreds in hybrid combinations across environments. GCA effects of inbreds for grain yield and other measured traits were larger than those of the SCA effects in all environments. The relative importance of GCA to SCA effects for grain yield and other traits increased from stress to non-stress environments with the additive genetic effects accounting for the major portion of the total genetic variation under all research environments. The HSGCA method classified the lines into three groups and was the most efficient because it had the highest breeding efficiency (40%) in the test environments followed by the HGCAMT, the SNP marker-based GD, and the SCA effects of grain-yield methods. Inbred TZEI 19 was identified as the best tester across research environments based on HSGCA method. Hybrids ENT 11 x TZEI 19 and TZEI 1 x TZEI 19 were the most outstanding and should be tested extensively in on-farm trials and commercialized.

Comparison of the results of the combining ability and heterotic grouping study involving the IITA and CIMMYT white inbreds with the results of a similar study involving the yellow endosperm early IITA and CIMMYT inbreds under similar contrasting environments revealed some interesting trends. In both studies, both GCA and SCA mean squares were significant for most measured traits, but there was a preponderance of GCA over SCA, indicating that early generation testing will be effective and selection of promising hybrids will be successful based solely on the prediction from GCA effects in both the white and yellow inbreds. Furthermore, the grouping of the inbreds by the HSGCA and the HGCAMT methods was closely related to the germplasm source and their combining abilities for the two different endosperm inbreds. However, while the HSGCA method was the most effective for grouping of the white endosperm inbreds, the HGCAMT was superior to the HSGCA method in the grouping of the yellow endosperm inbreds. The differences in the results of the grouping based on the HGCAMT and the HSGCA methods in the present study and those of the earlier authors could be attributed to the fewer number of traits with significant GCA effects in the white endosperm inbreds. This suggests that in a situation where we have just few traits with significant and positive GCA effects, the efficiency of the HGCAMT method may be compromised. Under such circumstance, it may be desirable to use both the GCA effects of multiple traits and the SCA effects of grain yield for a more efficient grouping of the inbred lines. There appears to be a need to confirm this hypothesis.

The choice of proven testers is another crucial factor that determines progress in maize hybrid development. Seed industry in sub-Saharan Africa is still at the infant stage, and adoption and use of hybrids by farmers are greatly constrained due to the extent of research, number of available seed companies, poor financial capability of existing seed companies to maintain genetic materials, and low financial status (purchasing power of the farmers). Tropical inbred lines exhibit poor vigor compared with temperate inbreds, and productivity of single-cross hybrid seeds from these inbreds is poor. This, in turn, leads to high production cost of the hybrid seeds, and most farmers cannot afford to buy them. Hybrids require high inputs such as fertilizer, herbicides, and pesticides to express their high production potentials, but most farmers in the sub-region are resource-poor and cannot afford it. Therefore, scientists of SSA have invested considerable research efforts and resources to identify single-cross testers to facilitate the development of three-way and double-cross hybrids and inbred testers for topcross hybrid development rather than for the development of single-cross hybrids for release to farmers. Proven testers were not available in the tropical germplasm at IITA.

At the initial stage of hybrid development, testers such as Mo17 and B73 derived from temperate germplasm were used. But the results of crosses of tropical lines with temperate testers were not producing desirable results. After a while, testers were identified among the late/intermediate maize germplasm which were adopted for early and extra-early maize germplasm.

Agbaje et al. (2008) used TZi 4001 and Ku1414 in a line x tester study to identify heterotic groups, but none of the testers could sufficiently cluster the lines into clear heterotic groups. Several diallel and NCII studies under stress and non-stress conditions have been conducted during the last decade. For example, Badu-Apraku et al. (2016a) examined the combining ability of selected IITA and CIMMYT inbreds for grain yield and other traits and classified the lines into heterotic groups using heterotic specific combining ability (SCA) and general combining ability (GCA) (HSGCA), single nucleotide polymorphism-based genetic distance (SNP-GD), and GCA effects of multiple trait (HGCAMT) methods. The authors reported that the HGCAMT is an efficient heterotic grouping method and offers a great opportunity for grouping the numerous IITA inbreds that are yet to be grouped. Furthermore, the results of this study confirmed that molecular markers could be used in grouping IITA inbreds that are yet to be field-tested. The efficiency of the heterotic grouping methods, SCA effects of grain yield, HSGCA, HGCAMT, and SNP-based GD methods varied with the type of genetic material under study. The results of these studies have led to the identification of several testers under contrasting stress conditions, and more recently, some excellent testers have been identified across multiple stresses (Annor and Badu-Apraku 2016; Badu-Apraku et al. 2015a, b, 2016). Through genetic studies conducted during the last decade, the HSGCA, HGCMAT, and molecular markers such as SNP and SSR have been confirmed as invaluable for the grouping of the numerous tropical inbreds that have been developed in SSA (Badu-Apraku et al. 2015a, 2016). The challenge now is to use these proven grouping methods to classify the numerous inbreds that are yet to be field-tested to allow planned crosses to be made and facilitate the development of superior hybrids. There is also a need to refine the heterotic groups that have been identified and to identify more efficient testers. Furthermore, much more research efforts need to be devoted to the development of proven testers for improving nutritional quality of maize in terms of provitamin A, quality protein content, and micronutrients. Presented in Tables 7.3, 7.4, 7.5, 7.6, 7.7, 7.8, and 7.9 are the elite testers of early and extra-early maturing tropical testers of all endosperm types that have been identified and their characteristics. Also presented are the single-cross hybrids of the different grain types for production of three-way and double-cross hybrids.

7.5 Conclusions

Early and extra-early maize germplasm showed clearly that genetic diversity is of primary importance in the display of heterosis. Inbred lines from different heterotic groups produced higher-yielding hybrids than those of lines from within the same heterotic group. Although GCA seems to be of great importance in hybrid production, SCA cannot be neglected in the process, especially for grain yield.

Table 7.3 Characteristics of extra-early maturing white inbred testers

Testers	Desirable attributes of inbred tester	Weaknesses of inbred tester	Tester combiners
TZEEI 21	Negative and significant GCA effect for stay-green characteristic under drought. Negative and significant GCA effect for *Striga* damage.	Lack of positive significant GCA for grain yield under *Striga*, low N, and drought. Lack of significant and negative GCA for number of emerged *Striga* plants.	TZEEI 6, TZEEI 38, TZEEI 37, TZEEI 29, TZEEI 90, TZEEI 4, TZEEI 39, TZEEI 3, TZEEI 32, TZEEI 55, TZEEI 54, TZEEI 57, and TZEEI 14
TZEEI 29	Positive and significant GCA effect for grain yield under *Striga.* Negative and significant GCA effect for number of emerged *Striga* plants and *Striga* damage	Lack of significant positive GCA effect for grain yield under drought and low N. Lack of negative and significant GCA for stay-green characteristic under drought and low N.	TZEEI 4, TZEEI 39, TZEEI 3, TZEEI 32, TZEEI 55, TZEEI 54, TZEEI 57, TZEEI 14, TZEEI 21, TZEEI 49, TZEEI 46, and TZEEI 13
TZEEI 14	Significant positive GCA effects for grain yield under *Striga* infestation. Negative and significant GCA effect for *Striga* damage.	Lack of significant and positive GCA effects for grain yield under low N and drought. Lack of negative significant GCA for number of emerged *Striga* plants and stay-green character under drought and low N.	TZEEI 6, TZEEI 38, TZEEI 37, TZEEI 29, TZEEI 90, TZEEI 4, TZEEI 39, TZEEI 3, TZEEI 32, TZEEI 21, TZEEI 49, TZEEI 46, and TZEEI 13
TZEEI 13	Significant and positive GCA effects for grain yield under *Striga* and low N. Significant and negative GCA effect for stay-green character under low N and *Striga* damage.	Lack of significant and positive GCA effects for grain yield under drought. Lack of negative significant GCA for *Striga* emergence and stay-green character under drought.	TZEEI 6, TZEEI 38, TZEEI 37, TZEEI 29, TZEEI 90, TZEEI 4, TZEEI 39, TZEEI 3, TZEEI 32, TZEEI 55, TZEEI 54, TZEEI 57, and TZEEI 14

(continued)

Table 7.3 (continued)

Testers	Desirable attributes of inbred tester	Weaknesses of inbred tester	Tester combiners
TZdEEI 50	Positive and significant GCA effect for grain yield under *Striga* and drought. Negative and significant GCA effect for *Striga* damage.	Lack of significant positive GCA effect for grain yield under low N. Lack of negative and significant GCA for stay-green character under low N. Lack of significant negative GCA effects for number of emerged *Striga* plants.	TZdEEI 21, TZdEEI 25, TZdEEI 42, TZdEEI 45, TZdEEI 46, TZdEEI 68, TZdEEI 69, TZdEEI 85, TZdEEI 105, TZdEEI 108, TZdEEI 44, TZdEEI 49, TZdEEI 51, TZdEEI 56, TZdEEI 71, TZdEEI 75, TZdEEI 90, TZdEEI 100, TZdEEI 103, TZdEEI 104, TZdEEI 16, TZdEEI 17, TZdEEI 20, TZdEEI 31, TZdEEI 33, TZdEEI 54, TZdEEI 58, TZdEEI 66, TZdEEI 70, TZdEEI 76, TZdEEI 78, TZdEEI 94, TZdEEI 95, TZdEEI 102, TZdEEI 22, TZdEEI 23, TZdEEI 24, TZdEEI 34, TZdEEI 43, TZdEEI 55, TZdEEI 62, TZdEEI 73, TZdEEI 74, TZdEEI 80, TZdEEI 81, TZdEEI 82, TZdEEI 84, TZdEEI 91, TZdEEI 96, TZdEEI 99, and TZdEEI 107

The molecular marker approach complements the multivariate approach in classifying inbred lines to heterotic groups. Inbred lines from CIMMYT and IITA appear to belong to different heterotic groups, and they combine very well in producing high-yielding hybrids. Testers for CIMMYT inbred lines were identified from IITA lines and vice versa, as well as testers for yellow and white early and extra-early IITA inbred lines under the various stress and non-stress environmental conditions. Classification of the same inbred to different heterotic groups in different studies frequently occurs in maize breeding. To overcome this problem, some earlier workers proposed a method designated heterotic groups' specific and general combining ability (HSGCA) that combines both SCA and GCA effects for heterotic grouping of lines. Though found effective when applied for grouping early and extra-early maize lines in SSA, the method was based only on grain yield. Therefore, a modification of the method designated HGCAMT was proposed in the studies summarized here. The method, which is the genetic value measuring the relationship among genotypes based on the GCA of multiple traits i to n, was found to be a more appropriate method for assigning inbred lines into heterotic groups particularly under stress conditions and when GCA is more important than SCA in genetic studies.

Table 7.4 Characteristics of extra-early maturing yellow and provitamin A inbred testers

Tester group	Grain color	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZEEI 58	Yellow	Positive and significant GCA effect for grain yield under *Striga.*	Lack of significant negative GCA for number of emerged *Striga* plants and *Striga* damage. Lack of significant negative GCA for stay-green characteristic under low N.	TZEEI 95, TZEEI 72, TZEEI 83, TZEEI 93, TZEEI 82, TZEEI 66, TZEEI 64, TZEEI 76, TZEEI 68, TZEEI 89, TZEEI 63, TZEEI 88, TZdEEI 5, TZdEEI 7, TZdEEI 12, TZEEI 95, TZdEEI 4, and TZdEEI 13
TZEEI 63	Yellow		Lack of significant negative GCA for *Striga* emergence and damage. Lack of significant negative GCA for stay-green character under low N.	TZEEI 95, TZEEI 72, TZEEI 83, TZEEI 93, TZEEI 82, TZEEI 66, TZEEI 58, TZEEI 73, TZEEI 87, TZEEI 67, TZEEI 94, TZEEI 81, TZEEI 79, TZEEI 96, TZdEEI 5, TZdEEI 7, TZdEEI 12, TZdEEI 4, and TZdEEI 13
TZEEI 79	Yellow	Significant positive GCA effects for grain yield under *Striga* and low N. Significant negative GCA effects for *Striga* damage and stay-green character under low N.	Lack of significant negative GCA for number of emerged *Striga* plants and stay-green character under drought. Lack of significant positive GCA effects for grain yield under drought.	TZEEI 95, TZEEI 72, TZEEI 83, TZEEI 93, TZEEI 82, TZEEI 66, TZEEI 64, TZEEI 76, TZEEI 68, TZEEI 89, TZEEI 63, TZEEI 88, TZdEEI 5, TZdEEI 7, TZdEEI 12, TZdEEI 4, and TZdEEI 13
TZEEI 95	Yellow	Significant negative GCA effects for grain yield under low N and *Striga.* Significant negative GCA effects for number of emerged *Striga* plants.	Lack of significant negative GCA for stay-green characteristic under low N. Lack of significant negative GCA for *Striga* damage.	TZEEI 64, TZEEI 76, TZEEI 68, TZEEI 89, TZEEI 63, TZEEI 88, TZEEI 58, TZEEI 73, TZEEI 87, TZEEI 67, TZEEI 94, TZEEI 81, TZEEI 79, TZEEI 96, TZdEEI 1, TZdEEI 9, and TZdEEI 11

(continued)

Table 7.4 (continued)

Tester group	Grain color	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZdEEI 7	Yellow	Significant negative GCA effects for *Striga* damage.	Lack of significant negative GCA effects for number of emerged *Striga* plants Lack of significant negative GCA effects for stay-green characteristic under drought and low N.	TZdEEI 1, TZdEEI 9, TZdEEI 11, TZEEI 58, TZEEI 63 and TZEEI 79, TZdEEI 4 and TZdEEI 13, TZEEI 64, TZEEI 76, TZEEI 68, TZEEI 89, TZEEI 63, TZEEI 88, TZEEI 58, TZEEI 73, TZEEI 87, TZEEI 67, TZEEI 94, TZEEI 81, TZEEI 79, and TZEEI 96
TZdEEI 12	Yellow	Significant negative GCA effects for *Striga* damage.	Lack of significant negative GCA effects for number of emerged *Striga* plants under *Striga*. Lack of significant stay green characteristic under drought.	TZdEEI 1, TZdEEI 9, TZdEEI 11, TZEEI 58, TZEEI 63 and TZEEI 79, TZdEEI 4, and TZdEEI 13
TZEEI 81	Yellow	Significant negative GCA effects for grain yield under low N and *Striga*. Significant negative GCA effects for *Striga* damage.	Lack of significant negative GCA effects for number of emerged *Striga* plants. Lack of significant negative GCA effects for stay-green character under low N.	TZEEI 95, TZEEI 72, TZEEI 83, TZEEI 93, TZEEI 82, TZEEI 66, TZEEI 64, TZEEI 76, TZEEI 68, TZEEI 89, TZEEI 63, TZEEI 88, TZdEEI 5, TZdEEI 7, TZdEEI 12, TZEEI 95, TZdEEI 4, and TZdEEI 13
TZEEI 67	Yellow	Significant and negative GCA effects for grain yield under low N and *Striga*. Significant and negative GCA effects for grain yield under low N and *Striga*.	Lack of significant and negative GCA effects for number of emerged *Striga* plants and *Striga* damage. Lack of significant and negative GCA effects for stay-green characteristic under low N.	TZEEI 95, TZEEI 72, TZEEI 83, TZEEI 93, TZEEI 82, TZEEI 66, TZEEI 64, TZEEI 76, TZEEI 68, TZEEI 89, TZEEI 63, TZEEI 88, TZdEEI 5, TZdEEI 7, TZdEEI 12, TZEEI 95, TZdEEI, 4 and TZdEEI 13

(continued)

Table 7.4 (continued)

Tester group	Grain color	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZEEIOR 30	Orange	Positive and significant GCA effects for grain yield under *Striga*. Positive and significant GCA effects for stay-green characteristic under low N. Positive and significant GCA effects for *Striga* damage	Lack of significant and positive GCA effects for grain yield under drought.	TZEEIOR 11, TZEEI 76, TZEEI 81, TZEEIOR 92, TZEEIOR 197, TZEEIOR 249, TZEEIOR 251, TZEEIOR 35, TZEEIOR 42, TZEEI 79, TZEEIOR 109, TZEEIOR 139, TZEEIOR 140, TZEEIOR 146, TZdEEI 13, TZEEI 58, TZEEI 69, TZEEI 82, TZEEI 96, TZEEI 63, TZEEI 64, TZEEI 68, TZEEI 73, TZEEI 95, and TZEEIOR 102
TZEEIOR 197	Orange	Positive and significant GCA effects for grain yield under drought and low N. Positive and significant GCA effects for grain yield under *Striga*	Lack of significant and positive GCA effects for grain yield under drought.	TZEEIOR 35, TZEEIOR 42, TZEEI 79, TZEEIOR 109, TZEEIOR 139, TZEEIOR 140, TZEEIOR 146, TZdEEI 13, TZEEI 58, TZEEI 69, TZEEI 82 and TZEEI 96, TZEEI 63, TZEEI 64, TZEEI 68, TZEEI 73, TZEEI 95, TZEEIOR 102, TZdEEI 7, TZdEEI 9, TZdEEI 12, TZEEIOR 30, TZEEIOR 41, TZEEIOR 47, TZEEIOR 76, TZEEIOR 97, TZEEIOR 99, TZEEIOR 123, TZEEIOR 125, and TZEEIOR 161

Table 7.5 Characteristics of early-maturing white inbred testers

Tester group	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZEI 7	Significant and positive GCA effects for grain yield under low N. Significant and negative GCA effects for stay-green characteristic under drought.	Lack of significant and positive GCA effects for grain yield under drought. Lack of significant and negative GCA effects for stay-green under low N.	TZEI 3A, ENT 3, TZEI 1, TZEI 48, TZEI 63, TZEI 65, TZEI 82, TZEI 19, TZEI 22, TZEI 100, TZEI 198, TZEI 229, and TZEI 56, TZEI 386, TZEI 387, TZEI 398, TZdEI 198, TZEI 188, TZEI 368, TZEI 357, TZdEI 102, TZEI 7, TZEI 332, and TZEI 371
TZEI 31		Lack of significant and positive GCA effects for grain yield under *Striga.* Lack of significant and negative GCA effects for number of emerged *Striga* plants and *Striga* damage.	TZEI 3A, TZEI 100, TZEI 361, TZEI 386, TZEI 387, TZEI 398, TZdEI 198, TZEI 188, TZEI 368, TZEI 357, TZdEI 102, TZEI 7, TZEI 18, TZEI 107, TZEI 357, TZEI 390, TZEI 229
TZEI 18		Lack of positive and significant GCA effects for grain yield under *Striga* infestation. Lack of negative and significant GCA effects for number of emerged *Striga* plants and *Striga* damage.	ENT 3, TZEI 3A, TZEI 1, TZEI 48, TZEI 63, TZEI 65, TZEI 82, TZEI 19, TZEI 22, TZEI 100, TZEI 198, TZEI 229, and TZEI 56, TZEI 386, TZEI 387, TZEI 398, TZdEI 198, TZEI 188, TZEI 368, TZEI 357, TZdEI 102, TZEI 7, TZEI 332, and TZEI 371
TZEI 19		Lack of significant and positive GCA effects for grain yield under drought and low N.	ENT 7, ENT 10, ENT 11, ENT 12, ENT 16, TZEI 18, TZEI 30, TZEI 7 ENT 3, TZEI 1, TZEI 48, and TZEI 63
TZdEI 352	Significant and positive GCA effects for grain yield under artificial *Striga* infestation and optimal growing environments. Significant and negative GCA effects for *Striga* damage at 8 and 10 WAP. Significant and negative GCA for number of emerged *Striga* plants at 10 WAP. Tolerance to drought stress.		TZEI 5, TZEI 31, TZEI 56, TZEI 18, TZEI 80, TZEI 296, TZdEI 120, TZdEI 425, TZEI 326, TZEI 352, TZEI 383, TZEI 355 and TZEI 410, TZdEI 485, TZdEI 479, TZdEI 399, TZdEI 396, TZdEI 357, TZdEI 441, TZdEI 84, TZdEI 315, TZdEI 378, TZdEI 314, TZdEI 202, TZdEI 120, TZdEI 551, TZdEI 492, TZdEI 98, TZdEI 157, TZdEI 131, TZdEI 124, TZdEI 82, and TZdEI 71

(continued)

Table 7.5 (continued)

Tester group	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZdEI 100	Positive and significant GCA effects for grain yield under *Striga* infestation. Negative and significant GCA effects for *Striga* damage.	Lack of significant and negative GCA effects for number of emerged *Striga* plants.	TZEI 386, TZEI 387, TZEI 398, TZdEI 198, TZEI 188, TZEI 368, TZEI 357, TZdEI 102, TZEI 7, TZEI 18, TZEI 107, TZEI 357, TZEI 390, TZEI 229, TZEI 31, TZEI 332, and TZEI 371

Table 7.6 Characteristics of early yellow maturing and provitamin A inbred testers

Tester group	Grain color	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZEI 129	Yellow	Significant and positive GCA effects for grain yield under drought and low N.	Lack of significant and negative GCA effects for stay-green characteristic under low N and drought.	ENT 17, TZEI 123, TZEI 12, TZEI 149, TZEI 158, TZEI 161, TZEI 178, TZEI 8, TZEI 23, ENT 13, and ENT 4
TZEI 17	Yellow	Significant and positive GCA effects for grain yield under low N. Significant and negative GCA effects for stay-green characteristic under drought stress.	Lack of significant and positive GCA effects for grain yield under drought. Lack of significant and negative GCA effects for stay green characteristic under low N.	ENT 17, TZEI 123, TZEI 12, TZEI 149, TZEI 158, TZEI 161, TZEI 178, TZEI 8, TZEI 23, ENT 13, and ENT 4
TZEI 23	Yellow	Positive and significant GCA effects for grain yield under *Striga* infestation. Significant and negative GCA effect for *Striga* damage.	Lack of significant and positive GCA effects for grain yield under low N and drought. Lack of significant and negative GCA effects for stay-green characteristic under low N and drought.	ENT 17, TZEI 123, TZEI 12, TZEI 129, TZEI 17, TZEI 16, ENT 13, and ENT 4

(continued)

Table 7.6 (continued)

Tester group	Grain color	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
ENT 13	Yellow	Positive and significant GCA effects for grain yield under drought and low N.	Lack of significant and negative GCA effects for stay-green characteristic under low N and drought.	ENT 17, TZEI 123, TZEI 12, TZEI 149, TZEI 158, TZEI 161, TZEI 178, TZEI 8, TZEI 23, TZEI 129, TZEI 17, and TZEI 16
TZEI 10	Yellow	Negative and significant GCA effects for number of emerged *Striga* plants.	Lack of significant and positive GCA effects for grain yield under *Striga*, low N, and drought. Lack of significant and negative GCA effects for *Striga* damage and stay-green characteristic under low N.	TZEI 430, TZEI 470, TZEI 472, TZEI 507, TZEI 449, TZEI 450, TZEI 16, TZEI 433, TZEI 439, TZEI 443, TZEI 461, TZEI 474, TZEI 483, TZEI 484, TZEI 495, TZEI 515, TZEI 516, TZEI 518, TZEI 522, TZEI 455, TZEI 494, TZEI 160, TZEI 415, TZEI 428, TZEI 442, TZEI 464, TZEI 508, TZEI 520, TZEI 161, TZEI 173, ENT 8, ENT 17
TZEI 563	Yellow	Negative and significant GCA effect for number of emerged *Striga* plants.	Lack of significant and positive GCA effect for grain yield under *Striga.*	TZEI 601, TZEI 552, TZEI 558, TZEI 534, TZEI 603, TZEI 549, TZEI 604, TZEI 557, TZEI 608, TZEI 492, TZEI 459, TZEI 561, TZEI 503, TZdEI 51, TZEI 595, TZEI 572, TZEI 587, TZEI 23, TZEI 598, TZEI 124, TZEI 609, TZEI 559, TZEI 582, TZEI 544, TZEI 422, TZEI 615, TZEI 617, TZEI 585, TZEI 560, TZEI 620, TZEI 547, TZEI511, TZEI 562, TZEI 10, TZEI600, TZEI 619, TZEI 554, TZEI 584, TZEI 502, TZEI 602, TZEI 567, TZEI 539, TZEI 594, TZEI 574, TZEI 578, TZEI 496, TZEI 550, TZEI 466, TZEI 426, TZEI 129, TZEI 551, ENT 13

(continued)

Table 7.6 (continued)

Tester group	Grain color	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZEI 595	Yellow	Negative and significant GCA effect for number of emerged *Striga* plants. Negative and significant GCA effect for anthesis–silking interval across environments.	Lack of significant and positive GCA effect for grain yield under *Striga* infestation.	TZEI 601, TZEI 552, TZEI 558, TZEI 534, TZEI 603, TZEI 549, TZEI 604, TZEI 557, TZEI 608, TZEI 492, TZEI 459, TZEI 561, TZEI 503, TZdEI 51, TZEI 610, TZEI 416, TZEI 586, TZEI 576, TZEI 540, TZEI 597, TZEI 599, TZEI 571, TZEI 563, TZEI 448, TZEI 25
TZEIOR 108	Orange	Significant and positive GCA effects for grain yield under drought and *Striga* infestation.		TZEIOR 9, TZEIOR 11, TZEIOR 12, TZEIOR 13, TZEIOR 42, TZEIOR 24, TZEI 10, TZEI 17, TZEIOR 57, TZEIOR 56, TZEIOR 58, TZEIOR 59, TZEIOR 60
TZEI 129	Orange	Significant and positive GCA effects for grain yield under drought and *Striga* infestation.		TZEI 432,TZEI 441,TZEI 182,TZEI 24,TZEI 175, TZEI 430,TZEI 470,TZEI 472,TZEI 507,TZEI 449,TZEI 450,TZEI 16, TZEI 433,TZEI 439,TZEI 443,TZEI 461,TZEI 474,TZEI 483,TZEI 484,TZEI 495,TZEI 515,TZEI 516,TZEI 518,TZEI 522,TZEI 455,TZEI 494,TZEI 160, TZEI 442,TZEI 464,TZEI 508,TZEI 520,TZEI 161,TZEI 173,ENT 8, ENT 17
TZEIORQ 40	Orange	Significant and positive GCA effects for grain yield under low N.	Lack of significant and negative GCA effects for stay-green under low N.	TZEIORQ 45, TZEIORQ 23, TZEIORQ 24, TZEIORQ 44,TZEIORQ 6, TZEIORQ 15, TZEIORQ 41, TZEIORQ 43, TZEIORQ 7, TZEIORQ 29, TZEIORQ 11, TZEIORQ 59, TZEIORQ 48, TZEIORQ 2, TZEIORQ 70, TZEQI 82

(continued)

Table 7.6 (continued)

Tester group	Grain color	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZEIORQ 43	Orange	Significant and positive GCA effects for grain yield under drought and low N.	Lack of significant and negative GCA effects for stay-green characteristic under low N.	TZEIORQ 45, TZEIORQ 23, TZEIORQ 24, TZEIORQ 44, TZEIORQ 29, TZEIORQ 11, TZEIORQ 59, TZEIORQ 48, TZEIORQ 2, TZEIORQ 70, TZEQI 82, TZEIORQ 69, TZEIORQ 20, TZEIORQ 26, TZEIORQ 5, TZEIORQ 40, TZEIORQ 42, TZEIORQ 47, TZEIORQ 13
TZEIORQ 44	Orange	Significant and positive GCA effects for grain yield under drought and low N.	Lack of significant and negative GCA effects for stay-green under low N.	TZEIORQ 29, TZEIORQ 11, TZEIORQ 59, TZEIORQ 48, TZEIORQ 2, TZEIORQ 70, TZEQI 82, TZEIORQ 69, TZEIORQ 20, TZEIORQ 26, TZEIORQ 5, TZEIORQ 40, TZEIORQ 42, TZEIORQ 47, TZEIORQ 13, TZEIORQ 6, TZEIORQ 15, TZEIORQ 41, TZEIORQ 43, TZEIORQ 7
TZEIORQ 59	Orange	Significant positive GCA effects for grain yield under drought and low N. Significant negative GCA effects for stay-green characteristic under drought and low N.	Lack of significant and negative GCA effects for anthesis–silking interval under drought.	TZEIORQ 69, TZEIORQ 20, TZEIORQ 26, TZEIORQ 5, TZEIORQ 40, TZEIORQ 42, TZEIORQ 47, TZEIORQ 13, TZEIORQ 6, TZEIORQ 15, TZEIORQ 41, TZEIORQ 43, TZEIORQ 7, TZEIORQ 45, TZEIORQ 23, TZEIORQ 24, TZEIORQ 44

Table 7.7 Characteristics of extra-early maturing and early-maturing QPM white inbred testers

Tester group	Grain color	Maturity group	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZEEQI 7	White	Extra-early	Positive and significant GCA for grain yield under drought and low N.	Lack of negative and significant stay-green character under low N and drought.	TZEEQI 60, TZEEQI 109, TZEEQI 134, TZEEQI 183, TZEEQI 3, TZEEQI 8, TZEEQI 102, TZEEQI 44, TZEEQI 11, TZEEQI 52, TZEEQI 101, TZEEQI 144, TZEEQI 63, TZEEQI 190, TZEEQI 38, TZEEQI 145, TZEEQI 96, TZEEQI 66, and TZEEQI 157
TZEEQI 134	White	Extra-early	Positive and significant GCA for grain yield under drought and low N.	Lack of negative and significant stay-green character under low N and drought.	TZEEQI 1, TZEEQI 7, TZEEQI 61, TZEEQI 181, ZEEQI 137, TZEEQI 3, TZEEQI 8, TZEEQI 102, TZEEQI 44, TZEEQI 11, TZEEQI 52, TZEEQI 101, TZEEQI 144, TZEEQI 63, TZEEQI 190, TZEEQI 38, TZEEQI 145, TZEEQI 96, TZEEQI 66 and TZEEQI 157
TZEQI 6	White	Early	Significant and positive GCA effects for grain yield under low N. Significant and negative GCA effects for *Striga* damage and number of emerged *Striga* plants.	Lack of significant and positive GCA for grain yield under drought. Lack of significant and positive GCA for grain yield under *Striga*.	TZEQI 15, TZEQI 24, TZEQI 34, TZEQI 39, TZEQI 44, TZEQI 45, TZEQI 49, TZEQI 55, TZEQI 56, TZEQI 59, and TZEQI 60

(continued)

Table 7.7 (continued)

Tester group	Grain color	Maturity group	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZEQI 55	White	Early	Significant and positive GCA effects for grain yield under low N and *Striga.* Significant and negative GCA effects for stay-green character under drought and low N.	Lack of significant and positive GCA for grain yield under drought. Lack of significant and negative GCA effects for *Striga* damage and number emerged *Striga* plants.	TZEQI 14, TZEQI 16, TZEQI 17, TZEQI 18, TZEQI 23, TZEQI 25, TZEQI 26, TZEQI 27, TZEQI 28, TZEQI 29, TZEQI 30, TZEQI 4, TZEQI 5, TZEQI 6, TZEQI 12, TZEQI 13, TZEQ, 22, TZEQI 33, and TZEQI 35
TZEQI 87	Yellow	Early	Significant and positive GCA effects for grain yield under *Striga.* Significant and negative GCA effects for stay-green characteristic under drought and low N. Significant and negative GCA effects for *Striga* damage.	Lack of significant and positive GCA effects for grain yield under drought and low N. Lack of significant and negative GCA effects for number of emerged *Striga* plants.	TZEQI 80, TZEQI 81, TZEQI 82, TZEQI 91, TZEQI 93, TZEQI 92
TZEQI 91	Yellow	Early	Significant and positive GCA effects for grain yield under *Striga.* Significant and positive GCA effects for grain yield under drought and low N.	Lack of significant and negative GCA effects for *Striga* damage and number of emerged *Striga* plants. Lack of significant and negative GCA effects for stay-green characteristic under drought and low N.	TZEQI 74, TZEQI 87, TZEQI 89, TZEQI 84, TZEQI 76, TZEQI 77, TZEQI 78, TZEQI 79, TZEQI 80, TZEQI 81, TZEQI 82

Table 7.8 Characteristics of early-maturing white and yellow QPM inbred testers

Tester group	Grain color	Desirable attributes of inbred tester	Defects of inbred tester	Tester combiners
TZEQI 6	White	Significant and positive GCA effects for grain yield under low N. Significant and negative GCA effects for *Striga* damage and number of emerged *Striga* plants.	Lack of significant and positive GCA for grain yield under drought. Lack of significant and positive GCA for grain yield under *Striga*.	TZEQI 15, TZEQI 24, TZEQI 34, TZEQI 39, TZEQI 44, TZEQI 45, TZEQI 49, TZEQI 55, TZEQI 56, TZEQI 59, and TZEQI 60
TZEQI 55	White	Significant and positive GCA effects for grain yield under low N and *Striga*. Significant and negative GCA effects for stay-green characteristic under drought and low N.	Lack of significant and positive GCA for grain yield under drought. Lack of significant and negative GCA effects for *Striga* damage and number of emerged *Striga* plants.	TZEQI 14, TZEQI 16, TZEQI 17, TZEQI 18, TZEQI 23, TZEQI 25, TZEQI 26, TZEQI 27, TZEQI 28, TZEQI 29, TZEQI 30, TZEQI 4, TZEQI 5, TZEQI 6, TZEQI 12, TZEQI 13, TZEQ, 22, TZEQI 33, and TZEQI 35
TZEQI 87	Yellow	Significant and positive GCA effects for grain yield under *Striga*. Significant and negative GCA effects for stay-green character under drought and low N. Significant and negative GCA effects for *Striga* damage.	Lack of significant and positive GCA effects for grain yield under drought and low N. Lack of significant negative GCA effects for number of emerged *Striga* plants.	TZEQI 80, TZEQI 81, TZEQI 82, TZEQI 91, TZEQI 93, and TZEQI 92
TZEQI 91	Yellow	Significant and positive GCA effects for grain yield under *Striga*. Significant and positive GCA effects for grain yield under drought and low N.	Lack of significant and negative GCA effects for *Striga* damage and number of emerged *Striga* plants. Lack of significant and negative GCA effects for stay-green characteristic under drought and low N.	TZEQI 74, TZEQI 87, TZEQI 89, TZEQI 84, TZEQI 76, TZEQI 77, TZEQI 78, TZEQI 79, TZEQI 80, TZEQI 81, TZEQI 82

Table 7.9 Characteristics of early and extra-early single-cross testers

Testers	Maturity and color	Desirable attributes of the parental inbred lines and the tester	Tester combiners
TZEI 7 x TZdEI 352	Early/ white	Both TZEI 7 and TZdEI 352 had positive and significant GCA effect for grain yield under *Striga*-infested and *Striga*-free environments. TZdEI 352 had negative and significant GCA effect for *Striga* damage and emerged *Striga* plants (10 WAP). TZEI 7 and TZdEI 352 belong to the same heterotic group.	TZEI 5, TZEI 31, TZEI 56, TZEI 18, TZEI 80, TZEI 296, TZdEI 120, TZdEI 425, TZEI 326, TZEI 352, TZEI 383, TZEI 355, and TZEI 410
TZEI 462 x TZEI 10	Early/ yellow	TZEI 462 had positive and significant GCA effect for grain yield under *Striga* and low N. TZEI 10 had positive and significant GCA effect for grain yield under *Striga* and negative and significant GCA effect for *Striga* damage and emerged *Striga* plants (10 WAP). TZEI 462 and TZEI 10 belong to the same heterotic group.	TZEI 428, TZEI 450, TZEI 439, TZEI 442, TZEI 461, TZEI 464, TZEI 449, TZEI 483, TZEI 484, TZEI 182, TZEI 470, TZEI 472, TZEI 24, TZEI 515, TZEI 516, TZEI 518, TZEI 507, TZEI 455, TZEI 160, TZEI 161, TZEI 415, TZEI 430, TZEI 433, TZEI 441, TZEI 124, TZEI 432, ENT 13, ENT 8, and ENT 17
TZEI 584 x ENT 13	Early/ yellow	TZEI 584 had positive and significant GCA effect for grain yield under *Striga.* ENT 13 had positive and significant GCA effect for grain yield under *Striga.* TZEI 584 and ENT 13 belong to the same heterotic group.	TZEI 601, TZEI 552, TZEI 558, TZEI 534, TZEI 603, TZEI 549, TZEI 604, TZEI 557, TZEI 608, TZEI 492, TZEI 459, TZEI 561, TZEI 503, TZdEI 51, TZEI 610, TZEI 416, TZEI 586, TZEI 576, TZEI 540, TZEI 597, TZEI 599, TZEI 571, TZEI 563, TZEI 448, TZEI 25
TZEI 124 x ENT 13	Early/ yellow	TZEI 124 × ENT 13 had positive and significant SCA effects for grain yield across environments. TZEI 124 had positive and significant GCA effect for grain yield across environments. ENT 13 had positive and significant GCA effect for grain yield across environments. TZEI 124 and ENT 13 belong to the same heterotic group.	TZEI 601, TZEI 517, TZEI 610, TZEI 422, TZEI 519, TZEI 492, TZEI 23, TZEI 557, TZEI 534, TZEI 511, TZEI 503, TZEI 459, TZEI 608, TZEI 603, TZEI 539, TZEI 496, TZEI 598, TZEI 426, TZEI 25, TZEI 617, TZEI 572, TZEI 558, TZEI 551, TZEI 574, TZEI 587, TZEI 416, TZEI 615, TZEI 609, TZEI 547, TZEI 604, TZEI 10, TZEI 447, TZEI 600, TZEI 561, TZEI 549, TZEI 552, TZdEI 51

(continued)

Table 7.9 (continued)

Testers	Maturity and color	Desirable attributes of the parental inbred lines and the tester	Tester combiners
TZEI 584 x ENT 13	Early/ yellow	TZEI 584 × ENT 13 had positive and significant SCA effect for grain yield across environments. TZEI 584 had positive and significant GCA effect for grain yield under *Striga.* TZEI 584 had positive and significant GCA effect for grain yield across environments. ENT 13 had positive and significant GCA effect for grain yield across environments. TZEI 584 and ENT 13 belong to the same heterotic group.	TZEI 601, TZEI 517, TZEI 610, TZEI 422, TZEI 519, TZEI 492, TZEI 23, TZEI 557, TZEI 534, TZEI 511, TZEI 503, TZEI 459, TZEI 608, TZEI 603, TZEI 539, TZEI 496, TZEI 598, TZEI 426, TZEI 25, TZEI 617, TZEI 572, TZEI 558, TZEI 551, TZEI 574, TZEI 587, TZEI 416, TZEI 615, TZEI 609, TZEI 547, TZEI 604, TZEI 10, TZEI 447, TZEI 600, TZEI 561, TZEI 549, TZEI 552, TZdEI 51
TZEI 550 x ENT 13	Early/ yellow	TZEI 550 × ENT 13 had positive and significant SCA effect for grain yield across environments. TZEI 124 had positive and significant GCA effect for grain yield across environments. ENT 13 had positive and significant GCA effect for grain yield across environments. TZEI 550 and ENT 13 belong to the same heterotic group.	TZEI 601, TZEI 517, TZEI 610, TZEI 422, TZEI 519, TZEI 492, TZEI 23, TZEI 557, TZEI 534, TZEI 511, TZEI 503, TZEI 459, TZEI 608, TZEI 603, TZEI 539, TZEI 496, TZEI 598, TZEI 426, TZEI 25, TZEI 617, TZEI 572, TZEI 558, TZEI 551, TZEI 574, TZEI 587, TZEI 416, TZEI 615, TZEI 609, TZEI 547, TZEI 604, TZEI 10, TZEI 447, TZEI 600, TZEI 561, TZEI 549, TZEI 552, TZdEI 51
TZEI 586 x ENT 13	Early/ yellow	TZEI 586 × ENT 13 had positive and significant SCA effect for grain yield across environments. TZEI 586 had positive and significant GCA effect for grain yield under *Striga.* TZEI 124 had positive and significant GCA effect for grain yield across environments. ENT 13 had positive and significant GCA effect for grain yield across environments. TZEI 586 and ENT 13 belong to the same heterotic group.	TZEI 601, TZEI 517, TZEI 610, TZEI 422, TZEI 519, TZEI 492, TZEI 23, TZEI 557, TZEI 534, TZEI 511, TZEI 503, TZEI 459, TZEI 608, TZEI 603, TZEI 539, TZEI 496, TZEI 598, TZEI 426, TZEI 25, TZEI 617, TZEI 572, TZEI 558, TZEI 551, TZEI 574, TZEI 587, TZEI 416, TZEI 615, TZEI 609, TZEI 547, TZEI 604, TZEI 10, TZEI 447, TZEI 600, TZEI 561, TZEI 549, TZEI 552, TZdEI 51

(continued)

Table 7.9 (continued)

Testers	Maturity and color	Desirable attributes of the parental inbred lines and the tester	Tester combiners
TZEQI 34 x TZEQI 55	Early/ white QPM	TZEQI 34 had significant positive GCA effect for grain yield under drought, low N, and across environments. TZEQI 34 had significant negative GCA effect for *Striga* damage (10 WAP) and emerged *Striga* plants (10 WAP). TZEQI 55 had significant positive GCA effect for grain yield under low N, *Striga*, and across environments. TZEQI 34 and TZEQI 55 had significant negative GCA effect for stay-green characteristic. TZEQI 34 and TZEQI 55 belong to the same heterotic group.	TZEQI 4, TZEQI 5, TZEQI 6, TZEQI 12, TZEQI 13, TZEQI 22, TZEQI 33, TZEQI 35, TZEQI 14, TZEQI 16, TZEQI 17, TZEQI 18, TZEQI 23, TZEQI 25, TZEQI 26, TZEQI 27, TZEQI 28, TZEQI 29, and TZEQI 30
TZEQI 6 x TZEQI 12	Early/ white QPM	TZEQI 6 had significant positive GCA effect for grain yield under low N and across environments. TZEQI 12 had significant positive GCA effect for grain yield under low N, *Striga*, and across environments. TZEQI 6 and TZEQI 12 had significant negative GCA effect for *Striga* damage and emerged *Striga* plants (10 WAP). TZEQI 6 and TZEQI 12 belong to the same heterotic group.	TZEQI 14, TZEQI 16, TZEQI 17, TZEQI 18, TZEQI 23, TZEQI 25, TZEQI 26, TZEQI 27, TZEQI 28, TZEQI 29, TZEQI 30.TZEQI 15, TZEQI 24, TZEQI 34, TZEQI 39, TZEQI 44, TZEQI 45, TZEQI 49, TZEQI 55, TZEQI 56, TZEQI 59, and TZEQI 60
TZEQI 87 x TZEQI 89	Early/ yellow QPM	TZEQI 87 had significant and positive GCA effect for grain yield under *Striga* and across drought, low N, and *Striga* environments. TZEQI 87 had significant negative GCA effect for stay-green characteristic under drought and low N. TZEQI 89 had significant GCA effect for grain yield under drought, low N, optimal and across environments. TZEQI 87 and TZEQI 89 belong to the same heterotic group.	TZEQI 84, TZEQI 91, TZEQI 92, and TZEQI 93

(continued)

Table 7.9 (continued)

Testers	Maturity and color	Desirable attributes of the parental inbred lines and the tester	Tester combiners
TZEQI 92 x TZEQI 93	Early/ yellow QPM	TZEQI 92 had positive and significant GCA effect for grain yield under drought, low N, *Striga*, and optimal and across environments. TZEQI 92 had significant negative GCA effect for *Striga* damage (10 WAP). TZEQI 93 had significant and positive GCA effects for grain yield under drought, low N, optimal and across environments.	TZEQI 74, TZEQI 89, TZEQI 87, TZEQI 76, TZEQI 78, TZEQI 79, TZEQI 77, TZEQI 80, TZEQI 82, and TZEQI 81
TZEIORQ 42 x TZEIORQ 20	Early PVA QPM	TZEIORQ 42 had positive and significant GCA effect for grain yield under drought, low N, and optimal and across environments. TZEIORQ 20 had significant and positive GCA effects for grain yield under drought and low N. TZEIORQ 42 and TZEIORQ 20 belong to the same heterotic group.	TZEIORQ 45, TZEIORQ 23, TZEIORQ 24, TZEIORQ 44, TZEIORQ 6, TZEIORQ 15, TZEIORQ 41, TZEIORQ 43, TZEIORQ 7, TZEIORQ 29, TZEIORQ 11, TZEIORQ 59, TZEIORQ 48, TZEIORQ 2, TZEIORQ 70, TZEQI 82
TZEEI 29 x TZdEEI 23	Extra-early white	TZEEI 29 had significant positive GCA effect for grain yield under *Striga.* TZEEI 29 had significant negative GCA effect for *Striga* damage and emerged *Striga* plants (10 WAP). TZdEEI 23 had significant positive GCA effect for grain yield under drought. TZdEEI 23 had significant negative GCA effect for stay-green characteristic under drought. TZEEI 29 and TZdEEI 23 belong to the same heterotic group.	TZEEI 4, TZEEI 39, TZEEI 3, TZEEI 32, TZEEI 55, TZEEI 54, TZEEI 57, TZEEI 14, TZEEI 21, TZEEI 49, TZEEI 46, and TZEEI 13

(continued)

Table 7.9 (continued)

Testers	Maturity and color	Desirable attributes of the parental inbred lines and the tester	Tester combiners
TZdEEI 34 x TZdEEI 50	Extra-early white	TZdEEI 34 had significant positive GCA effect for grain yield under Striga, low N, and optimal environments. TZdEEI 50 had significant positive GCA effect for grain yield under *Striga* and drought. TZdEEI 34 and TZdEEI 50 had significant negative GCA effect for *Striga* damage (10 WAP)	TZdEEI 21, TZdEEI 25, TZdEEI 42, TZdEEI 45, TZdEEI 46, TZdEEI 68, TZdEEI 69, TZdEEI 85, TZdEEI 105, TZdEEI 108, TZdEEI 44, TZdEEI 49, TZdEEI 51, TZdEEI 56, TZdEEI 71, TZdEEI 75, TZdEEI 90, TZdEEI 100, TZdEEI 103, TZdEEI 104, TZdEEI 16, TZdEEI 17, TZdEEI 20, TZdEEI 31, TZdEEI 33, TZdEEI 54, TZdEEI 58, TZdEEI 66, TZdEEI 70, TZdEEI 76, TZdEEI 78, TZdEEI 94, TZdEEI 95, TZdEEI 102, TZdEEI 22, TZdEEI 23, TZdEEI 24, TZdEEI 34, TZdEEI 43, TZdEEI 55,TZdEEI 62, TZdEEI 73, TZdEEI 74,TZdEEI 80, TZdEEI 81, TZdEEI 82,TZdEEI 84, TZdEEI 91, TZdEEI 96,TZdEEI 99, and TZdEEI 107
TZdEEI 11 x TZEEI 79	Extra-early yellow	TZdEEI 11 had significant positive GCA effect for grain yield under drought. TZEEI 79 had significant negative GCA effect for *Striga* damage (10 WAP). TZdEEI 11 and TZEEI 79 belong to the same heterotic group.	TZdEEI 4, TZdEEI 13, TZdEEI 5, TZEEI 63, TZdEEI 7, TZdEEI 12, and TZdEEI 95
TZdEEI 7 x TZdEEI 12	Extra-early yellow	TZdEEI 7 and TZdEEI 12 had positive and significant GCA effect for grain yield under *Striga*. TZdEEI 7 and TZdEEI 12 belong to the same heterotic group. TZdEEI 7 and TZdEEI 12 had negative and significant GCA effect for *Striga* damage (10 WAP). TZdEEI 12 had positive and significant GCA effect for grain yield under drought.	TZdEEI 1, TZdEEI 9, TZdEEI 11, TZdEEI 4, TZdEEI 13, TZEEI 58, and TZEEI 79

(continued)

Table 7.9 (continued)

Testers	Maturity and color	Desirable attributes of the parental inbred lines and the tester	Tester combiners
TZEEI 95 x TZEEI 79	Extra-early yellow	TZEEI 95 had significant and negative GCA effects for grain yield under low N and *Striga*. TZEEI 95 had significant and negative GCA effects for number of emerged *Striga* plants.	TZEEI 64, TZEEI 76, TZEEI 68, TZEEI 89, TZEEI 63, TZEEI 88, TZEEI 58, TZEEI 73, TZEEI 87, TZEEI 67, TZEEI 94, TZEEI 81, TZEEI 96, TZdEEI 1, TZdEEI 9, TZdEEI 11, TZEEI 72, TZEEI 83, TZEEI 93, TZEEI 82, TZEEI 66, TZdEEI 5, TZdEEI 7, TZdEEI 12, TZdEEI 4, and TZdEEI 13
TZEEIOR 109 x TZEEIOR 197	Extra-early PVA	TZEEIOR 109 and TZEEIOR 197 had significant and positive GCA effects for grain yield across *Striga*, drought, and optimal environments. TZEEIOR 109 and TZEEIOR belong to the same heterotic group. TZEEIOR 197 had significant and negative GCA effect for *Striga* damage at 10 WAP.	TZEEIOR 22, TZEEIOR 24, TZEEIOR 26, TZEEIOR 27, TZEEIOR 28, TZEEIOR 41, TZEEIOR 45, TZEEIOR 97, TZEEIOR 140, TZEEIOR 142, TZEEIOR 205, TZEEIOR 209, TZEEIOR 233, TZEEIOR 234, TZEEIOR 250, and TZEEIOR 251
TZEEIOR 205 x TZEEIOR 250	Extra-early PVA	TZEEIOR 205 and TZEEIOR 250 had significant and positive GCA effects for grain yield across *Striga*, drought, and optimal environments. TZEEIOR 205 and TZEEIOR 250 belong to the same heterotic group. TZEEIOR 250 had significant and negative GCA effect for stay-green characteristic.	TZEEIOR 22, TZEEIOR 24, TZEEIOR 26, TZEEIOR 27, TZEEIOR 28, TZEEIOR 41, TZEEIOR 45, TZEEIOR 30, TZEEIOR 109, TZEEIOR 197, and TZEEIOR 202

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Chapter 8
Molecular Approaches to Maize Improvement

8.1 Introduction

The prime objective of crop improvement is to identify individuals in the heterogeneous population with favorable alleles present at the highest proportion of loci involved in the expression of key traits (Goodman et al. 1987). Conventional plant breeding is based on increasing the chances of selecting such individuals from populations generated from matings. Selection has usually been carried out at the whole-plant or phenotypic level which represents the outcome of the interaction between genotype and environment. Phenotypic selection has resulted in tremendous genetic gains in crops but is severely limited when faced with traits that are largely modulated by the environment (Cooper et al. 2006). Furthermore, the nature of some traits can make the testing procedure complex, unreliable, and expensive. Under such circumstances, indirect selection using molecular markers becomes an efficient complementary breeding tool. The idea is that when target traits can be easily identified and linked with one or more markers, then the marker loci can be used as a surrogate for the trait, resulting in greatly enhanced breeding efficiency. Thus, molecular or marker-assisted breeding (MB) involves the use of DNA markers instead of phenotypic selection to speed up the process of development and release of cultivars. Marker-assisted breeding can be useful for selecting quantitatively inherited traits that are difficult or expensive to measure, exhibit low heritability, and/or are expressed late during the developmental process. At certain points in the breeding program, the genotypes are evaluated in the field to ensure that they express the desired trait. The MB is preferable to conventional breeding when phenotypic screening is particularly expensive or laborious as in situations where root traits, osmotic adjustment, disease resistance, and drought tolerance are being screened; when phenotyping is possible only after flowering, linked marker is codominant, and target gene is dominant; and where environmental influence is strong

B. Badu-Apraku, M.A.B. Fakorede, *Advances in Genetic Enhancement of Early and Extra-Early Maize for Sub-Saharan Africa*,
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(low heritability), as in cases when pyramiding multiple resistant genes and when marker profiles can be obtained from seeds.

There are three different approaches to MB. These are marker-assisted selection (MAS), marker-assisted backcrossing (MABC), and marker-assisted recurrent selection (MARS). Marker-assisted selection involves the transfer of a limited number of loci (e.g., transgene, disease resistance loci, etc.) from one genetic background to another. The MABC involves the selection of individuals with specific alleles for traits controlled by a limited number of loci (up to 6–8). The MARS involves the identification and selection of several genomic regions (up to 20 or even more) for complex traits within a single population.

8.2 Marker-Assisted Selection (MAS)

Marker-assisted selection is an indirect selection process where a trait of interest is selected based on a marker (morphological, biochemical, or DNA/RNA variation) linked to a trait of interest (e.g., productivity, disease resistance, abiotic stress tolerance, and quality), rather than on the trait itself (Ribaut et al. 2001; Rosyara 2006). For example, using MAS to select individuals with disease resistance involves identifying a marker allele that is linked with disease resistance rather than the level of disease resistance. The assumption is that the marker associates at high frequency with the gene or QTL of interest, due to genetic linkage, i.e., close proximity, on the chromosome, of the marker locus and the disease resistance-determining locus.

8.2.1 Types of Markers

There are two broad categories of markers. These are:

Morphological markers Morphological markers are often detectable by the eye, by simple visual inspection. Examples of morphological markers include the presence or absence of an awn, leaf sheath coloration, and plant height. The majority of MAS work in the present era uses DNA-based markers in well-characterized crops such as maize and tomato, where several genes that determine morphological traits have been mapped to specific locations of chromosomes.

Biochemical markers A protein that can be extracted and observed, for example, isozymes and storage proteins:

- *Cytological* markers—The chromosomal banding produced by different stains, for example, G banding.
- *DNA-based or molecular* markers—A unique gene (DNA sequence), occurring in proximity to the gene or locus of interest, can be identified by a range of molecular techniques such as RFLP, RAPD, AFLP, DAF, SCAR, microsatellite, or single nucleotide polymorphism (SNP) detection.

The major advantages of the molecular over the other classes of markers are that their number is potentially unlimited, their dispersion across the genome is complete, their expression is unaffected by the environment, and their assessment is independent of the stage of plant development (Lee 1995). The gene of interest directly causes production of protein(s) or RNA that produce a desired trait or phenotype, whereas markers (a DNA sequence or the morphological or biochemical markers produced due to the DNA) are genetically linked to the gene of interest. The gene of interest and the marker tend to move together during segregation of gametes due to their proximity on the same chromosome and concomitant reduction in recombination (chromosome crossover events) between the marker and gene of interest. For some traits, the gene of interest has been discovered, and the presence of desirable alleles can be directly assayed with a high level of confidence. However, if the gene of interest is not known, markers linked to the gene of interest can still be used to select for individuals with desirable alleles of the gene of interest. When markers are used, there may be some inaccurate results due to inaccurate tests for the marker. There also can be false-positive results when markers are used, due to recombination between the marker of interest and gene (or QTL). A perfect marker would elicit no false-positive results. The term “perfect marker” is sometimes used when tests are performed to detect a SNP or other DNA polymorphism in the gene of interest if that SNP or other polymorphism is the direct cause of the trait of interest. The term “marker” is still appropriate to use when directly assaying the gene of interest, because the test of genotype is an indirect test of the trait or phenotype of interest (https://en.wikipedia.org/wiki/Marker-assistedselection).

8.2.2 *Important Properties of Markers for MAS*

An ideal marker should be easily recognized among all possible phenotypes (homo- and heterozygotes) from all different alleles. It should demonstrate measurable differences in expression between trait types and gene of interest alleles, early in the development of the organism. The testing for the marker has had variable success depending on the allele at the marker locus or the allele at the target locus. Low or null interaction among markers allows the use of many at the same time in a segregating population. Finally, the abundance of the markers and whether or not the markers are polymorphic are important in determining the value of the markers.

8.2.3 *Disadvantages of Morphological Markers*

Morphological markers have several general deficits that reduce their usefulness. These include the delay of marker expression until late into the development of the organism, dominance, deleterious effects, pleiotropy, confounding effects of genes unrelated to the gene or trait of interest but which also affect the morphological marker (epistasis), rare polymorphism, and frequent confounding effects of environmental factors which influence the morphological characteristics of the organism.

To avoid problems characteristic of morphological markers, DNA-based markers have been developed. They are highly polymorphic, exhibit simple inheritance (often codominant), are abundant throughout the genome, are easy and fast to detect, and exhibit minimum pleiotropic effects, and detection is not dependent on the developmental stage of the organism. Numerous markers have been mapped to different chromosomes in several crops including rice, wheat, maize, and soybean. Those markers have been used in diversity analysis, parentage detection, DNA fingerprinting, and prediction of hybrid performance. Molecular markers are useful in indirect selection processes, enabling manual selection of individuals for further propagation.

8.2.4 Selection for Major Genes Linked to Markers

"Major genes" that are responsible for economically important characteristics are frequent in plants. Such characteristics include disease resistance, male sterility, self-incompatibility, and others related to shape, color, and architecture of whole plants and are often of mono- or oligogenic in nature. The marker loci that are tightly linked to major genes can be used for selection and are sometimes more efficient than direct selection for the target gene. Such advantages in efficiency may be due, for example, to higher expression of the marker mRNA in such cases that the marker is actually a gene. Alternatively, in cases where the target gene of interest differs between two alleles by a difficult-to-detect single nucleotide polymorphism, an external marker may be present as the most realistic option.

8.2.5 Favorable Situations for Molecular Marker Selection

There are several examples of the use of molecular markers in the selection of a genetic trait. These include situations where:

- The selected character is expressed late during plant growth and development, such as flowering periods, so that it is not necessary to wait for the maize plant to become fully matured before arrangements can be made for the next growth cycle.
- The expression of the target gene is recessive so that individual plants which are heterozygous positive for the recessive allele can be crossed to produce some homozygous offspring with the desired trait.
- There is requirement for the presence of special conditions in order to invoke expression of the target gene(s), as in the case of breeding for disease and pest resistance where inoculation with the disease or exposure to pests would otherwise

be required. This advantage derives from the errors due to unreliable inoculation methods and the fact that field inoculation with the pathogen is not allowed in many areas for safety reasons. Moreover, problems in the recognition of the environmentally unstable genes can be eluded.

- The phenotype is affected by two or more unlinked genes (epistasis), for example, selection for multiple genes which provide resistance against diseases or insect pests for gene pyramiding.

The cost of genotyping (an example of a molecular marker assay) is reducing, while the cost of phenotyping is increasing particularly in developed countries, thus increasing the attractiveness of MAS as the development of the technology continues (https://en.wikipedia.org/wiki/Marker-assisted_selection).

8.2.6 Steps for MAS

Generally, the first step is to map the gene or quantitative trait locus (QTL) of interest first by using different techniques and then using this information for marker-assisted selection. Generally, the markers to be used should be close to gene of interest (<5 recombination unit or cM) in order to ensure that only minor fraction of the selected individuals will be recombinants. Generally, not only a single marker but rather two markers are used in order to reduce the chances of an error due to homologous recombination. For example, if two flanking markers are used at the same time with an interval between them of approximately 20 cM, there is higher probability (99%) for recovery of the target gene.

8.3 QTL Mapping Techniques

8.3.1 Quantitative Trait Locus and QTL Mapping

In plants, QTL mapping is generally achieved using biparental cross populations; a cross between two parents which have a contrasting phenotype for the trait of interest is developed. Commonly used populations are recombinant inbred lines (RILs), doubled haploids (DH), backcross, and F_2. Linkage between the phenotype and markers which have already been mapped is tested in these populations in order to determine the position of the QTL. Such techniques are based on linkage and are therefore referred to as "linkage mapping."

8.3.1.1 Single-Step MAS and QTL Mapping

In contrast to two-step QTL mapping and MAS, a single-step method for breeding typical plant populations has been developed (Rosyara et al. 2007, 2009). In such an approach, in the first few breeding cycles, markers linked to the trait of interest are identified by QTL mapping, and later the same information is used in the same population. In this approach, pedigree structure is created from families that are obtained by crossing number of parents (in three-way or double crosses). Both phenotyping and genotyping are done using molecular markers mapped to the possible location of QTL of interest. This will identify markers and their favorable alleles. Once these favorable marker alleles are identified, the frequency of such alleles will be increased, and response to marker-assisted selection is determined. Marker alleles with desirable effects are further used in subsequent selection cycles.

8.4 High-Throughput Genotyping Techniques

Recently high-throughput genotyping techniques have been developed that allow marker-assisted screening of genotypes. This will help breeders in shifting traditional breeding to marker-assisted selection. One example of such automation is using DNA isolation robots, capillary electrophoresis, and pipetting robots.

One recent example of capillary system is Applied Biosystems 3130 Genetic Analyzer. This is the latest generation of four-capillary electrophoresis instruments for the low- to medium-throughput laboratories.

8.5 Use of MAS for Backcross Breeding

A minimum of five or six backcross generations are normally required to transfer a gene of interest from a donor to a recurrent parent. The recovery of the recurrent genotype can be accelerated with the use of molecular markers. If the F_1 is heterozygous for the marker locus, individuals with the recurrent parent allele(s) at the marker locus in first or subsequent backcross generations will also carry a chromosome tagged by the marker.

8.6 Marker-Assisted Gene Pyramiding

Gene pyramiding has been proposed and applied to enhance resistance to diseases and insects by selecting for two or more than two genes at a time. For example, in rice, such pyramids have been developed against bacterial blight and blast. The advantage of using markers is that it allows selection for QTL-allele-linked markers that have the same phenotypic effect.

8.7 Forward Selection

Forward selection is a selection for a desirable trait or gene. This is in contrast to background selection, which focuses on eliminating unwanted contribution of genetic materials, typically from a donor parent during introgression of genes. It has been proposed for several decades that molecular markers can be used to assist progress with forward selection.

8.8 Using Molecular Markers to Assist with Forward Selection

The possibility of using molecular markers to assist with forward selection was the result of the rapid increase in the number of available molecular markers, beginning with RFLP markers in the 1980s (Tanksley and Hewitt 1988) and more recently with SSRs and SNPs. Before using molecular markers to conduct forward selection, suitable marker(s) must be identified. A suitable marker is defined based on three factors: (1) marker properties, (2) association with desired trait, and (3) genetic distance between marker and trait.

8.8.1 Marker Properties

Desirable characteristics of molecular markers to be used for marker-assisted selection include codominant inheritance, reproducibility, low cost of marker development and genotyping, and capacity to be run on a high-throughput scale. For these reasons, SNPs (and to some extent SSRs) are currently in widespread use in molecular marker applications. Khan et al. (2007) provided an example of developing suitable molecular markers for use in marker-assisted selection. Previous quantitative trait locus (QTL) mapping studies identified a major QTL associated with fire blight resistance in apple (Calenge et al. 2005; Khan et al. 2006). In this initial study, RAPD and AFLP markers were associated with this QTL. However, RAPD and AFLP markers are not suitable for marker-assisted selection due to their dominant nature and potential issues of reproducibility between laboratories. Therefore, Khan et al. (2007) developed SCAR markers from the RAPD and AFLP markers for use in marker-assisted selection for resistance to fire blight in apple. SCAR markers are codominant and can be reproduced between laboratories.

8.8.2 Marker Association with Desired Trait

After a desirable trait has been identified as possessing a trait of special interest to a breeding program, the next step is to study the genetic nature of the trait. Phenotypic and genotypic data from molecular markers can help determine the number and nature of gene(s)/QTLs controlling a trait by detecting associations between markers and traits.

A variety of methods are available for identifying markers associated with a trait, including single-marker trait analysis, simple interval mapping, multiple interval mapping, and composite interval mapping. All these methods require the development of mapping populations, and some methods require the development of a genetic map. It is important to confirm associations between markers in traits in breeding populations to make sure the association holds true in that population. Associations between a marker and a trait may not hold true in other populations due to undetected interactions with other genes (epistasis) (Tanksley and Hewitt 1988). In the case of quantitative traits, there may be interactions between genes and environment, making the phenotype dependent on the environment (Knoll and Ejeta 2008).

8.8.3 Genetic Distance Between Marker and Trait

To effectively use a molecular marker to conduct forward selection, the marker must be tightly linked with the associated trait. Ideally, the genes conferring the trait were previously cloned, and the molecular markers were developed within the gene sequences. This ensures that there are no recombination events between the marker and gene. Although this may be possible for some genes, such as the RB gene in potato that confers resistance to late blight, it is generally not the case (Colton et al. 2006; Song et al. 2003). Commonly, the molecular marker is located some distance from the gene. When selection is based on a single marker, there is a chance that genetic recombination will occur between the marker and gene, resulting in loss of the gene. The chance of recombination is dependent on the genetic distance between the marker and gene. The farther apart the marker and gene, the more likely a recombination event between them.

To circumvent the potential for recombination between a marker and gene, researchers have promoted selection based on markers that flank the gene (flanking markers) (Hospital and Charcosset 1997; Soller and Plotkinhazan 1977; Tanksley 1983). By selecting based on the marker genotype of flanking markers, breeders can identify recombination events between one of the markers and the gene. If there was a crossover between a marker and gene, the two markers, which are on either side of the gene, would have different genotypes. The chance that double crossovers occurred is small and related to the distance between flanking markers (distance between marker and gene and distance between gene and the second marker).

Selection based on flanking markers, however, may lead to keeping extra genes that are located between the molecular markers in addition to the desired gene. This can be problematic if desired and undesired traits are closely linked. This again reinforces the concept of identifying molecular markers as closely linked to the desired gene as possible.

8.9 Empirical Results of Marker-Assisted Selection

The goal of selection is to increase the frequency of beneficial alleles in a breeding population to increase genetic gain over time (Falconer and Mackay 1996). Improvement of quantitative traits has relied mainly on phenotypic selection where the breeding value of each line is estimated from a limited number of phenotypic evaluations. Successful selection requires accurate estimates of breeding values to identify lines to be used as parents or advanced in the breeding program for additional testing. The breeding value of an individual is equal to the summation of all additive effects across all genes the individual carries (Falconer and Mackay 1996). Estimating the breeding value of a line using limited phenotypic evaluations is inaccurate for traits with low heritability due to the larger relative importance of environment compared to genotype (Bernardo 2010). Therefore, selection methods that more accurately measure the genetic component of the trait are needed to improve gains in breeding. Traditional marker-assisted selection was proposed as an indirect selection method to select individuals based on their marker allele constitution (Lande and Thompson 1990). Marker-assisted selection exploits the tight linkage between QTL and nearby markers and was suggested as an easier, faster, and more efficient selection method (Hospital 2009). However, the use of traditional marker-assisted selection has been limited in complex traits because of low power to detect QTL and bias in the estimated marker effects (Beavis 1994; Melchinger et al. 1998; Bernardo 2010). Another drawback of traditional marker-assisted selection is that it splits the selection task into two steps: identifying markers linked to QTL through QTL mapping followed by using linked markers to identify individuals carrying favorable alleles. The initial step of QTL mapping represents an impediment for the practical use of traditional marker-assisted selection because of the need to assemble or create a mapping population, evaluate and genotype individuals, and identify markers linked to QTL. Additional efforts are required to evaluate the mapped QTL to confirm they were not falsely declared (Bernardo 2004, 2010; Navara and Smith 2014). In addition, traditional methods of QTL mapping, such as biparental mapping, are limited to the alleles from the two parents and do not represent the entire genetic diversity of the breeding program. Several studies have compared traditional marker-assisted selection with phenotypic selection in crop species including sweet corn (Yousef and Juvik 2001), maize (Flint-Garcia et al. 2003; Abalo et al. 2009), wheat (Davies et al. 2006; Wilde et al. 2007), and soybean (Lamkey et al. 2013). Mixed results were observed in these studies, and in several cases, phenotypic selection was superior to marker-assisted selection (Flint-Garcia et al. 2003; Davies et al. 2006; Wilde et al. 2007; Lamkey et al. 2013). A possible reason for the lack of effectiveness of marker-assisted selection is that only significant markers are used in line selection; thus, only a portion of the total genetic variance is captured by markers (Bernardo and Yu 2007; Heffner et al. 2009; Bernardo 2010).

Genomic selection is a relatively new practice in plant breeding programs that does not require QTL mapping. It aims at improving quantitatively inherited traits by exploiting abundant marker information (Meuwissen et al. 2001; Hayes et al. 2009; Lorenz et al. 2011). Unlike the traditional marker-assisted selection program, genomic selection does not involve the identification of significant markers. In contrast, all markers are used with genomic selection to choose best performing lines, thereby reducing the two-step process required for traditional marker-assisted selection to a one-step selection procedure that captures all the genetic variance explained by markers. In barley, for example, several prediction models have been evaluated, and ridge regression best linear unbiased prediction (RR-BLUP) has been found to be similar in accuracy to models that consider the underlying genetic architecture of a trait such as Bayes Cπ and Bayes LASSO or nonlinear prediction models that account for both additive and nonadditive gene actions such as Gaussian and exponential models (Lorenz et al. 2012; Sallam et al. 2015). The adoption of genomic selection in plant breeding programs can lead to an improved selection gain when compared with phenotypic or traditional marker-assisted selection (Bernardo and Yu 2007; Heffner et al. 2009; Jannink 2010; Yabe et al. 2013). With phenotypic selection, selection of breeding lines at the early stages of evaluation is often done in few environments. Because genomic selection uses estimates of marker effects based on many breeding lines evaluated across multiple environments, it has the potential to provide more reliable breeding value estimates than when a limited number of trials are used in phenotypic selection. Several studies have compared phenotypic selection and/or traditional marker-assisted selection to genomic selection using simulated data (Bernardo and Yu 2007; Jannink 2010; Yabe et al. 2013) and empirical data (Massman et al. 2012; Asoro et al. 2013; Rutkoski et al. 2015). These studies suggest that the use of genomic selection in a breeding program can increase the rate of gain from selection. In a simulation study in maize, Bernardo and Yu (2007) reported that the response to genomic selection exceeded traditional marker-assisted selection for low and moderate heritable traits. There is a need for additional studies with empirical data involving traits with different genetic architecture to compare the effectiveness of genomic and phenotypic selection.

Genomic and phenotypic selections were compared by Wilde et al. (2007) in five sets of selection candidates from a barley breeding program. In each set, about 96 breeding lines were genotyped with 1536 SNP markers and phenotyped for yield, FHB severity, and DON concentration. A set of 168 lines and the same set of SNP markers were used to train a prediction model and predict the performance of the selection candidates using RR-BLUP. The best performing 10% of the breeding lines in each selection candidate set were selected using both methods and evaluated again in several trials. Similar significant response to selection using genomic and phenotypic selection for FHB severity and DON concentration was observed, while no significant responses were observed for yield using either method. For all traits, genomic selection significantly increased genetic similarity compared to the selection candidates. In addition, genomic selection resulted in an increase in the frequency of favorable alleles compared to phenotypic selection. Three indirect selection methods for DON concentration (predicted FHB severity, empirical FHB severity, and predicted DON concentration) performed similarly to direct phenotypic selection for DON but differed considerably in cost. It was concluded that the use of genomic selection for yield and FHB breeding in barley should result in similar gains from response to selection obtained using phenotypic selection, but with a shorter breeding cycle time and lower cost.

8.10 Search for Novel Genes for Resistance to *Striga hermonthica* Through MAS

Marker-assisted recurrent selection (MARS) could speed up maize breeding process because pre-flowering data could be used to obtain genotypic information for selection and controlled pollination should be possible compared to laborious and expensive field evaluations involved in phenotypic recurrent selection methods. However, a limited number of studies have been conducted on the use of MARS in maize in West and Central Africa (WCA).

Striga is one of the most important biological constraints limiting maize production in sub-Saharan Africa. Yield losses may reach 100% and may cause farmers to abandon their fields. The incidence and severity of the parasite are particularly high in the savannahs of WCA (Berner et al. 1996). In WCA alone, it is estimated that 40 million hectares in cereal production are severely infested by *Striga* spp., while nearly 70 million ha have moderate levels of infestation (Lagoke et al. 1991). *Striga hermonthica* (Del.) Benth and *Striga asiatica* (L.) Kuntze cause the greatest economic damage to maize. Maize breeders at IITA have used hybridization, inbreeding, and recurrent selection to concentrate favorable alleles for resistance to *Striga*. Several populations, varieties, hybrids, and inbred lines with moderate levels of resistance have been developed and distributed to the national maize programs. So far, the moderate level of resistance to *Striga* identified to date and incorporated in maize in WCA is quantitatively inherited, and no cases of immunity have been reported (Kim 1994; Kling et al. 1996). The available resistance, therefore, does not limit the reproduction of the parasite. There is, therefore, a need for novel resistance genes that support little or no *S. hermonthica* emergence.

By combining marker-assisted selection (MAS) methods with conventional breeding schemes, the overall selection gain and, therefore, the efficiency of a breeding program could be increased. Identification of molecular markers that are linked to *Striga* resistance can expedite the development of resistant cultivars using appropriate marker-assisted selection (MAS) strategies. An accession of teosinte (*Zea diploperennis*) that supports little or no *S. hermonthica* emergence was identified at IITA and crossed to normal maize adapted to the lowland tropics of WCA. Several promising inbred lines supporting fewer emerged *Striga* plants were selected from a backcross population involving the Z. *diploperennis* accession. A project was initiated at IITA in 1998 to map the *Striga* resistance genes of three BC_4S_2 genotypes (607-2-1, 91-5-1, 44-6-1) derived from *Z. diploperennis* backcross population to facilitate rapid transfer of these genes to elite maize inbred lines by MAS backcrossing. Each of the three selected S_2 lines was crossed to two locally adapted and susceptible inbred parents, 1393 and 5057, to obtain a total of six F_1 crosses. Each F_1 was selfed to generate F_2 plants. Field evaluations showed that there was greater phenotypic variation in the numbers of emerged *Striga* per plant and *Striga* damage symptoms rating in the 607-2-1 × 1393 segregating population than in the other two populations. Thus, the 607-2-1 × 1393 segregating population was genotyped with SSR and AFLP markers that were polymorphic with the parents to map the *Striga* resistance genes derived from *Z. diploperennis* backcross population. The results of the studies confirmed the existence of genetic variation for *Striga* resistance in the population. It was also shown that traits that are indicators of resistance to *Striga* such as *Striga* damage symptom rating, number of emerged *Striga* plants, number of ears at harvest, and grain yield are quantitatively inherited. Some SSR and AFLP markers associated with QTLs affecting *Striga* damage symptom rating and the numbers of ears at harvest and grain yield under *Striga* infestation have been identified for the first time in a maize population with genes from *Z. diploperennis*. These QTLs were consistently expressed across test environments representing different *Striga* populations and were anchored at a few common marker intervals in the same linkage groups. The markers with significant association to reduced *Striga* damage symptom rating and increased numbers of ears at harvest and grain yield could be used as potential candidate markers for simultaneous improvement of these traits in maize. The use of these markers for selection may eliminate the bulk of *Striga*-susceptible genotypes, which in turn may significantly reduce the amount of screening required to breed maize for resistance to *S. hermonthica*. There is a need for these putative markers to be confirmed in different populations with diverse genetic backgrounds and to validate and evaluate the utility of markers associated with *Striga* resistance.

The integration of accurate phenotypic data with molecular approaches will facilitate the identification of effective and consistent markers for marker-assisted recurrent selection. Four early-maturing inbred lines (TZEI 1, TZEI 2, TZEI 11, and TZEI 17) with contrasting reactions to drought but with complementary agronomic traits and resistance to *S. hermonthica* were selected based on the available field data and intercrossed in 2007 to form two biparental crosses, namely, TZEI 1 × TZEI 2 and TZEI 17 × TZEI 11. The objective of the program was to generate superior early-maturing DT inbred lines with combined resistance to *Striga* and higher levels of tolerance to drought. The two biparental crosses, TZEI 1 × TZEI 2 (BBA4) and TZEI 17 × TZEI 11 (BBA2), were selected for marker-assisted recurrent selection. A total of 270 S_2 lines derived from TZEI 1 × TZEI 2 were crossed to the tester, TZEI 19, in 2008. The resulting 270 testcrosses were evaluated at Mokwa and Abuja under artificial *Striga* infestation in 2009. These testcrosses were also evaluated at Ikenne and Bagauda in Nigeria and Kiboko in Zimbabwe under controlled drought stress in 2009/2010 and under optimal growing conditions at Ikenne in 2010. Similarly, 382 S_2 lines of the second cross involved in the marker-assisted selection, TZEI 17 × TZEI 11, were crossed to the tester, TZEI 23, in the 2009/2010 dry season nursey at Ibadan. The resulting testcrosses were evaluated under artificial *Striga* infestation at Mokwa and Abuja in 2010 and under optimal growing conditions at Ikenne in 2010 and under controlled drought stress at Bagauda in

Nigeria and Chiredzi in Zimbabwe in 2010. The testcrosses were also evaluated under induced drought stress at Ikenne during the 2010/2011 dry season. Leaf samples were harvested from the S_2 lines of the two populations in the field for DNA extraction.

In an effort to advance each of the populations to cycle 1 stage of recurrent selection, based on the results of the multilocation trials, the top 10% $F_{3:2}$ lines of the testcrosses involving (TZEI 1 × TZEI 2) and TZEI 19 were selected based on the BLUP values and planted for recombination to form the (TZEI 1 × TZEI 2) Syn C1 in 2011. A balanced composite made from the selected C_1 population was planted for genotyping. Based on SNP data and the summary results, the base index which integrated grain yield, anthesis–silking interval, plant and ear aspects, stay-green characteristic, *Striga* damage at 8 and 10 WAP, and number of emerged *Striga* plants at 8 and 10 WAP was computed. The top 10% of plants were selected using the base index and recombined to form (TZEI 1 × TZEI 2) Syn C_2 using GEBV in 2012. A balanced composite made from the selected C_2 population was planted for genotyping. Based on SNP data and the summary results, the top 10% of plants were selected using the base index and recombined to form (TZEI 1 × TZEI 2) Syn C_3 using GEBV in 2013. Similarly, the top 10% $F_{3:2}$ lines of the testcrosses involving (TZEI 17 × TZEI 11) and TZEI 23 were recombined to form the (TZEI 17 × TZEI 11) Syn C_1. A balanced composite of the selected C_1 population was planted for genotyping. Based on SNP data and the summary results, the top 10% of plants were selected using the base index and recombined to form (TZEI 17 × TZEI 11) Syn C_2 using GEBV in 2012. Furthermore, balanced composite of (TZEI 17 × TZEI 11) Syn C_2 was planted for genotyping. Based on SNP data and the summary results, the top 10% of plants were selected and recombined in the 2012/2013 dry season in IITA-Ibadan to form (TZEI 17 × TZEI 11) Syn C3 using GEBV.

Fifty S_1 families were generated from the C_0, C_1, C_2, and C_3 of the two populations during the 2013 growing season. A total of 200 S_1 families from the four cycles of each population were crossed to a tester (i.e., TZEI 7 for BBA4 population and TZEI 23 for BBA2 population) during the 2013/2014 dry season. The testcrosses were evaluated under artificial *Striga* infestation at Abuja and Mokwa, terminal drought stress at Bagauda, and optimal growing conditions at Ikenne and Mokwa. In addition, the testcrosses were evaluated under induced drought stress at Ikenne during the 2014/2015 dry season. In addition, 60 S_1 families were generated from each of the C_0, C_1, C_2, and C_3 of the 2 populations during the 2013 growing season. A total of 240 S_1 families from the four cycles of each population were used to determine the genetic gains from MARS under drought stress, *Striga* infestation, and optimal growing conditions. Furthermore, the effects of MARS on the genetic diversity of the different cycles of selection of the populations were studied. Results revealed that under *Striga*, grain yield increased from C_0 to C_1 but declined from C_1 through C_3, while *Striga* damage at 10 weeks after planting (WAP) decreased from C_0 to C_1 but increased from C_1 through C_3. The number of emerged *Striga* plants at 10 WAP was steady between C_0 and C_2 but decreased in C_3. Across *Striga*-free environments, yield was steady from C_0 through C_2 but decreased in C_3. Genetic variances and heritabilities of most traits were highest at C_2 under both research conditions. In the C_0, ear aspect (EASP), ears per plant, ear height, and SDR 10 WAP were the important secondary traits accounting for about 81.2% of the total variation in grain yield. In C_1 and C_3, however, EASP, SDR 2, and ear rot were the reliable secondary traits and explained 78.8 and 79.3% of the total variation in grain yield. It was concluded that one cycle of PS improved grain yield and *Striga* tolerance, while two cycles of MARS improved *Striga* resistance in the population. The relative importance of secondary traits was altered during one cycle of PS; thereafter, two cycles of MARS maintained but did not improve the relative importance of the secondary traits. The increase in genetic variance for grain yield from C_0 to C_1 across *Striga*-infested environments suggested that PS was effective in maintaining the variability for grain yield in the population. In contrast, the decrease in genetic variance for grain yield obtained at C_3 compared to C_1 implied that MARS depleted the variability for grain yield in the population. Similar trends were observed for the genetic variances for *Striga* damage and the number of emerged *Striga* plants at 10 WAP, indicating the need for introgression of new sources of *Striga* resistance genes into the population. Across *Striga*-free environments, a similar trend was observed for the genetic variance of grain yield. The reduced heritability estimates for grain yield in C_3 compared to C_1 across each test environment indicated that there will be little or no progress from selection in the advanced cycles of the population. The decrease in genetic variability during MARS seems a plausible reason for the concomitant decrease in grain yield in the present study. It was concluded that one cycle of PS improved mean performance and genetic variability of grain yield and *Striga* tolerance in TZE 1 × TZEI 2 maize population, but MAS was not effective in further improvement of the population. In contrast to the results of Talabi et al. (2016) (unpublished), Beyene et al. (2015) investigated genetic gains in grain yield from genomic selection (GS) in eight biparental maize populations under managed drought stress environments and obtained higher gains from GS compared to conventional pedigree-based PS.

Substantial progress has been made by IITA in improving the available early maize varieties, populations, inbreds, and hybrids for resistance to *Striga*. However, many of the released early varieties still support a considerable number of *Striga* plants, which may ultimately flower, set seed, and increase the *Striga* seed bank in the soil. An increase in the level of resistance to *Striga* in the available germplasm is therefore an important breeding goal in maize. A high level of resistance was found in perennial teosinte, *Zea diploperennis* (Kling et al. 2000). Therefore, IITA in addition to exploiting the genetic variation present in cultivated maize has introgressed resistance genes from perennial teosinte, *Zea diploperennis*, to cultivated maize of tropical adaptation, and backcross progeny with high levels of resistance has been selected from the crosses, and intermediate-maturing inbreds with novel genes for *Striga* resistance have been developed (Kling et al. 2000; Menkir et al. 2006). Several early and extra-early drought-tolerant inbreds containing novel *Striga* resistance genes from the *Zea diploperennis* have also been developed in IITA (Amegbor et al. 2017).

Markers linked to specific genes may be used to facilitate selection of desired genotypes through MAS. The identification and characterization of quantitative trait loci (QTL) will help to identify genomic regions associated with the expression of complex traits and their precise genetic contribution at target loci. The use of molecular tools will complement conventional breeding approach and speed up the breeding process, thereby facilitating the release of new superior high-yielding maize hybrids which combine *Striga* resistance and drought tolerance genes and significantly outyield the commercial varieties within a short period. So far, no QTLs have been identified for *Strig*a resistance in maize. Therefore, there is an urgent need to identify QTLs for *Striga* resistance to facilitate the rapid and efficient transfer of the genes into other maize genotypes and develop drought-tolerant hybrids with combined resistance to *Striga* for commercialization in the sub-region. The use of molecular approaches such as identification of quantitative trait loci controlling *Striga* resistance in maize can also contribute significantly to the understanding and knowledge of the genetic basis of maize performance under *Striga* infestation. This information is crucial to the success of the IITA Maize Improvement Program and will be invaluable in designing cost-effective breeding approaches aimed at improving sustainability and stability of grain yield under low soil nitrogen, drought, and *Striga* infestation. The genotyping of the mapping population for linkage mapping of *Striga* resistance has been outsourced to the Institute of Genomic Diversity facility at Cornell University, USA. The objective of this study is to identify the QTLs associated with *Striga* resistance in two early-maturing mapping populations using SNP markers.

8.11 Development of Mapping Populations for QTL Analyses for *Striga* Resistance

Crosses were made between selected *Striga* resistance inbred lines and susceptible inbred lines designated as P_1 and P_2 to generate F_1 progenies. The two contrasting inbred lines were selected based on preliminary evaluation of the lines under *Striga*-infested conditions. The F_1 generation was backcrossed to the susceptible parental inbreds to obtain BC_1P_2. The F_1's were also self-pollinated to obtain the F_2 generation. The BC_1P_2 was selfed to generate the BC_2F_1 population and the F_2 advanced to F_3. Three hundred $F_{3:2}$ lines were generated and phenotyped at Mokwa and Abuja, in *Striga* endemic Southern Guinea savanna of Nigeria. Studies are presently going on at the Cornell University where QTLs for *Striga* resistance would be identified, validated, and used for marker-assisted selection to develop superior new varieties for *Striga* endemic areas of sub-Saharan Africa.

Genotypic differences in response of maize to nitrogen fertilizers have been reported (Bertin and Gallais 2000). Genetic studies evaluating N response in breeding lines and hybrids suggest polygenic inheritance (Pollmer et al. 1979). Molecular markers can be used to study the inheritance of complex traits and identify specific loci associated with the expression of these traits. Once a desired trait has been identified in a segregating population, specific chromosome segments controlling variation for the trait can be localized using RFLPs or some other type of genetic marker system (Beavis et al. 1991). In maize, the genetic dissection of complex traits for abiotic stress responses has focused primarily on drought tolerance (Ribaut et al. 1996, 1997; Tuberosa et al. 2002). Morris et al. (2003) evaluated the benefits of molecular markers in breeding programs, and Ribaut and Ragot (2007) reported marker-assisted selection experiments used to improve grain yield under moisture stress and low temperature. Limited studies have been carried out to understand the genetic response of segregating populations to field soil deficiencies such as low P (Reiter et al. 1991) or low N (Agrama et al. 1999; Hirel et al. 2001). Ribaut et al. (2007) identified eight quantitative trait loci (QTL) for GY under low N. Of these, two were also detected under high N which could be used for the identification of genotypes with tolerance to low-N stress and also with high yield under optimal conditions. The development of molecular marker technologies offers powerful alternative methods for examining the relationships between physiological traits controlling the response of maize to N, thereby contributing to a better understanding of metabolic pathways and physiological processes (Limami and de Vienne 2001).

In maize, the genetic dissection of complex traits for abiotic stress responses has focused mainly on drought tolerance (Ribaut et al. 1996, 1997; Tuberosa et al. 2002). The advantage of using molecular markers in breeding programs has been evaluated (Morris et al. 2003), and marker-assisted selection experiments to improve grain yield under moisture stress and low temperatures have been reported (Ribaut and Ragot 2007). Not as much attention has been paid to the understanding of the genetic response of segregating populations to field soil deficiencies such as low P (Reiter et al. 1991) or low N (Agrama et al. 1999; Hirel et al. 2001). However, the genetic basis for nitrogen use efficiency (NUE) has received some research attention. Agrama et al. (1999) investigated quantitative trait loci (QTL) for correlated secondary traits of NUE using a set of $F_{2:3}$ populations derived from two inbred lines, B73 and G79, and identified six QTLs for grain yield under low-N conditions and five QTLs under high N. Hirel et al. (2001) reported that QTLs for NUE were correlated with agronomic and physiological traits. Maize QTLs for nitrogen use efficiency (NUE) have been reported for vegetative growth and grain-filling periods of a mapping population evaluated under N and without N (Bertin and Gallais 2001; Hirel et al. 2001).

Heritability of GY and other associated traits under low-N conditions is generally low with large environmental effects. Consequently, the use of marker-assisted selection (MAS) could be a very effective strategy in breeding for tolerance to low N (Zhou 2010). However, the effectiveness of MAS depends on the precise localization of the QTL using the representative breeding germplasm and identification of tightly linked, easy-to-use molecular markers. Results of most studies in maize have utilized SSRs for linkage map construction and QTL mapping. With the availability of whole sequence genome information in maize (Gore et al. 2009), SNPs are physically anchored and provide an ideal platform for linkage mapping and QTL identification. The use of SNP markers has emerged as a powerful tool for many genetic applications due to the low assay cost, high genomic abundance, locus specificity, codominant inheritance, simple documentation, potential for high-throughput analysis, and relatively low genotyping error rates (Rafalski 2002; Schlotterer 2004).

Numerous SNP markers, mostly developed from DNA sequences of known genes, are now available for use in maize. Their applications in maize breeding include genetic diversity analysis, linkage map construction, marker-trait association or quantitative trait locus (QTL) mapping, and MAS (Lü et al. 2011). Markers, shown to be linked to specific genes, may be used to facilitate selection of desired genotypes through MAS. QTLs identified in elite breeding germplasm are of direct relevance for crop improvement through knowledge-based breeding and can be immediately used for MAS approaches (Würschum 2012; Wang et al. 2012a, b).

8.12 Contribution of Molecular Breeding to Maize Improvement

The potential of MB to contribute significantly to crop improvement has been overemphasized since the identification of the first quantitative trait loci (QTL) in the 1980s because scientists had largely underestimated the impact of gene networks and their interactions on plant phenotype (Ribaut et al. 2002). With the availability of more sophisticated statistical approaches, which allow the characterization of both QTL and the QTL × environment interactions, as well as the contributions made by plant models, some of these limitations have now been largely overcome, resulting in MAB having a great potential to contribute to maize breeding. Presently, the use of markers to track transgenes or pyramid favorable alleles determining a significant proportion of the phenotypic variance is possible for many crops, including maize. The number of reports asserting the successes of MB in dealing with polygenic traits has been significantly increasing. In addition, it is now generally widely accepted that the role of MB goes beyond the manipulation of elite alleles at a few loci in biparental segregating populations. Presently, there is a need for validation of the genetic gain of favorable alleles. Once this is achieved, markers could be easily developed and employed. This validation step remains a major hurdle in the establishment of a large set of markers appropriate for deployment in maize breeding programs. However, considering the technological and methodological progress achieved in genomics in recent years, the potential of MB to complement phenotypic selection and increase maize productivity will increase significantly in the near future.

8.13 Identification of Novel Alleles in Gene Bank Accessions

A particularly promising application of molecular markers has been to identify novel alleles present in gene bank accessions (Dwivedi et al. 2007). The CGIAR crop research centers and public research institutions throughout the world, including some national programs in developing countries, have spent many years collecting and conserving plant genetic material to prevent the loss of different types of crops and their wild relatives (Spooner et al. 2005). These collections represent a reservoir of genetic diversity that is a valuable resource for gene discovery in crop species. In addition, broad-scale genomics programs have begun to sample these genetic resources to survey the level of phenotypic variation within species with a view to developing novel strategies for crop improvement (Fernie et al. 2006). Although exotic germplasm has been extensively exploited as a source of variation for monogenic traits, relatively little work has been devoted to polygenic traits governed by QTL. Although the identification and introgression of favorable alleles from wild relatives have been successfully reported for several crops, much more work needs to be done to identify elite alleles in exotic maize germplasm.

8.14 QTL Mapping and Pyramiding of Genes for Biotic and Abiotic Stresses

One of the achievements of the plant biotechnology revolution for the last two decades has been the development of molecular genetics and associated technologies, which have led to the development of an improved understanding of the basis of inheritance of agronomic traits. The genomic segments or QTL involved in the determination of phenotype can be identified from the analysis of phenotypic data in conjunction with allelic segregation at loci distributed throughout the genome. Because of this, the mode of inheritance, as well as the gene action underlying the QTL, can be deduced (Lander and Botstein 1989). As with the improvement in marker technologies, the statistical tools needed for QTL mapping have evolved from a rudimentary to a very sophisticated level (Borevitz 2004). Current approaches are based on multiple regression methods, using least squares or generalized least squares estimation methods, mixed model approaches such as maximum likelihood, and Markov chain Monte Carlo (MCMC) algorithms, which use Bayesian statistics to estimate posterior probabilities by sampling from the data. In parallel, with progress in the characterization of genetic effects at QTL and refinement of QTL peak position through meta-analysis (Chardon et al. 2004), advances have also been made in understanding the impact of the environment on plant phenotype. The mapping of QTL for multiple traits has allowed for the quantification of QEI (Jian and Zeng 1995), and more recently, approaches using factorial regression models have been applied to model both QEI and genotype by environment interaction (GEI), using genetic and environmental co-variables in the same model (Vargas et al. 2006).

The power of DNA markers is their ability to select for genotypes carrying a favorable allelic composition at all marked loci. Favorable QTL alleles can be used to transfer one or more discrete genomic segments from a donor to an elite cultivar by backcrossing or to conduct marker-assisted population improvement by the stacking of favorable alleles into individuals selected on the basis of marker genotype.

Marker-assisted backcrossing (MABC), in which a chosen allele at a marker locus is transferred from a donor to a recipient line, has been widely used to introgress favorable alleles into elite material which lacks a specific characteristic. A suite of genome-wide markers helps to expedite the progress of the backcrossing process, since it allows the simultaneous selection of the donor allele at the target locus and the rapid recovery of the recurrent parent alleles elsewhere (Tanksley et al. 1989). Although a number of parameters influence the choice of selection strategy, the design of a workable MABC program is relatively straightforward, and genetic gain can be predicted by simulation (Ribaut et al. 2002; Frisch and Melchinger 2005). MABC is an efficient means of transferring a single favorable allele (e.g., a transgene or a major QTL) into a range of genetic backgrounds or of improving a particular genotype for a given trait (Ribaut and Ragot 2007). This latter approach is particularly important when breeding for foodstuffs, where the development of new germplasm is challenging because the new product needs to fit the requirements of local consumers and be better than products already available. For this reason, the introgression of superior alleles via MABC to improve popular cultivars for a specific trait is perhaps the most suitable application of MAS in the developing world. Although such application of molecular markers may make its biggest short-term impact in developing countries, in the long term the strategy is limited because its output can at best only generate an improved version of an existing genotype. To exploit the advantage of combining superior alleles from two or more parental lines, other MAS approaches need to be considered and are outlined in the following sections. In practice, plant performance reflects the integration of several traits, and consequently an ideotype will generally be a complex one. Stam (1995) provides the explanation as to why, in the case of biparental populations, ideotypes cannot be expected to occur in a selfing generation of realistic size. Similarly, because of the number of loci involved and the relative contribution of each parent, the ideotype will generally not be attainable through MABC. The MARS schemes, which involve several successive generations of intercrossing selections based on molecular marker genotype, in addition to the use of multi-trait selection indices, may allow a closer approach to the ideotype (Peleman and Van Der Voort 2003). Other approaches suggest the selection to be conducted in large segregating populations (few thousands of genotypes) to fix elite alleles at few selected loci in a single step of selection conducted at an early stage of recombination (Ribaut and Betran 1999). As expected, the use of markers in breeding programs has been adopted primarily for the manipulation of simply inherited traits, for which a limited number of the most significant QTL can impact the phenotypic variance. Examples of some achievements in maize breeding through molecular markers are the development of quality protein maize (QPM) through marker-assisted transfer of opaque-2 gene in backcross programs (Dreher et al. 2000), backcross marker-assisted selection for drought tolerance, and recurrent selection for grain moisture and earliness (Ribaut and Ragot 2007). In addition, genes identified through MBC include maize leaf rust resistance Rp1 D (Collins et al. 1999) and flowering time QTL Vgt1 (Salvi et al. 2002) and root abscisic acid QTL, ABA1 (Ribaut 2007).

A review of gene-marker associations for disease resistance and quality traits in various crops was recently presented by Francia et al. (2005). Other current crop-specific reviews have described the status quo in various extensively studied crops, such as rice (Ashikari and Matsuoka 2006), maize (Ribaut and Ragot 2007), wheat (Bonnett et al. 2005), less-studied cereals such as pearl millet (Serraj et al. 2005), or legumes (Dwivedi et al. 2006; Miklas et al. 2006). The mapping of SNPs on the linkage groups was not different from what was mapped by Zaidi et al. (2015) and Almeida et al. (2013) using similar markers. However, the orientation, size, and distances differed. This could be attributed to the type and size of the population and number of markers used. The length of the linkage map was smaller than that reported by other authors (Zaidi et al. 2015; Almeida et al. 2013). It was, however, bigger than that reported by Šimić et al. (2009), who found a linkage map length of 484.6 cM using SSR markers. The differences in the sizes of the linkage maps may be attributed to the type of marker and the number of markers used.

QTL analysis resulted in the identification of a total of 13 QTLs for 6 different traits under low-N environments (9 QTLs) and high-N environments (4 QTLs). Some QTLs detected for different traits were overlapping in some specific genomic regions. Chromosome 10 harbored overlapping QTL for GY, DTS, and ASI. They were all flanked by the SNP markers PZA01292_1 and PZB0049_1 but had different peak marker positions. These QTLs may have had pleiotropic effects, thus explaining the correlation observed among the traits. Similar overlapping genomic regions for GY and ASI on chromosome 10 were reported by Ribaut et al. (1997) and Malosetti et al. (2008). This explains the reason for the strong correlation of ASI with GY across a broad range of germplasm suggesting the possibility of a cluster of tightly linked loci orchestrating low-N tolerance through coordinated expression of these traits. Higher heritability was recorded for ASI and DTS than for GY for both low-N and high-N environments. This suggests that understanding the genetic basis of ASI and DTS will aid in designing efficient marker-based breeding strategies for enhanced GY under low-N environments. Some earlier studies have reported QTL for yield and secondary traits on chromosome 10 under optimal and water stress conditions (Li et al. 2010; Zheng et al. 2009). Adofo-Boateng (unpublished) mapped QTLs for GY, SG, and EPP to the same location on chromosome 1 at a marker peak of 58.0. She attributed this to be due to the physiological relationship and strong correlation between them. Close linkage between GYP and EPP has been reported by numerous researchers using classical analysis (Agrama 1996; Sabadin et al. 2008; Ifie et al. 2015). The mapping of the traits in the same region could indicate that this region might be a hot spot for yield traits and transferring this region will lead to varieties with multiple traits. Agrama et al. (1999) and Ribaut et al. (2007) detected QTLs for GY under low N on chromosome 1. QTL detected for EPP on chromosome 1 under low N was also reported by Ribaut et al. (1997) under drought stress. The identification of common genomic regions for the regulation of some traits under drought and low-N conditions has important implications for breeding maize. Many drought areas are located in developing countries, where, for economic reasons, N supply is insufficient. Based on phenotypic data, Bänziger et al. (2002) and Badu-Apraku et al. (2013) suggested that selection for tolerance to mid-season drought stress led to morphological and physiological changes that increased yield under N deficiency.

The quest for stress resistance, high yield, and good quality is unending for crop breeders, so the desirable crop production characteristics of functional stay-green genotypes make them very attractive. Beavis et al. (1994), using restriction fragment length polymorphism (RFLP) markers, identified three and five stay-green QTLs in an F_4 and a topcross maize population generated from B73_Mo17. Zheng et al. (2009), using SSR markers, detected 14 QTLs in an F_2 population.

Adofo-Boateng (2015) identified three QTLs for SG: one under high N on chromosome 8 and two under low N on chromosomes 1 and 4. It was explained that the few QTLs detected in this study may probably be due to the differences in the parental lines used, the segregation population, genetic map, or agroecological conditions. Wang et al. (2012a) also identified QTLs for SG on chromosomes 1 and 4, indicating that chromosomes 1 and 4 were important in controlling SG. A QTL for plant height (qpht) was detected on chromosome 1 with a phenotypic variation of 9.6%. Plant height was also shown to be correlated with yield; hence, it is an important trait for selection. Other researchers have mapped this QTL at other locations. For example, Ribaut et al. (2007) mapped five QTLs for PHT on chromosomes 3, 4, 6, 9, and 10. The QTL identified in this study was different from that of Ribaut et al. (2007), suggesting that it belongs to a new chromosome associated with PHT in maize and that plant height in maize is controlled by polygenes. Due to additive effects, nine QTLs (qgy-10-1, qdts-1, qsg-8, qsg-1, qsg-4, qasi-6, qasi-10, qepp-1, qpht-1) could increase phenotypic values of traits, while the other four (qgy-1, qgy-10-2, qdts-5, qdts-10) could decrease them to some extent.

A total of 13 QTLs were identified on a linkage map spanning a total length of 622.7 cM, with a marker density of 3.9 cM. The localization of grain-yield QTLs with some of the yield-related traits is an excellent indication of strong association. Identification of QTLs of secondary traits that improve crop growth and performance especially under low-N environments will certainly assist breeders in rapid introgression of these genomic regions into desired elite germplasm. Five QTLs (qgy-1, qts-1, qsg-1, qsg-4, and qasi-6) for GY, DTS, SG, ASI, and EPP, respectively, were close to their adjacent markers, with an interval of 0.7–5.2 cM between them, and this explains phenotypic variance from 9% to 21%, suggesting that the markers are linked with the gene controlling the trait and could be considered for marker-assisted selection (MAS). Other QTLs identified were far from their linked markers, greater than or equal to 10 cM, and thus, it is necessary to find more molecular markers for these given chromosomal regions. Fine mapping of the QTLs with high p-values should be carried out to increase the possibility of using the significant marker for marker-assisted breeding. Finally, validation of these QTLs in another mapping population is necessary before using these markers in MAS.

8.15 The Challenges and Opportunities of Molecular Breeding to Improve Plant Breeding Efficiency

Ribaut and Ragot (2007) reported that since the development of molecular biology, the potential of MB contributing significantly to crop improvement has been controversial. With the identification of the first quantitative trait loci (QTL) in the 1980s, the ability of molecular markers to streamline the selection of complex traits has been oversold because scientists have largely underestimated the impact of gene networks and their interactions on plant phenotype. Some of these limitations have now been overcome, as a result of the development of more sophisticated statistical approaches which have facilitated the characterization of both QTL and the QTL by environment interactions (QEI), as well as the contributions made by plant models. Presently, the use of markers to track transgenes or stack favorable alleles determining a significant proportion of the phenotypic variance can be routinely carried out for many crops. There are a number of reports asserting the successes of MB in dealing with polygenic traits, and the number has been increasing. Furthermore, it is now generally accepted that the role of MB extends beyond the manipulation of elite alleles at a few loci in biparental segregating populations. There is a need to evolve new strategies to fully exploit the large amount of information emerging from the genomics technologies and various genome sequencing efforts. QTL, functional genomics, and association studies are complementary approaches and should be used to quantify the genetic effects of specific alleles at target loci. Once the genetic gain of favorable alleles has been validated, allele-based markers can be easily developed and exploited. This validation step remains a major bottleneck in the establishment of a large set of markers appropriate for deployment in plant breeding. However, considering the progress that has been made in genomics so far, it is clear that the potential of MB to complement phenotypic selection and improve crop productivity is set to increase significantly in the foreseeable future.

The present challenge is to convert the large amount of genetic information into a large set of markers useful for breeding and to integrate such markers into a sustainable breeding scheme. In essence, the priority lies in the development of efficient MB strategies aimed at plant improvement. The major advantages of molecular over the other classes of markers are that their number is potentially unlimited, their dispersion across the genome is complete, their expression is unaffected by the environment, and their assessment is independent of the stage of plant development (Lee 1995).

The potential of wild species and landraces as sources of genetic variation for crop improvement was recognized early in the twentieth century (Tanksley and McCouch 1997). A particularly promising application of molecular markers has been to identify novel superior alleles present in gene bank accessions (Dwivedi et al. 2007). The research centers of CGIAR and public research institutions all over the world, including some national programs in developing countries, have spent many years collecting and conserving plant genetic material (including seeds, cuttings, and tissues) to prevent the loss of different types of crops and their wild relatives (Spooner et al. 2005). These collections represent reservoirs of genetic diversity for gene discovery in crop species. In addition, broad-scale genomics programs have begun to sample these genetic resources to survey the level of phenotypic variation within species with a view to develop novel strategies for plant improvement (Fernie et al. 2006). Although exotic germplasm has been extensively exploited as a source of variation for monogenic traits, limited work has been devoted to complex traits typically governed by QTL. Although the identification and introgression of favorable alleles from wild relatives have been successfully reported for several crops, with spectacular results achieved in tomato (Fridman et al. 2004) and maize (Amegbor et al. 2017), much more work needs to be done to identify elite alleles in exotic germplasm. One of the achievements of the plant biotechnology revolution for the last two decades has been the development of molecular genetics and associated technologies, which have led to the development of an improved understanding of the basis of inheritance of agronomic traits. The genomic segments or QTL involved in the determination of phenotype can be identified from the analysis of phenotypic data in conjunction with allelic segregation at loci distributed throughout the genome. Because of this, the mode of inheritance, as well as the gene action underlying the QTL, can be deduced (Lander and Botstein 1989). As with the improvement in marker technologies, the statistical tools needed for QTL mapping have evolved from a rudimentary to a very sophisticated level (Borevitz 2004). Current approaches are based on multiple regression methods, using least squares or generalized least squares estimation methods, mixed model approaches such as maximum likelihood, and Markov chain Monte Carlo (MCMC) algorithms, which use Bayesian statistics to estimate posterior probabilities by sampling from the data. In parallel, with progress in the characterization of genetic effects at QTL and refinement of QTL peak position through meta-analysis (Chardon et al. 2004), progress has also been made in understanding the effect of the environment on plant phenotype. The mapping of QTL for multiple traits has allowed for the quantification of QEI (Jian and Zeng 1995), and more recently, approaches using factorial regression models have been applied to model both QEI and genotype by environment interaction (GEI), using genetic and environmental co-variables in the same model (Vargas et al. 2006). The major challenges of molecular breeding in maize improvement include high cost of each single data point availability and complexity of molecular platforms, lack of reliability of marker profiling and scoring (SSR vs SNP), degree of polymorphism, lack of availability of equipment and technical expertise, problems of integration of molecular breeding in maize improvement, lack of resources of programs for developing high-density SNP platforms in maize and problems in optimizing MARS and GWS procedures, problems in identifying genes/QTLs for yield potential and stability, problems in identifying high-yielding, stable genotypes (low G × E × M), lack of closer collaboration with breeders in developing countries, and the need for training of breeders to integrate MB in their breeding programs.

Molecular breeding has a great potential to contribute to maize improvement. The use of markers to track transgenes or pyramid favorable alleles determining a significant proportion of the phenotypic variance is possible for many crops, including maize. However, there is a need to address the major challenges of MB including high cost of each single data point availability and complexity of molecular platforms, lack of reliability of marker profiling and degree of polymorphism, lack of availability of equipment and technical expertise, problems of integration of MB in maize improvement, lack of resources of programs for developing high-density SNP platforms in maize and lack of closer collaboration between breeders in developing countries, and the need for training of breeders to integrate MB in their breeding programs.

8.16 Conclusion

Results of studies comparing traditional MAB with phenotypic selection in maize in SSA have shown that in several cases phenotypic selection has been superior to marker-assisted selection. However, presently, sophisticated statistical approaches, which allow the characterization of QTL and the QTL × environment interactions, are available. As a result, MB has a great potential to contribute to maize improvement in SSA if there could be closer collaboration between breeders in developed countries and breeders in developing countries as well as training of national program breeders to integrate MB in their breeding programs. A promising application of molecular markers has been the identification of novel genes present in gene bank accessions. The CGIAR centers, including some national programs in developing countries, have spent resources collecting and conserving plant genetic resources to prevent the loss of different types of crops and their wild relatives. Much more work needs to be done to identify elite alleles in exotic germplasm using molecular tools.

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Part III
Breeding for Specific Traits

Chapter 9
Breeding of Quality Protein and Provitamin A Maize

9.1 Introduction and Justification

An estimated 842 million people worldwide are malnourished. Most of these people live in developing countries of Africa—especially, SSA—and Asia (Jauhar 2006). Although significant progress has been made in improving the nutritional status of vulnerable groups in sub-Saharan Africa during the past 15 years, the region has one of the highest populations of malnourished people among all regions of the world. A considerable proportion of people in West and Central Africa (WCA) still do not have access to nutritionally adequate food to guarantee healthy living. Childhood and maternal underweight is responsible for millions of death in the sub-region. Among the top preventable health risks globally, malnutrition was ranked first and HIV/AIDS fourth according to the World Health Report of 2002. The potential therefore exists to address the problem of malnutrition in Africa through biofortification. Maize has such a critical nutritional role to play in addressing the problem of malnutrition in Africa through biofortification because it is the most important staple food crop across sub-Saharan Africa. Traditionally, maize is consumed as a starchy base in a variety of forms including gruels, porridge, and pastes. It is also used as porridge for weaning children (2–3 months, until the children are completely weaned at the age of 15–24 months) and preschool children (3–5 years) without protein supplements. The normal maize has a major defect as human food because the protein is deficient in two essential amino acids, lysine, and tryptophan. Consequently, infants fed on normal maize without any balanced protein supplements suffer from diseases such as kwashiorkor which is a fatal syndrome characterized by initial growth failure, irritability, skin lesions, edema, and fatty liver. The consumption of quality protein maize (QPM) which is high in lysine may lead to

B. Badu-Apraku, M.A.B. Fakorede, *Advances in Genetic Enhancement of Early and Extra-Early Maize for Sub-Saharan Africa*,
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improved absorption of Zn and Fe in the human digestive system and thus contribute to improved micronutrient status.

A number of factors qualify maize as the crop of choice for biofortification to address nutrition problem in WCA. For example, the per capita consumption of maize varies from 30 to 90 kg per year in the coastal countries of WCA and rose to an average of 0.5% per year from 1988 to 1977. Maize is used as the main constituent of the local weaning foods. Unfortunately, its use as weaning food for children in WCA is often without protein supplements. QPM offers a unique opportunity to impact positively on the nutrition of malnourished people of WCA because it may supply as much as 70–73% of the human protein requirements compared to 46% for normal maize. The biological value of QPM is estimated at 80% compared to 40–57% for normal maize and 86% for eggs. The protein of QPM has 90% of the relative value (RV) of milk.

Feeding experiments with rats, swine, young children, and adult humans have established the superiority of QPM over normal maize. It is possible for children to meet 90% of their protein requirements by consuming 175 g of QPM per day. In a feeding trial with malnourished children, it was found that the growth rate obtained for children fed on QPM was similar to that obtained for cow milk formula (Graham et al. 1990). Therefore, QPM breeding appears to hold a promise for alleviating protein-related malnourishment among the poor.

9.2 Principles of QPM Germplasm Development

QPM development is based on the opaque-2 mutant. Studies of these mutants at CIMMYT showed that the soft floury phenotype of the mutants was modified to hard vitreous endosperm in certain genetic backgrounds (Vasal et al. 1980). The conversion of opaque-2 into QPM is based primarily on genetic modifiers. Modifiers are minor genes and exert their influence largely by intensifying or diminishing the expression of major genes. Modifiers stimulate the opaque-2 gene to produce kernels with desirable characteristics. Studies have provided evidence of maternal effect for endosperm hardness. Endosperm hardness in F_1 is usually higher when hard endosperm lines are used as female parents. Endosperm hardness and lysine content in F_1 kernels are usually significantly lower when the two parents involved in a cross are characterized by hard endosperm. Consequently, crossing genotypes with soft and hard endosperm or those with semihard endosperm would be a practical way to obtain high-lysine content and retain endosperm hardness. For kernel and protein quality, additive genetic effects appear to be more important. Heritability values are high for endosperm hardness and oil content and only moderate for protein content.

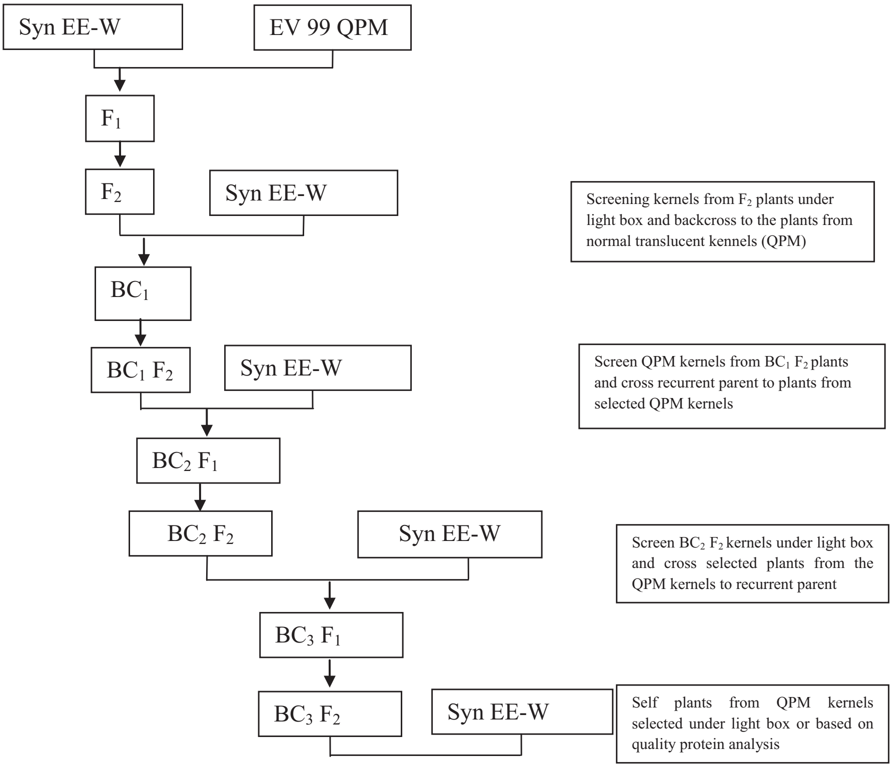
9.3 Breeding Methods for the Selection of Opaque-2 (o-2) and Favorable Genetic Background

9.3.1 Backcross and Pedigree Breeding Methods

The backcross breeding method has been used extensively for the conversion of normal endosperm maize to QPM. However, the pedigree breeding method is the most widely used for the development of new inbred lines that combine the desirable traits of two or more parental genotypes. If the QPM parent is unadapted, the backcross method is the logical breeding method. However, if the QPM parent can also contribute to improved adaptation, quality, and yield, the pedigree method would be appropriate for handling the segregating generations.

In converting a normal endosperm maize variety to QPM, the QPM source is used as the donor parent, while the normal endosperm variety is used as the recurrent parent. Streak-resistant QPM populations and pools used as sources of opaque-2 gene for the development of QPM varieties in the IITA Maize Program include Pop 61-SR BC3, Pool 15-SR QPM, Pool 18-SR QPM, EV8763-SR, and EV8766-SR BC6. The backcross method is effective when the character under transfer has moderate to high heritability as is the case for the QPM trait. Following the initial cross, a series of backcrosses to the recurrent parent is made during which the QPM trait is maintained by selection. At the end of the backcrossing breeding program, the o-2 gene under transfer will be heterozygous, and selfing after the last backcross produces individuals homozygous for the o-2 gene. The method reproduces the genotype and phenotype of the recurrent parent with precision, the only difference now being the QPM trait.

In choosing the recurrent parent, an adapted variety widely cultivated and already accepted by farmers should be a natural choice. For single-cross hybrids, one of the two inbred parents of a widely cultivated hybrid is converted to QPM. Thus, backcross breeding method can be used in the conversion of a population (Fig. 9.1) or an inbred line (Fig. 9.2) to QPM. In the case of conversion of a normal endosperm population to QPM, the use of adequate number of plants of the recurrent parent is required to recapture the variability of the latter. This will prevent genetic drift and ensure that the new population possesses the agricultural characteristics of the original population. Usually six backcrosses, coupled with rigid selection in the early generations, have proved satisfactory in many backcross breeding programs. Our experience at IITA has shown that with an elite genotype used as the donor parent, it may not be necessary to have as many as six backcrosses. Partial conversion with few backcrosses, usually two to three backcrosses, followed by identification of individuals with the desired endosperm characteristics may produce satisfactory results at minimal cost.



Screening kernels from F_2 plants under light box and backcross to the plants from normal translucent kennels (QPM)

Screen QPM kernels from BC_1 F_2 plants and cross recurrent parent to plants from selected QPM kernels

Screen BC_2 F_2 kernels under light box and cross selected plants from the QPM kernels to recurrent parent

Self plants from QPM kernels selected under light box or based on quality protein analysis

Fig. 9.1 Scheme for converting a normal endosperm variety to QPM

9.4 Recurrent Selection

Recurrent selection is an effective breeding method for placing the opaque-2 gene in a much broader genetic background and thus provides great opportunities for identifying superior QPM genotypes. The breeding method has been effective for modifying endosperm texture (hard, vitreous) and eliminating most of the defects associated with the opaque-2 gene without reducing protein quality.

9.5 QPM Germplasm Development in WCA

To fit into diverse agroecological zones in WCA, extra-early, early, intermediate, and late normal endosperm maize populations, varieties, and inbred lines that possess resistance/tolerance to drought and important biotic stresses, including maize streak virus (MSV), *Striga*, and downy mildew, have been converted to QPM. To maintain or further improve the levels of *Striga* resistance/tolerance already achieved, the conversion is carried out under artificial *Striga* infestation. A similar strategy has been

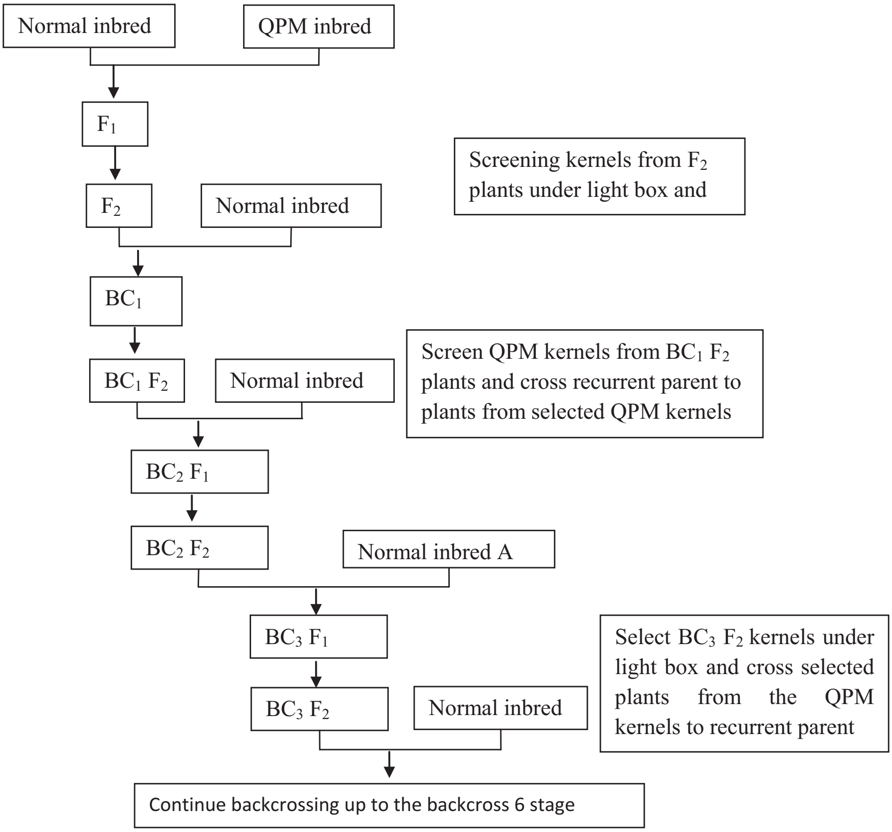


Fig. 9.2 Backcross breeding procedure for converting normal endosperm maize to QPM

deployed for MSV for which artificial infestation with viruliferous leafhoppers—the vector of the virus—is used to maintain good levels of MSV resistance in germplasm converted to QPM.

9.6 Strategies for QPM Development at IITA

The strategies for the development of QPM varieties at IITA have been all-encompassing. QPM lines from CIMMYT have been used as sources of genes for high lysine and tryptophan. Those with desirable agronomic features have been used to broaden the genetic base of adapted germplasm. Following the conversion of normal endosperm populations and pools with MSV to QPM, inbred lines have been extracted from such populations. In addition to these, elite inbred lines have been converted to QPM at IITA by backcrossing, and new QPM inbred lines also developed following hybridization between QPM and normal endosperm lines and handling of the segregating generations by the pedigree method.

The first QPM variety released in WCA was Obatanpa GH. This variety has been widely adopted by farmers and consumers in Ghana. Presently, it covers more than 50% of the maize hectarage (650,000 ha) in Ghana (Dankyi et al. 2005). It has also been released formally or informally in several other African countries including Benin (as Faaba), Togo, Mali (as Debunyuman), Guinea, Burkina Faso, Côte d'Ivoire, Senegal, Cameroon, Nigeria (as SAMMAZ 14), Mozambique (Susuma), Uganda, Ethiopia, Zimbabwe, Swaziland, Malawi, and Southern Africa (Badu-Apraku et al. 2004). The cultivar is also serving as a source of inbred lines for the development of QPM hybrids and synthetic varieties in several maize breeding programs in Africa. Obatanpa GH possesses good levels of resistance to the maize streak virus (MSV) and lowland rust (incited by *Puccinia polysora* Underw.) and moderate levels of resistance to blight [caused by *Bipolaris maydis* (Nisikado Miyake) Shoemaker]. The variety was derived from Population 63 SR, a white dent QPM, adapted to the lowland tropics. Population 63 SR is a composite of intermediate-maturing tropical maize germplasm originally formed by CIMMYT, Mexico. IITA incorporated genes for MSV resistance into the population. Following multilocational testing of Pop 63 SR in Ghana between 1987 and 1989 (Badu-Apraku et al. 2006), the population was identified as an outstanding source for new QPM varieties. The major defects of the population as a source of QPM at that time were the low level of streak resistance; poor husk cover; the presence of high percentage of soft, chalky kernels; and low grain-yield potential. While a visiting scientist in IITA-Ibadan in 1989, Dr. Baffour Badu-Apraku initiated a breeding program to extract a streak-resistant, high-yielding QPM variety with improved husk cover, appropriate hard endosperm modification, as well as elevated levels of lysine and tryptophan. A bulk of Pop 63 SR was planted at IITA, Ibadan (78,389 N, 38,939 E), Nigeria. About 9 days after planting, S_0 plants were infested with viruliferous leafhoppers (*Cicadulina* spp.). Two weeks later, the streak-susceptible plants were rogued out followed by the selfing of the agronomically desirable and streak-resistant S_0 plants. At harvest, about 500 S_1 ears from agronomically desirable S_0 plants with good husk cover were screened under a light box, and kernels with the desirable endosperm modification were selected. Kernels with appropriate endosperm modification selected from 250 ears were planted ear-to-row in a recombination block in the field at Ibadan. The S_1 plants were advanced to the second cycle of recombination under artificial infestation with viruliferous leafhoppers. This was followed by screening of the selected ears for desirable kernel modification under the light box. The selected kernels of each ear were planted ear-to-row for advancement to the S_1 stage by selfing under artificial MSV infection. At harvest, about 250 S_1 ears selected from plants with good husk cover and other agronomically desirable characteristics were planted ear-to-row in a recombination block at Fumesua (18,369 W, 68,459 N) in Ghana. In addition, about 30 kernels from each S_1 ear were dispatched to CIMMYT, Mexico, for tryptophan and lysine analyses. Based on the results from laboratory analyses, 80 S_1 lines with high levels of the two essential amino acids were taken through two cycles of recombination with special emphasis on selection for improved husk cover, grain yield, and desirable kernel characteristics. The resulting variety was designated Obatanpa indicating "good nursing mother" in the Ghanaian local dialect. Several multilocation trials were conducted in contrasting environments in Ghana. Results showed that Obatanpa was superior or comparable in grain yield and other agronomic characters to the top-improved intermediate- and late-maturing normal endosperm maize varieties in Ghana (Twumasi-Afriyie et al. 1997; Sallah et al. 1997). Furthermore, results of feeding trials with piglets and chicken showed that Obatanpa was superior in nutritional value and could be used as a replacement for normal endosperm maize in animal feeds with economic advantage (Okai et al. 1994; Osei et al. 1994). Because of its outstanding performance and the improved levels of lysine and tryptophan, Obatanpa was released for commercialization in Ghana in 1992. As an open-pollinated cultivar, it has been important to upgrade the genetic purity of Obatanpa periodically since its release in 1992. For instance, in 2001 the lysine and tryptophan levels of the grains of Obatanpa were monitored and found to be lower than desirable. Moreover, some plants were observed to be segregating for susceptibility to the MSV. In an effort to upgrade the lysine and tryptophan content of the variety, 277 half-sib families selected from Obatanpa were analyzed for the two essential amino acids in the QPM laboratory at CIMMYT, Mexico. Based on the results of the laboratory analysis, 40 families with high levels of lysine and tryptophan were selected for recombination to reconstitute the variety during the off-season of 2001 in Ghana. Furthermore, a program was initiated during the major season of 2002 to upgrade the level of streak resistance of the reconstituted variety. More than 500 families selected from the reconstituted Obatanpa were dispatched to IITA-Côte d'Ivoire for upgrading of the streak resistance level. The seed of the families was planted under artificial infestation with viruliferous leafhoppers at Ferkessédougou (9839 N, 58,109 W), Côte d'Ivoire. About 3 weeks after planting, the streak-susceptible plants were rogued out. This was followed by selfing of the streak-resistant plants with agronomically desirable characteristics at flowering. At harvest, the selected S_1 ears were recombined under artificial streak infestation in Ibadan during the off-season of 2003 to reconstitute the new version of Obatanpa, which was designated, Obatanpa GH. Five QPM hybrids, six open-pollinated QPM varieties including the new and old versions of Obatanpa, and three normal endosperm varieties were evaluated at seven locations in the forest and forest–savanna ecologies of Ghana during the major and minor planting seasons of 2004 (Table 9.1). The results revealed that Obatanpa GH was the highest-yielding open-pollinated variety with a grain yield of 4.96 Mg ha^{-1} compared to 3.56 Mg ha^{-1} for the normal endosperm local check. Obatanpa GH had a plant height of 205 cm and silked at 55 days after planting. Results of 19 on-farm trials conducted in the northern Guinea savanna zone of the Republic of Benin in 2004 revealed that Obatanpa GH had an average grain yield of 3.67 Mg ha^{-1}, which was comparable to that of the popular *Striga* and drought-tolerant normal endosperm variety, EV 97 IWDT STR (3.37 Mg ha^{-1}). However, Obatanpa GH was superior to the released normal endosperm local check (2.66 Mg ha^{-1}). Results of laboratory analyses of Obatanpa GH for total protein and tryptophan at IITA in 2005 indicated that it contains 10.0% total protein in the grain

Table 9.1 Grain yield, days to mid-silking, and plant height of late- and medium-maturing maize varieties evaluated at seven locations in Ghana during the major and minor seasons of 2004

Variety	Characteristics	Grain yield (kg/ha)	Mid-silk (days)	Plant height (cm)
GH 9163SRS715-1-1-1	Pop 63 SR, QPM, intermediate maturity	5736	52	196
GH 9163SRS850-2-2-1-2	Pop 63 SR, QPM, intermediate maturity	5442	52	203
Mamaba	Three-way hybrid, QPM, intermediate maturity	5090	52	195
GH8762SRS8DT42-2-2-5-1	Three-way hybrid, QPM, intermediate maturity	5030	54	199
GH9163SRS8DT42-2-2-5-2	Three-way hybrid, QPM, intermediate maturity	4986	54	200
Obatanpa (old)	Pop 63 SR, OPV, QPM, intermediate maturity	4968	54	208
Obatanpa (new)	Pop 63 SR, OPV, QPM, intermediate maturity	4958	55	205
EV02 Obat-L	Obatanpa, OPV, QPM, intermediate	4824	55	207
CIDA-ba	Three-way hybrid, QPM, intermediate maturity	4735	52	198
EV02 Obat Y-T	Obatanpa, OPV, QPM, intermediate maturity	4696	56	209
EV02 Obat Y-V	Obatanpa, QPV, QPM, intermediate maturity	4682	56	217
Dadaba	Three-way hybrid, QPM, intermediate maturity	4502	55	195
Okomasa	Late normal endosperm, OPV	4423	57	221
Abeleehi	I normal endosperm, OPV, intermediate maturity	4305	54	197
GH9866	OPV, QPM, intermediate maturity	4052	55	204
Kwadaso local	Normal endosperm OPV, late maturity	3559	57	209
Grand mean		4749	54	204
Lsd (5%)		374	1	9
CV (%)		17	3	9

with 0.88% tryptophan in the protein. In contrast, the normal endosperm check possessed 9.6% total protein with 0.49% tryptophan in the protein of the grain.

A major goal of the IITA Maize Improvement Program since 1980 has been to mitigate the effects of the two major constraints on maize production and productivity in WCA, *Striga hermonthica*, and drought. Toward this end, several high-yielding, early, and extra-early *Striga*-resistant and/or drought-tolerant normal endosperm populations, varieties, hybrids, and inbred lines have been developed in the program. Inbreeding, hybridization, and recurrent selection have all been used in the program. Our strategy for converting normal maize into QPM has focused largely on crossing elite populations and varieties to QPM donor sources followed by selection of genetic modifiers which stimulate the opaque-2 gene to produce kernels with desirable characteristics. The sources of the QPM trait used in the conversion program for the normal endosperm, white early-maturing germplasm were Pool 15 SR QPM and DMR-ESR-W QPM (both white-grained) and Pool 18 SR QPM (yellow grained) for the yellow materials (Table 9.1). The extra-early white variety, EV 99 QPM, has been used as the donor for the conversion of the normal endosperm, extra-early maturing, white populations, varieties, and inbred lines to QPM. Seven early *Striga*-resistant and/or drought-tolerant, elite, normal endosperm maize varieties and populations (TZE-W Pop DT STR C_3, EV DT-W 99 STR C_1, 98 Syn WEC STR C_0, TZE-W Pop × 1368 STR C_1, TZE-Y Pop DT STR C_3, TZE-Y Pop C_0 S_6, and EV DT –Y 2000 STR C_0) and four extra-early (TZEE-W Pop C_3, 2000 Syn EE-W, TZEE-Y Pop STR C_3, and 99 TZEE-Y STR) were crossed in 2002 to QPM donors for partial conversion to QPM.

Available information indicates the presence of maternal effects for endosperm hardness of F_1 kernels, but no such effect exists in F_2 kernels. Therefore, endosperm hardness in F_1 is usually higher when hard endosperm parents are used as females. Endosperm hardness and lysine content in F_1 kernels are usually significantly less than both parents when hard × hard endosperm combinations were analyzed. Therefore, combinations involving both soft and hard endosperm parents or between semihard endosperm parents are a more practical way to obtain higher-lysine content and maintain the endosperm hardness. Consequently, in all our conversion programs, hard endosperm normal maize parents were used as the females in F_1 crosses, while the donor parent had semihard QPM endosperm. The F_1 crosses were advanced to the F_2 stage and screened under the light box in 2003. The F_2 kernels with good endosperm modification were selected and advanced to the BC_1F_1 stage by backcrossing to the respective recurrent parents. Following a generation of backcrossing to the respective recurrent parents, more than 350 S_1 plants were extracted from each backcross population. The kernels from selected ears were then screened under the light box for desirable endosperm modification. During the conversion program, selection for the desirable endosperm modification was based on a rating scale of 1–5 where:

1 = kernels completely translucent with no opaqueness
2 = 25% opaqueness
3 = 50% opaqueness
4 = 75% opaqueness
5 = 100% opaqueness

The S_1 kernels with a score of 2–3 were selected and advanced to the S_2 stage by selfing. Kernels with score 1 were not selected because while there was the probability of having the o-2 gene in the homozygous recessive condition (o_2o_2), kernels could also be heterozygous O2o2 or homozygous dominant (O_2O_2) in which case the kernel will be low in lysine and tryptophan. In contrast, kernels with score 4 were not selected because the probability of obtaining well-modified kernels in advanced generations was much lower. The type 5 kernels were rejected as the kernels had soft endosperm with no modifiers (Vivek et al. 2008). The S_2 kernels of each ear were screened under the light box, and those with a score of 2–3 were again selected, grown ear-to-row, and the agronomically desirable plants were selfed to obtain about 250 S_3 ears at harvest. At this stage, only the kernels of the S_3 ears with a score of 2 were selected under the light box and planted in isolation blocks for recombination to obtain the F_1 generations of each partially converted variety/population. The F_1 seed of each recombined backcross material was planted and advanced to the second cycle of recombination to obtain the extra-early and early QPM varieties and populations in the IITA Maize Program. This was followed by the analysis of seed samples of each F_2 population/variety for tryptophan content in the IITA laboratory. No conscious effort was made to select for *Striga* resistance or drought tolerance during the QPM conversions. However, we have used artificial *Striga* infestation to maintain good levels of *Striga* resistance in germplasm converted to QPM. Similarly, artificial infestation with viruliferous leafhoppers has been utilized to maintain good levels of maize streak virus resistance in converted germplasm.

The procedure for the conversion of selected drought and/or *Striga*-resistant early and extra-early of QPM inbred lines is very similar to that used for the conversion of the early and extra-early varieties to QPM. Following one generation of backcrossing to the respective recurrent parents, more than 350 S_1 plants were extracted from each backcross population, and the kernels from selected ears were screened under the light box for the appropriate endosperm modification. The S_1 kernels with a score of 2−3 were selected for selfing to the S_2 stage. During the following season, the S_2 kernels of each ear were screened under the light box, and those with scores of 2–3 were identified, grown ear-to-row, and the agronomically desirable plants were advanced through selfing to obtain about 250 S_3 ears from each backcross source population at harvest. The 250 ears from each backcross were evaluated under managed drought stress at Ikenne and artificial *Striga* infestation at Mokwa and Abuja. Based on the evaluations, the top 25% S_3 lines were selected from each source population and advanced to S_6 stage using pedigree selection under optimal growing conditions. Selection under *Striga* infestation was achieved using a base index which integrated *Striga* damage at 8 and 10 WAP, number of emerged *Striga* plants at 8 and 10 WAP, number of ears per plant (EPP), and grain yield under artificial *Striga* infestation. On the other hand, selection under drought stress was achieved using an index integrating grain yield, EPP, anthesis–silking interval, ear aspect, and stay-green characteristic. Through this program, 73 white-grained and 23 yellow-grained QPM inbreds with drought and/or *Striga* resistance as well as streak resistance have been developed (Table 9.2) and are undergoing testing in hybrid combinations.

Table 9.2 Characteristics of early- and extra-early maturing, normal endosperm and QPM varieties evaluated in *Striga*-infested and *Striga*-free environments in Nigeria, 2006–2008

Cultivars	Code	Parentage	Grain type	Reaction to biotic/abiotic stresses	% Protein	% Tryptophan in protein
Early-maturing cultivars						
98 SYN WEC	SYNWC	(Pool 16 DT × 1368 STR) S_4 F_2	White dent/flint	Resistant to *Striga*	9.51	0.724
98 SYN WEC STR QPM C_0	SYNWQ	(Pool 16 DT × 1368 STR) S_4 F2 × QPM source	White dent/flint	Resistant to *Striga*	9.26	1.014
DM ESR-W QPM	DMRQ	DM ESR-W × QPM source	White flint	Susceptible to *Striga* and drought	9.29	1.086
EV DT-W 99 STR C_1	EDTW	(TZE-W pop × 1368 STR) TZE-W pop S_4F_2 set 1	White dent/flint	Tolerant to drought and *Striga* resistant	9.81	0.761
EV DT-W 99 STR QPM C_0	EDTWQ	(TZE-W pop × 1368 STR) TZE-W pop S4F_2 set 1 × QPM source	White dent/flint	Tolerant to drought and *Striga* resistant	10.28	1.146
EV DT-Y 2000 STR C_0	EDTY	TZE-Y pop STR S_4 F_2	Yellow flint	Tolerant to drought and *Striga* resistant	10.40	1.205
EV DT-Y 2000 STR QPM C_0	EDTYQ	TZE-Y pop STR S_4 F_2 × QPM source	Yellow flint	Tolerant to drought and *Striga* resistant	9.93	1.440
Pool 15 SR QPM C_1	P15Q	Various, QPM	White dent	Susceptible to *Striga* and drought	10.28	1.243
Pool 18 SR QPM C_1	P18Q	Various, QPM	Yellow flint	Susceptible to *Striga* and drought	11.07	1.115
Pop 61 SR BC_4 QPM	Pop61Q	Various, QPM	Yellow flint	Susceptible to *Striga* and drought	9.70	1.058
TZE-W pop DT STR C_4	TWC4	Local and introduced germplasm, SR source	White dent/flint	Tolerant to drought and *Striga* resistant	10.87	0.869
TZE-W pop STR QPM C_0	TWQ	TZE-W pop STR C_4 × QPM source	White dent/flint	Tolerant to drought and *Striga* resistant	9.80	1.058
TZE-W pop × 1368 STR QPM co	TWXQ	(TZE-W pop × 1368 STR) × QPM source	White dent/flint	Tolerant to drought and *Striga* resistant	10.04	1.092

(continued)

Table 9.2 (continued)

Cultivars	Code	Parentage	Grain type	Reaction to biotic/abiotic stresses	% Protein	% Tryptophan in protein
TZE-Y pop DT STR C_4	TYC4	Local and introduced germplasm, SR source	Yellow flint	Tolerant to drought and *Striga* resistant	9.30	0.750
TZE-Y pop STR QPM C_0	TYQ	TZE-Y pop STR C_4 × QPM source	Yellow flint	Tolerant to drought and *Striga* resistant	10.29	1.190
TZE-Y pop STR C_0 S_6 QPM C_0	TYS6Q	TZE-Y pop C_0S_6 × QPM source	Yellow flint	Tolerant to drought and *Striga* resistant	8.81	1.422
Extra-early maturing cultivars						
2000 Syn EE-W	SYN	TZEE-W pop STR S_4 F_2	White dent/flint	Drought escaping and *Strig*a resistant	9.37	0.731
2000 Syn EE-W QPM C_0	SYNQ	TZEE-W pop STR S_4 F_2 × QPM source	White dent	Drought escaping and *Striga* resistant	10.21	1.056
99 TZEF-Y STR	TZFY	Various	Yellow flint	Drought escaping and *Striga* tolerant	10.75	0.721
99 TZEF-Y STR QPM C_0	TZFYQ	99 TZEF-Y STR × QPM source	Yellow flint	Drought escaping and *Striga* resistant	10.54	1.071
EV 99 QPM	EV99Q	TZEE-W SR BC_3 × QPM source	White dent/flint	*Striga* susceptible	9.54	1.027
TZEE-W pop STR C_4	TZW_4	Local and introduced extra-early germplasm	White dent/flint	Drought escaping and *Strig*a resistant	10.34	0.873
TZEE-W pop STR QPM C_0	TZWQ	Local and introduced extra-early germplasm × QPM source	White dent/flint	Drought escaping and *Striga* resistant	10.63	0.966
TZEE-Y pop STR C_4	T_{ZY}	Local and introduced extra-early germplasm	Yellow flint	Drought escaping and *Striga* resistant	10.38	0.582
TZEE-Y pop STR QPM C_0	TZYQ	Local and introduced extra-early germplasm × QPM source	Yellow flint	Drought escaping and *Striga* resistant	10.49	0.927

9.7 QPM Parental Inbred and Hybrid Testing

A total of 93 early QPM lines at S_6 stage comprising of 71 white-grained and 22 yellow-grained endosperms developed in the IITA Maize Improvement Program were given TZEQI designations and analyzed for lysine and tryptophan contents at the IITA Nutrition Laboratory in August, 2010. Based on the analysis, the best 14 yellow endosperm QPM lines were planted, and single-cross hybrids were generated using diallel mating scheme. The diallel crosses were evaluated under induced drought stress and well-watered conditions at Ikenne during the 2010/2011 and 2011/2012 dry seasons. Also, the best 30 white endosperm early-maturing QPM inbreds were selected, and single-cross hybrids were generated using design II mating scheme to determine the performance of selected drought-tolerant early QPM inbred lines and their crosses under drought stress and well-watered conditions and examine the combining abilities and inheritance patterns of the inbred lines to identify the best testers for use in our breeding program. The 150 hybrids plus six checks were evaluated across eight environments in 2012 and 2013. Results of the combined analysis showed that the single-cross hybrid, TZEQI 35 × TZEQI 59, was the highest yielding across environments and out yielded the best hybrid (TZEI 5 × TZEI 98) by 1%. General combining ability (GCA) and specific combining ability (SCA) effects were highly significant ($p < 0.01$) for grain yield and other measured traits when *Striga*-infested (data not shown), indicating that additive and nonadditive gene actions were both important in the control of the inheritance of grain yield and other traits in the inbreds. However, GCA effects for all traits were greater than SCA effects across *Striga*-infested environments. The GCA mean squares for *Striga* damage at 8 and 10 weeks after planting (WAP) were significant and about three times greater than those of the SCA, indicating that additive gene action played a major role in the inheritance of the *Striga* damage. In contrast, GCA and SCA mean squares were not significant for number of emerged *Striga* plants at 10 WAP but were significant at 8 WAP with preponderance of GCA over SCA, indicating that additive gene action modulated the inheritance of number of emerged *Striga* plants in the inbreds. These results indicated that the additive gene action was more important for grain yield and other traits in the set of the inbreds when *Striga*-infested. This suggested that *Striga* resistance in either of the parental inbred lines would be sufficient to obtain hybrids with an acceptable performance under *Striga* infestation.

There was preponderance of GCA-female effects over GCA-male effects for grain yield, plant, and ear aspects, suggesting that maternal effects played a predominant role in the inheritance of these traits. However, larger GCA-male than GCA-female effects for *Striga* damage at 8 and 10 weeks after planting was observed indicating that paternal effects modified *Striga* damage. The GCA effects of multiple traits (HGCAMT) method classified the inbred lines into three heterotic groups each under drought, low-N, and across test environments and four groups across *Striga*-infested environments. The SNP-based method placed the inbreds into three heterotic groups across research environments and was more efficient in the classification of the inbreds. The inbreds TZEQI 25, TZEQI 35, and TZEQI 55 were identified as the best male testers, TZEQI 6 and TZEQI 56 as the best female testers, and TZEQI 6 and TZEQI 55 as the best male/female testers across environments. Hybrids TZEQI 16 × TZEQI 55, TZEQI 35 × TZEQI 59, and TZEQI 6 × TZEQI 35 were identified as outstanding across environments and were recommended for commercialization to contribute to sustainable maize production, improved nutrition, and food security in SSA.

In another study, 91 diallel crosses, derived from 14 early-maturing, yellow endosperm QPM maize inbreds, were evaluated under *Striga*-infested environments at Mokwa and Abuja in Nigeria between 2011 and 2012. The objectives were to (i) examine the combining ability for grain yield of the set of early QPM yellow inbreds, (ii) determine the heterotic groups of the inbreds, (iii) identify the best testers for use in WCA, and (iv) determine the performance and stability of the inbreds in hybrid combinations under *Striga*-infested environments. Grain yield of the yellow QPM hybrids ranged from 1008 kg ha^{-1} for TZEQI 80 × TZEQI to 5074 kg ha^{-1} for TZEQI 78 × TZEQI 92 (data not shown). The most outstanding hybrid, TZEQI 78 × TZEQI 92, out yielded the best OPV check (2008 DTMA-Y STR) by 76%. The *Striga*-resistant hybrids were characterized by higher grain yield, better ear aspect, higher number of ears per plant, lower *Striga* damage, and lower number of emerged *Striga* plants at 8 and 10 WAP compared with the susceptible hybrids. The GGE biplot analysis identified TZEQI 78 × TZEQI 92, TZEQI 79 × TZEQI 92, and TZEQI 78 × TZEQI 91 as the highest-yielding and most stable hybrids across environments and should be promoted for adoption and commercialization in WCA.

The results of the combined analysis revealed that single-cross hybrid, TZEQI 78 × TZEQI 92, was the highest yielding across *Striga*-infested environments and outperformed the best yellow normal endosperm hybrid (TZEI 23 × TZEI 13) by 32%. The GCA and SCA effects were highly significant ($p < 0.01$) for grain yield and other measured traits when *Striga*-infested (data not shown), indicating that additive and nonadditive gene actions were both important in the control of the inheritance of grain yield and other traits of the inbreds. However, GCA effects for all traits were greater than SCA effects across *Striga*-infested environments (data not shown). The GCA mean squares for *Striga* damage at 8 and 10 weeks after planting (WAP) were significant and about three times greater than those of the SCA, indicating that additive gene action played a major role in the inheritance of the *Striga* damage. In contrast, GCA and SCA mean squares were not significant for a number of emerged *Striga* plants at 10 WAP but were significant at 8 WAP with preponderance of GCA over SCA, indicating that additive gene action modulated the inheritance of a number of emerged *Striga* plants in the inbreds. These results indicated that the additive gene action was more important for grain yield and other traits in the set of the inbreds when *Striga*-infested. This suggests that *Striga* resistance in either of the parental inbred lines would be sufficient to obtain hybrids with an acceptable performance under *Striga* infestation.

The GCA effect of an inbred determines its relative importance as a tester for the improvement of a target trait in a population and as a parent for the development of synthetic varieties and hybrids. Genotypes that are outstanding in terms of GCA and SCA for grain yield and other agronomic traits could be employed for the development of heterotic populations for further improvement and for developing high-yielding synthetic varieties and hybrids (Akinwale et al. 2014). In the present study, significant and positive GCA effects were observed for grain yield of the inbreds TZEQI 89, TZEQI 91, TZEQI 92, and TZEQI 93 under drought, low-N, and optimal environments; TZEQI 78, TZEQI 87, TZEQI 91, and TZEQI 92 under *Strig*a infestation; and TZEQI 87, TZEQI 89, TZEQI 91, TZEQI 92, and TZEQI 93 across research environments indicating that these inbreds possess favorable alleles for grain yield and would contribute high grain yields to their progenies. Significant and negative GCA effects were observed for the stay-green characteristic of inbred TZEQI 82 and of TZEQI 87 under drought stress and under low N indicating that the two inbreds will transmit the trait to their progenies or will slow down the rate of leaf senescence. These inbreds could be used to improve this trait in QPM germplasm. Under *Striga* infestation, significant negative GCA effects were detected for *Striga* damage at 10 WAP for inbreds TZEQI 87 and TZEQI 92 indicating that the inbreds were tolerant to *Striga* damage and could be used to improve other QPM germplasm. Also, TZEQI 84 showed significant negative GCA effects for the number of emerged *Striga* plants at 8 and 10 WAP, indicating that the inbred possesses genes for resistance to *Striga* that could be introgressed into QPM germplasm. The inbred TZEQI 93 showed significant negative GCA effects for days to silking and ASI under drought, low-N, *Striga*-infested, optimal, and across research environments suggesting that it will contribute favorable alleles for earliness to the progenies under the contrasting environments. Inbreds TZEQI 74 and TZEQI 87 showed significant positive GCA effects for EPP under each research environment and across the four, indicating that they would contribute favorable alleles to the trait in their progenies.

To assign inbred lines into heterotic groups, heterotic group's specific and general combining ability (HSGCA) method proposed by Fan et al. (2008) and general combining ability effects of grain yield and other traits (HGCAMT) method proposed by Badu-Apraku et al. (2013) were used. The estimated GCA effects of the inbred parents for each environment were subjected to GGE biplot analysis to assess the relationships among inbreds, environments, and inbred × environment interaction. Furthermore, the GGE biplot was used to obtain information on the performance and yield stability of the single-cross hybrids (Yan 2001). The inbred lines were classified into three heterotic groups based on the GCA effects of multiple traits (HGCAMT) of inbred lines and three groups based on heterotic groups' specific and general combining ability (HSGCA). There was close correspondence between classification based on HSGCA and the HGCAMT methods, indicating the effectiveness of the two methods in classifying inbred lines. TZEQI 78, TZEQI 89, TZEQI 87, and TZEQI 82 were identified as the best inbred testers. Inbreds TZEQI 87 and TZEQI 91 had the highest GCA effects and TZEQI 89 the lowest. Inbred TZEQI 78 was identified as the most stable across *Striga*-infested environments (Figure not shown).

Ninety-six extra-early QPM hybrids were generated by crossing 24 selected extra-early inbred lines in sets using North Carolina Design II mating scheme to determine the performance of the drought-tolerant lines and their crosses under drought stress, well-watered conditions, and low- and high-N environments. Also, the combining abilities and inheritance patterns of the inbred lines were determined and the best testers identified for use in our breeding program. The 96 hybrids plus four checks were evaluated at Ile-Ife and Mokwa under low- and high-N conditions in 2012 and 2013. Also, the hybrids were evaluated under terminal drought stress at Bagauda during the growing season of 2012 and 2013 and under induced drought stress and well-watered conditions at Ikenne during the 2011/2012 and 2012/2013 dry seasons. Results showed that general combining ability (GCA) effects were greater than specific combining ability (SCA) effects for all traits measured under stress and optimal conditions as well as across test environments suggesting that additive gene action was more important than nonadditive gene action in the 24 QPM inbred lines. The inbreds TZEEQI 7, TZEEQI 60, TZEEQI 61, TZEEQI 8, TZEEQI 11, TZEEQI 137, TZEEQI 63, TZEEQI 66, TZEEQI 44, and TZEEQI 157 possessed favorable alleles for stress tolerance and could be used for population improvement and development of stress-tolerant hybrids. The hybrids TZEEQI 183 × TZEEQI 7, TZEEQI 181 × TZEEQI 7, and TZEEQI 144 × TZEEQI 183 were high yielding and the most stable across environments and should be tested extensively in on-farm trials and commercialized in the sub-region. Narrow-sense heritability ranged from 19% for ear aspect to 63% for ear height under stress conditions and 5% for grain yield to 87% for plant height. This result indicated that many of these traits can be readily transmitted and direct phenotypic selection can be made since there is preponderance of additive gene effects for all the measured traits. The 24 inbred lines were classified into three heterotic groups based on the GCA effects of multiple traits of the inbreds. Inbred lines, TZEEQI 7 and TZEEQI 134, were identified as best testers for heterotic groups 1, 2, and 3, respectively, while TZEEQI 7 × TZEEQI 60 was the best single-cross tester. These testers could be utilized in QPM hybrid breeding programs to group other QPM inbred lines into heterotic groups. Inbred lines TZEEQI 7, TZEEQI 78, TZEEQI 111, TZEEQI 60, TZEEQI 61, and TZEEQI 137 were identified as stress (drought and low N) tolerant and may be used as germplasm sources for introgression of genes for tolerance to the two stresses into tropical extra-early QPM populations, as well as for the development of drought and low-nitrogen-tolerant hybrids in sub-Saharan Africa. The extra-early normal endosperm hybrid checks, TZEEI × TZEEI 29 and (TZEEI 21 × TZEEI 14) × TZEEI 29, were found to be superior in grain yield under all conditions compared to the extra-early QPM hybrids. This indicates that much more research effort should be devoted to breeding for high-yielding, drought, and low-nitrogen extra-early QPM hybrids. The extra-early QPM inbred lines, viz., TZEEQI 1, TZEEQI 7, TZEEQI 60, and TZEEQI 134, identified with high positive and significant GCA effects for grain yield can be crossed with other QPM inbred lines of different origins to identify high-performing single-cross hybrids for use as parents in QPM hybrids.

Inbred lines displaying significant and positive GCA effects for grain yield are most likely to contribute favorable alleles in a recurrent selection program and could be used as parents to develop synthetic population that could be improved for drought and low-N tolerance. Alternatively, such inbred lines could be used to develop outstanding hybrids for commercialization. The significant positive GCAm effects displayed for the grain yield of inbred TZEEQI 1 and GCAf effects for grain yield of TZEEQI 7, TZEEQI 60, and TZEEQI 134 under stress indicated that the inbreds would contribute favorable alleles for grain yield under stress when used as males and females, respectively. Similarly, the positive and significant GCAm and GCA_f effects displayed by TZEEQI 183 suggested that the inbreds could contribute to improved grain yield in their offspring when used either as male or female parent. The negative and significant GCAm and GCA_f effects of the stay-green characteristic for TZEEQI 109 suggested that the inbred would contribute alleles that would delay leaf senescence in its progenies when used either as male or female parent. In contrast, the negative and significant GCA_f effects exhibited by TZEEQI 102 indicated that the inbred would contribute to delayed leaf senescence in the progeny when used only as a female parent. The significant positive GCAm effects displayed for grain yield by the inbreds TZEEQI 1 and TZEEQI 60 and GCA_f effects by TZEEQI 109 as well as TZEEQI 137 under non-stress environment revealed that the inbreds would contribute favorable alleles for grain yield when used either as males or females under non-stress environments. Similarly, the positive and significant GCAm and GCA_f effects for grain yield displayed by inbreds TZEEQI 7 and TZEEQI 134 showed that the inbreds could contribute to improved grain yield in their offspring when used either as male or female parents.

9.8 Performance of QPM Open-Pollinated Varieties

During the conversion of the normal endosperm populations and varieties to QPM, no conscious effort was made to select for *Striga* resistance or drought tolerance. Even though there are several reports indicating that certain QPM genotypes have grain yields that are comparable to the yields of conventional varieties now under cultivation in developing countries and that several experimental varieties performed better than the checks in several regions of the world (National Research Council 1988), such reports were limited in WCA. There was therefore a need to determine how the available QPM varieties in the IITA Maize Program compared to their normal counterparts and to test extensively the available QPM varieties to promote their adoption and commercialization by farmers in WCA. Sixteen early- and nine extra-early maturing QPM and normal cultivars were evaluated in Nigeria from 2006 to 2008 to determine their performance in *Striga*-infested and *Striga*-free environments and to identify the most outstanding cultivars. Results showed that the extra-early normal maize cultivars, 2000 Syn EE-W and 99 TZEE-Y STR, were comparable in yield to the QPM versions under both research conditions. While TZEE-Y Pop STR C_4 was superior in grain yield to its QPM version only under *Striga*-free conditions, TZEE-W Pop STR C_4 was not only higher yielding than the

QPM version, under both test conditions, but was also superior in *Striga* resistance. In the early maturity group, TZE-W DT STR C_4 out yielded the QPM version by 21% under *Striga* infestation and by 10% when *Striga*-free. In contrast, the QPM cultivar, 98 Syn WEC STR QPM C_0, was higher yielding than the normal endosperm version, by 31% when *Striga*-infested. Analysis by GGE biplot revealed that two extra-early and three early-maturing cultivars had superior performance in both research environments. TZEE-W Pop STR QPM C_0 and EV DT-W 99 STR QPM C_0 were high yielding and stable when *Strig*a-infested, while TZE-Y Pop DT STR C_4, TZE-W Pop DT STR C_4, and TZE-Y Pop STR QPM C_0 were outstanding when *Striga*-free. It was striking that some products of the conversion program showed superior or comparable performance to the normal versions not only in terms of grain yield but also low *Striga* damage and emerged *Striga* plants (2000 Syn EE-W STR vs 2000syn EE-W STR QPM C_0, 98 Syn WEC vs 98 Syn WEC QPM C_0, EV DT-W 99 STR C_1 vs EV DT-W 99 STR QPM C_0). Furthermore, results of a trial involving 20 drought-tolerant early-maturing cultivars evaluated in 2008 at nine locations in drought-prone environments in Northern Nigeria indicated that the cultivars Tillering Early DT, EV DT-W 99 STR QPM C_0, EV DT-Y 2000 STR QPM C_0, and Pool 18-SR/AK 94 DMESRY were outstanding, out yielding the best local normal maize check by 8–51%. Based on the results of this trial, EV DT-W 99 STR QPM C_0 and EV DT-Y 2000 STR QPM C_0 which consistently showed superior performance across six locations were extensively tested on farm in the drought-prone and *Striga* endemic zones of Northern Nigeria through the funding support of the DTMA Project. Also, EV DT-W 99 STR QPM C_0 was undergoing extensive on-farm testing in Benin while it had been released in Ghana. In a similar trial in Ghana involving extra-early cultivars evaluated at two locations in the Upper West Region of Ghana, the highest-yielding QPM variety, TZEE-W Pop STR QPM C_0, had 34% higher grain yield than the QPM check variety (Buah et al. 2009). TZEE-W Pop STR QPM C_0 and TZEE-Y Pop STR QPM C_0 were released in Ghana in 2010. Similarly, based on the superior performance of TZEE-W Pop STR QPM C_0, 2000 Syn EE-W QPM C_0, and TZEE-Y Pop STR QPM C_0 in WA, the three cultivars were extensively tested in Ghana and Mali using the mother–baby on-farm testing approach and released (S. Buah, SARI; J. Kambiok, SARI; N. Coulibaly, IER, personal communications, 2009). The outstanding performance of the QPM varieties may be attributed to the large population sizes sampled during QPM conversion. This might have ensured that the favorable *Striga*-resistant and drought-tolerant alleles were maintained in the respective populations during selection for high grain yield, desirable agronomic characteristics, and appropriate endosperm modification. This demonstrated the effectiveness of the backcross, inbreeding, and hybridization methods adopted in our conversion program. Table 9.3 shows the grain yield and agronomic characteristics of extra-early QPM varieties at three locations in Nigeria. Grain yield of the five QPM varieties averaged 3.19 t ha^{-1} compared to 3.36 t ha^{-1} for the four normal endosperm reference checks. The mean grain yield of nine QPM varieties (3.48 t ha^{-1}) was comparable to the mean yield of five checks (3.41 t ha^{-1}) in three locations in Nigeria in 2 years (Table 9.3). Yield of the late

Table 9.3 Grain yield (kg ha^{-1}) and agronomic characters of extra-early QPM varieties evaluated at Mokwa, Zaria, and Ikenne, 2006–2007

Varieties	Grain yield (kg ha^{-1})	Days to silking	Plant height (cm)	Stalk lodging	Ear aspect
TZEE-W pop STR C4 (normal ref)	3911	54	165	3	3.8
TZEE-W pop STR QPM C0	3490	53	177	3	3.5
2000 Syn EE-W (normal ref)	3418	53	156	3	3.6
2000 Syn EE-W QPM C0	3278	53	163	3	3.7
TZEE-Y pop STR C4 (normal ref)	3275	54	174	3	3.6
TZEE-Y pop STR QPM C0	3261	53	159	3	3.8
99 TZEE-Y STR QPM C0	3085	54	162	2	3.6
99 TZEF-Y STR (normal ref)	2839	52	158	3	3.5
EV 99 QPM	2839	53	162	2	3.8
Grand mean	3266	53	164	3	3.7
LSD	400	1	9.5	1	0.3

Table 9.4 Grain yield and agronomic characters of intermediate/late-maturing QPM varieties evaluated at Ikenne, Mokwa, Zaria, and Saminaka in 2006 (source: Courtesy of A. Menkir, 2006)

Varieties	Grain yield (kg ha^{-1})	Days to silking	Plant height (cm)	Plant aspect	Ear aspect
Obatanpa/IWDC2 SYN F2* QPM	6397	56	217	2.4	2.3
Obatanpa/TZL COMP1 SYNW-1*2 QPM	6358	57	220	2.4	2.4
Pop 66 SR/TZUTSR-WSGY*2 (YQPM)	6150	55	224	2.8	2.5
Obatanpa GH	5992	56	225	2.8	2.3
POP66SR/ ACR91SUWAN-1-SRC1*2(YQPM)	5979	54	209	2.3	2.6
OBA SUPER II (yellow normal hybrid)	5840	57	208	2.6	2.3
Obatanpa	5787	55	219	2.7	2.4
POP66SR/DMR-LSRY*2 (YQPM)	5552	54	214	2.8	2.7
OBA SUPER I (white normal hybrid)	5499	57	205	2.8	2.4
Mean	5993	56	216	2.6	2.5
SE	271.6	0.4	4.3	0.1	0.1

varieties evaluated in four locations in Nigeria in 2006 ranged from 5.50 t ha^{-1} to 6.40 t ha^{-1} and averaged 5.97 t ha^{-1} for eight QPM varieties and 5.67 t ha^{-1} for two normal endosperm hybrids (Table 9.4). Yield of nine testcrosses averaged 7.38 t ha^{-1} in three locations in Nigeria in 2006 compared to 6.71 t ha^{-1} for two normal endosperm hybrid checks (Table 9.5). In all cases, the QPM varieties were comparable in yield performance to the normal endosperm counterparts.

Table 9.5 Grain yield and agronomic characters of testcrosses of intermediate/late-maturing QPM lines evaluated at Ikenne, Saminaka, and Zaria in 2006 (source: Courtesy of A. Menkir, 2006)

Entry	Grain yield (kg ha^{-1})	Days to silking	Plant height (cm)	Plant aspect	Ear aspect
AO618-30	7763	61	203	1.9	2.6
AO618-34	7629	60	228	2.7	2.6
AO618-27	7597	60	218	2.6	2.6
AO618-22	7462	61	216	2.6	2.6
AO618-25	7221	60	226	2.8	2.7
AO618-21	7123	62	203	2.8	2.5
AO618-15	6963	61	209	2.2	2.4
AO618-39	6906	61	224	2.9	2.2
OBA 98 (QPM hybrid check)	6739	58	214	3	2.9
OBA SUPER I (normal hybrid check)	6681	60	221	2.9	2.5
Mean	6358	61	215	2.7	2.6
SE	428	0.6	3.9	0.2	0.1

9.9 Progress in Developing Provitamin A QPM Inbreds, Varieties, and Hybrids

Vitamin A deficiency is a major health problem in SSA. The maize plant can accumulate significant quantity of provitamin A (PVA) in the endosperm and has rich genetic variation for PVA trait. Therefore, increasing PVA level in maize through breeding is a feasible approach for alleviating PVA deficiency. Most Africans subsist on cereal-based diet with low levels of vitamin A, whose deficiency affect more than 45 million children under 5 years of age in SSA (Menkir et al. 2014). Vitamin A deficiency depresses the immune system and increases susceptibility to diseases, diminishes possibility of survival from serious illness, and may cause night or complete blindness (Sommer and West 1996). Apart from PVA problem, maize production in SSA is constrained by *Striga hermonthica* parasitism, drought, and low soil nitrogen (low N). Therefore, there is need to develop and commercialize stress-tolerant PVA maize in the effort to fight malnutrition in SSA.

Since 2007, IITA's breeding strategy for early and extra-early maize has focused on simultaneous improvement of lysine, tryptophan, and/or β-carotene content of maize. The development of normal endosperm maize and QPM varieties high in β-carotene involves the screening of diverse germplasm to identify parental materials with consistently high levels of provitamin A as well as high levels of tolerance/resistance to drought, low N, and *Striga* for the development of synthetic varieties and hybrids. A program was initiated in 2007 to develop early (90–95 days to maturity) and extra-early (80–85 days to maturity) stress-tolerant (drought tolerant and *Striga* resistant), high-provitamin A varieties for WCA. To this end, the extra-early

Striga-resistant variety, 2004 TZEE-Y STR C_4; the extra-early *Striga*-resistant QPM variety, TZEE-Y STR QPM; the early drought- and *Striga*-resistant yellow variety, 2004 TZE-Y Pop DT STR C_4; and the drought- and *Striga*-resistant early QPM variety, TZE-Y Pop DT STR QPM, were crossed to two sources of high provitamin A [Syn –Y-STR-34-1-1-1-1-2-1-B-B-B-B-B/NC354/SYN-Y-STR-34-1-1-1 (OR1) and KU1409/DES/1409 (OR2)] from the IITA Maize Improvement Program to introgress the genes for high β-carotene into each of the eight varieties. This was followed by a cycle of backcrossing to each recurrent parent to recover earliness. The kernels of the BC_1F_1 of each material with deep orange color and/or appropriate endosperm modification under the light box in the case of the QPM materials were selected and selfed to the F_2 and subsequently the F_3 stages. The F_3 lines with the deep orange color were selected and recombined to form the extra-early provitamin A varieties, 2009 TZEE-OR1 STR, 2009 TZEE-OR2 STR, 2009 TZEE-OR1 STR QPM, and 2009 TZEE-OR2 STR QPM, and the early provitamin A varieties, 2009 TZE-OR1 STR, 2009 TZE-OR2 STR, 2009 TZE-OR1 STR QPM, and 2009 TZE-OR2 STR QPM. The varieties have been evaluated under both *Striga* infestation and drought since 2010 and have shown outstanding performance under these stresses. Furthermore, a program was initiated in 2011 to extract new generation of extra-early and early inbreds from the high-provitamin A normal endosperm varieties, 2009 TZEE-OR1 STR and 2009 TZE-OR1 STR, and the high-provitamin A QPM varieties, 2009 TZEE-OR2 STR QPM and 2009 TZE-OR2 DT STR QPM. The inbreds from each of the four varieties were advanced from the S_4 stage to the S_6 stage in 2014. A total of 123 and 73 newly developed inbreds from the early provitamin A varieties, 2009 TZE-OR1 STR and 2009 TZE-OR2 STR QPM, respectively, were evaluated for tolerance to managed drought stress during the 2014/2015 dry season at Ikenne. Furthermore, 224 inbred lines derived from the extra-early provitamin A variety, 2009 TZEE-OR1 STR, were evaluated for tolerance to drought at Ikenne, while the inbred lines developed from the 2009 TZEE-OR2 STR QPM variety were evaluated for drought tolerance at Ikenne and low N at Ile-Ife. Also, the newly developed inbred lines with normal endosperm were evaluated at Ikenne under induced drought stress in the 2014/2015 dry season, while the QPM inbreds were screened for the appropriate QPM endosperm modification in the QPM laboratory in IITA-Ibadan. Furthermore, selected inbreds are presently being analyzed for β-carotene content in the IITA and CIMMYT laboratories. The most promising inbreds with high levels of β-carotenes have been selected for evaluation in hybrid combinations to identify outstanding hybrids with high-provitamin A content. The inbred lines that have shown varying degrees of tolerance to drought and/or low N and *Striga* resistance were selected using the IITA base index and screened under the light box for the appropriate QPM endosperm modification. The early and extra-early inbred lines with orange endosperm color representing elevated levels of provitamin A were also considered, and provitamin A extra-early and early QPM lines were selected as parents for combining ability studies. The characteristics of the parental lines selected for the genetic studies; their reactions to drought, low N, and *Striga*; as well as the provitamin A levels have been determined (table not shown).

9.10 Combining Ability, Heterotic Patterns, and Performance of Provitamin A Inbreds and Hybrids Under Contrasting Environments

Maize production in SSA is constrained by *Striga hermonthica* parasitism, drought, and low soil nitrogen (low N). One hundred and thirty-two extra-early provitamin A maize hybrids derived from crosses between 33 extra-early provitamin A inbreds and 4 inbred testers were evaluated by Badu-Apraku et al. (2016) under *Striga*-infested, drought, low-N, and optimal environments in Nigeria, 2015–2016. The objectives of the study were to (i) estimate general combining ability (GCA) and specific combining ability (SCA) effects of grain yield and other traits of the extra-early provitamin A inbreds, (ii) classify the inbreds into heterotic groups, (iii) identify inbred testers, and (iv) assess the performance of the hybrids under contrasting environments. Results revealed preponderance of GCA over SCA for grain yield and other traits under contrasting environments. Inbreds TZEEIOR 30, TZEEIOR 41, TZEEIOR 42, TZEEIOR 97, TZEEIOR 109, and TZEEIOR 140 possessed genes for multiple stress tolerance and elevated levels of provitamin A (table not shown) and could be used to develop high-provitamin A stress-tolerant hybrids. Inbreds were classified into five groups under multiple stresses and three groups each under optimal and across environments. Inbreds TZEEIOR 197 and TZEEIOR 30 were identified as testers for heterotic groups 1 and 2. Hybrids TZEIOR 197 × TZdEEI 12 and TZEIOR 123 × TZdEEI 7 were the most stable and high yielding across multiple stress and non-stress environments and were recommended for further testing and commercialization in SSA.

Obeng-Bio (2017, unpublished) selected 24 lines as parents for the NCD 2 crosses, grouped them into six sets each containing four inbred lines to generate 96 hybrids. The characteristics of the parental lines selected and their reactions to drought and low-N stresses as well as the sets into which they were placed in the NCD 2 arrangement are shown in Table 9.6. The 96 hybrids plus four checks were evaluated under low-N conditions at Ile-Ife and Mokwa and under optimal environments at Ile-Ife, Mokwa, and Ikenne during the 2016 major growing season and managed drought stress during the 2016/2017 dry season in Nigeria. Results revealed that the SCA effects were larger than the GCA effects, with SCA accounting for 50.16–74.54% and GCA 25.46–49.84% of the total variation among hybrids for measured traits, across low-N and optimal environments, suggesting that hybrid production should be the focus of a breeding program using the set of inbred lines. The estimates of GCA effects for grain yield varied significantly among lines and between environments. The two-tailed t-tests performed to compare the relative contributions of GCA-female effects and GCA-male effects of the parental lines for grain yield and most of the measured traits were not significant under low-N, optimal, and across research environments indicating that the inheritance of the measured traits was equally controlled by both maternal and paternal effects. The results of the dendrogram constructed using the heterotic grouping method based on GCA of multiple traits (HGCAMT) proposed by Badu-Apraku et al. (2013) classified the

Table 9.6 The 24 provitamin A early QPM inbred lines selected for the NCD 2 crosses at Ibadan, Nigeria

S/N	Inbred	Pedigree	Reaction to drought stress	Reaction to low-N stress	SET
1	TZEIORQ 69	2009 TZE OR2 DT STR QPM S6 inb 57-2/2-2/2-1/1-1/2-1/1	Tolerant	Tolerant	A
2	TZEIORQ 29	2009 TZE OR2 DT STR QPM S6 inb 28-1/1-2/2-1/2-1/2-1/1	Tolerant	Susceptible	A
3	TZEIORQ 45	2009 TZE OR2 DT STR QPM S6 inb 35-2/3-3/3-4/4-3/4-1/1	Susceptible	Tolerant	A
4	TZEIORQ 48	2009 TZE OR2 DT STR QPM S6 inb 7-2/3-1/2-3/4-1/3-1/1	Tolerant	Susceptible	A
5	TZEIORQ 11	2009 TZE OR2 DT STR QPM S6 inb 7-1/3-1/2-1/2-4/4-1/1	Tolerant	Tolerant	B
6	TZEIORQ 20	2009 TZE OR2 DT STR QPM S6 inb 26-1/1-1/2-1/6-1/2-1/1	Tolerant	Tolerant	B
7	TZEIORQ 6	2009 TZE OR2 DT STR QPM S6 inb 2-2/3-2/3-2/4-1/5-1/1	Tolerant	Susceptible	B
8	TZEIORQ 44	2009 TZE OR2 DT STR QPM S6 inb 35-2/3-3/3-4/4-1/4-1/1	Tolerant	Susceptible	B
9	TZEIORQ 42	2009 TZE OR2 DT STR QPM S6 inb 35-2/3-3/3-2/4-2/2-1/1	Tolerant	Tolerant	C
10	TZEIORQ 59	2009 TZE OR2 DT STR QPM S6 inb 50-2/2-1/3-2/3-2/2-1/1	Tolerant	Tolerant	C
11	TZEIORQ 15	2009 TZE OR2 DT STR QPM S6 inb 7-2/3-1/2-3/4-1/3-1/1	Tolerant	Susceptible	C
12	TZEIORQ 23	2009 TZE OR2 DT STR QPM S6 inb 26-1/1-1/2-4/6-1/3-1/1	Tolerant	Susceptible	C
13	TZEQI 82	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 2-3-1-1-4-6	Tolerant	Tolerant	D
14	TZEIORQ 47	2009 TZE OR2 DT STR QPM S6 inb 35-3/3-3/3-1/3-2/2-1/1	Susceptible	Tolerant	D
15	TZEIORQ 7	2009 TZE OR2 DT STR QPM S6 inb 2-2/3-2/3-3/4-1/3-1/1	Tolerant	Susceptible	D
16	TZEIORQ 13	2009 TZE OR2 DT STR QPM S6 inb 35-2/3-3/3-4/4-1/4-1/1	Tolerant	Susceptible	D
17	TZEIORQ 2	2009 TZE OR2 DT STR QPM S6 inb 2-2/3-1/3-1/3-1/2-1/1	Tolerant	Tolerant	E
18	TZEIORQ 5	2009 TZE OR2 DT STR QPM S6 inb 2-2/3-2/3-1/4-3/3-1/1	Tolerant	Susceptible	E
19	TZEIORQ 26	2009 TZE OR2 DT STR QPM S6 inb 26-1/1-1/2-6/6-2/3-1/1	Tolerant	Tolerant	E
20	TZEIORQ 41	2009 TZE OR2 DT STR QPM S6 inb 35-2/3-3/3-4/4-1/4-1/1	Tolerant	Susceptible	E
21	TZEIORQ 24	2009 TZE OR2 DT STR QPM S6 inb 26-1/1-1/2-4/6-2/3-1/1	Tolerant	Tolerant	F
22	TZEIORQ 43	2009 TZE OR2 DT STR QPM S6 inb 35-2/3-3/3-3/4-1/2-1/1	Tolerant	Susceptible	F
23	TZEIORQ 40	2009 TZE OR2 DT STR QPM S6 inb 35-2/3-2/3-1/2-2/2-1/1	Susceptible	Tolerant	F
24	TZEIORQ 70	2009 TZE OR2 DT STR QPM S6 inb 35-2/3-3/3-4/4-1/4-1/1	Tolerant	Susceptible	F

inbreds into three groups (figures not shown). Group 1 consisted of TZEIORQ 69, TZEIORQ 5, TZEIORQ 20, TZEIORQ 15, TZEIORQ 6, TZEIORQ 41, TZEIORQ 40, TZEIORQ 43, and TZEIORQ 7; group 2 comprised TZEIORQ 45, TZEIORQ 44, TZEIORQ 42, TZEIORQ 26, TZEIORQ 47, TZEIORQ 23, and TZEIORQ 24, while TZEIORQ 29, TZEIORQ 11, TZEIORQ 59, TZEIORQ 13, TZEIORQ 48, TZEIORQ 2, TZEIORQ 70, and TZEQI 82 constituted group 3. TZEIORQ 43 had high grain yield under low-N environment, was placed in the first heterotic group, recorded significant positive GCA-female and GCA-male effects for grain yield, and was therefore the best tester for heterotic group 1. Furthermore, TZEIORQ 45 had high grain yield under low-N environments, was classified into the second heterotic group, recorded significant positive GCA-female and GCA-male effects for grain yield, and was therefore identified as the best tester for heterotic group 2. Also, TZEIORQ 59 recorded high grain yield under low-N environments, was classified into the third heterotic group, had high significant positive GCA-female and GCA-male effects, and was therefore identified as the best tester for heterotic group 3. The mean grain yield of the hybrids under low-N conditions ranged from 109.1 kg ha^{-1} for TZEIORQ 24 × TZEIORQ 26 to 5560 kg ha^{-1} for TZEIORQ 29 × TZEIORQ 43 with an overall mean of 2348 kg ha^{-1}. Also under optimal conditions, the mean grain yield varied from 36 kg ha^{-1} for TZEIORQ 26 × TZEIORQ 7 to 5938 kg ha^{-1} for TZEIORQ 69 × TZEIORQ 70. The best check TZEIOR 127 × TZEIOR 57 (provitamin A early hybrid) had grain yield of 3063 $kgha^{-1}$ under low-N environment and was ranked seventh among the 15 best-performing hybrids. However, apart from the best-performing hybrid TZEIORQ 29 × TZEIORQ 43, the grain yield of the six top-performing hybrids was not significantly different from that of the best normal endosperm provitamin A hybrid check (TZEIOR 127 × TZEIOR 57) under low-N and optimal environments. In addition, it was striking to note that TZEIORQ 43 × TZEIORQ 5 ranked 11th among the 15 best hybrids and performed similarly as the best check and had its inbreds placed in the same heterotic group. The parental lines of TZEIORQ 43 × TZEIORQ 5 recorded significant ($P > 0.05$) positive GCA-male and GCA-female effects, and the hybrid had a relatively good yielding ability to qualify its use as a seed parent in successful three-way and double-cross hybrids for high seed production. TZEIORQ 43 × TZEIORQ 5 was, therefore, identified as a potential single-cross hybrid tester. Out of the 100 hybrids evaluated across low-N environments, 66 including the two checks showed varying degrees of low-N stress tolerance. Average grain-yield reduction of 49.57% was recorded for the hybrids across low-N and optimal environments.

Additive main effects and multiplicative interaction (AMMI) biplot of grain yield and the first interaction principal component axis (IPCA 1) of 25 provitamin A early QPM hybrids (best 15 and worst 10 based on the base index) plus four checks evaluated across two low-N and three optimal environments in Nigeria in 2016 identified TZEIORQ 43 × TZEIORQ 2, TZEIORQ 7 × TZEIORQ 42, TZEQI 82 × TZEIORQ 42, and TZEIORQ 23 × TZEIORQ 11 as high-yielding and most stable hybrids. TZEIORQ 43 × TZEIORQ 2 showed the most outstanding yield and stability of performance across research environments.

Generally, high values were recorded for the narrow-sense heritability based on pooled estimates of male and female sums of squares for grain yield and other traits across research environments. Under low N, heritability estimates ranged from 0.42 for ears per plant to 0.81 for plant aspect, with grain yield recording 0.74. Under optimal environments, heritability estimates varied from 0.42 for days to silking to 0.88 for grain yield. The high-heritability values recorded among the hybrids for grain yield and other measured traits suggested a large amount of phenotypic variation for the measured traits of the hybrids due to genetic variation among the parental inbreds. Similarly, high percentages of mid-parent heterosis were recorded for grain yield and other traits particularly among the 15 top-performing hybrids with values ranging from 213.75% for TZEIORQ 42 × TZEIORQ 20 to 779.12% for TZEIORQ 29 × TZEIORQ 43. The high heterosis for grain yield among the best 15 hybrids suggested that the parental lines involved in the crosses possessed genes that are complementary, i.e., there appears to be transgressive segregation.

In another study, Olatise et al. (2017, unpublished) examined the GCA and SCA effects of grain yield and other traits of 42 extra-early PVA inbreds derived from *Zea diploperennis* across *Striga* and optimal growing environments, assessed the yield performance and stability of the inbreds and hybrids under contrasting environments, identified appropriate inbred testers for developing stress-tolerant hybrids, and classified the inbreds into contrasting heterotic groups using the heterotic groups' specific and general combining ability (HSGCA) and heterotic grouping based on GCA of multiple traits (HGCAMT) methods.

Results of the study revealed that under *Striga* infestation, the mean grain yield of the hybrids ranged from 1773kg ha^{-1} for TZEEIOR 125 X TZEEI 95 to 5707 kg ha^{-1} for TZEEIOR 251 X TZdEEI 7 with a mean of 3438 kg ha^{-1}. However, under induced drought stress, grain yield ranged from 719 kg ha^{-1} for TZdEEI 9 X TZdEEI 12 to 4235 kg ha^{-1} for TZEEIOR 11 X TZEEI 79, while it ranged from 4279 kg ha^{-1} for TZEEI 9 X TZEEI 79 to 6772 kg ha^{-1} for TZEEIOR 249 X TZEEI 7 under optimal growing conditions. Additive genetic effects for grain yield and most measured traits under each and across environments were generally more important than the nonadditive in the inheritance of the traits. The inbreds were classified into three heterotic groups across the research environments. TZEEIOR 197 X TZdEEI 7, TZEEIOR 251 X TZdEEI 7, and TZEEIOR 197 X TZEEI 79 were identified as high yielding and most stable across environments. These hybrids should be tested extensively in on-farm trials and commercialized in the sub-region. Inbred TZdEEI 7 had highly significant and positive GCA effects for grain yield across the research environments, indicating that it would be invaluable for improving the performance of other lines in hybrid combinations.

In another study, Badu-Apraku et al. (2016) determined the combining ability of 20 early provitamin A maize inbreds under multiple environments, classified the inbreds into heterotic groups using the heterotic grouping based on general combining ability (GCA) of multiple traits (HGCAMT) and the heterotic groups' specific combining ability (SCA) and GCA of grain yield (HSGCA) methods, identified inbred tester(s), and examined the performance of the inbreds in hybrid combinations. One hundred and ninety diallel crosses involving the 20 early provitamin A maize inbreds plus six yellow hybrid checks were evaluated under drought, *Striga*-infested, low-N, and optimal environments in Nigeria, 2016. Results showed significant mean squares for GCA and SCA effects of most traits across environments. However, there was a preponderance of the GCA over the SCA effects for most traits, suggesting that additive gene action was governing the inheritance of most traits in the set of inbred lines. The inbred lines were classified into three heterotic groups each by the HSGCA and HGCAMT methods. Only TZEI 129 was identified as an inbred tester across environments by the two methods. It was concluded that this tester could facilitate the development of superior provitamin A hybrid in SSA. The AMMI biplot identified the provitamin A hybrids TZEIOR 2 × TZEIOR 157 and TZEIOR 4 × TZEIOR 65 and the yellow hybrid check TZEI 124 × TZEI 25 as the most outstanding in terms of yield and stability across environments. It was recommended that the hybrids should be further tested and commercialized to improve food and nutrition security as well as alleviate poverty in the sub-region.

Konate (2017, unpublished) screened selected early-maturing provitamin A inbreds for tolerance/resistance to drought and *Striga* hermonthica and determined the provitamin contents; the combining ability and heterotic groups of the inbreds under *Striga*-infested, drought, optimal, and across environments; as well as the genetic diversity and population structure of the lines using the Diversity Array Technology (DArT) markers. A set of 155 early-maturing provitamin A maize inbred lines were screened under managed drought during the 2014/2015 dry season at Ikenne, and one hundred promising inbred lines were selected and characterized for genetic diversity using SNP markers, while fifty of the inbreds were analyzed for carotenoids contents. The inbreds were also evaluated under drought, *Striga*-infested, and optimal environments at four locations in Nigeria, 2015-2016. Fifty-six percent of the lines had provitamin A concentrations ranging from 5 to 9.60 μg/g. Results revealed lack of significant correlation of grain yield with α-carotene and β-carotene contents indicating that it is possible to select high-yielding inbred lines without affecting the provitamin A level. Grain yield of the inbreds across drought and *Striga*-infested environments ranged from 119 to 1971 with a mean of 893 kg ha^{-1}. Of the hundred early-maturing inbred lines evaluated under drought, 50 had positive base indices with 39 yielding above the mean grain yield. Cluster analysis based on the genetic distance classified the lines into five groups based predominantly on their pedigrees. Results of diallel analysis involving 17 selected inbred lines (136 single-cross hybrids) showed significant differences for all measured traits under drought, *Striga*-infested, optimal, and across stress environments except for anthesis–silking interval (ASI) under *Striga*-infested environments. The GCA and SCA effects were significant for grain yield and other traits under drought, *Striga*-infested, optimal, and across environments except the SCA effects for ASI, EPP under drought and *Striga* environments. Inbreds TZEIOR108, TZEI10, and TZEI17 had significant and positive GCA effects for grain yield across stress and non-stress environments. The inbreds TZEIOR108 and TZEI10 had significant negative GCA effects for *Striga* damage and number of emerged *Striga* plants indicating that the inbreds could be invaluable source of favorable alleles for improving *Striga* resistance/tolerance in tropical breeding population and for development of outstanding *Striga*-resistant hybrids.

There was preponderance of GCA effects over SCA effects for grain yield and most other traits under drought, *Striga*-infested, optimal, and across environments suggesting that additive gene effects were more important in the inheritance of these traits. The heterotic groups' specific and general combining ability (HSGCA) grouping method classified the lines into four main groups. The inbred lines TZEIOR108 and TZEI10 were identified as testers. Under drought, grain yield of hybrids ranged from 259 kg ha^{-1} for TZEIOR11 x TZEIOR12 to 5320 kg ha^{-1} for TZEIOR13 x TZEIOR 60. In contrast, grain yield under *Striga*-infested environments varied from 424 kg ha^{-1} for TZEIOR11 x TZEIOR12 to 3873 kg ha^{-1} for TZEIOR127 x TZEI10. Under optimal environments, the highest yielding hybrid was the commercial hybrid check (TZEI 124 x TZEI 25) with a yield of 6526 kg ha^{-1}.

The GGE biplot analysis identified the hybrids TZEIOR 57 x TZEIOR 108, TZEIOR 13 x TZEIOR 59, TZEIOR 60 x TZEIOR 108, TZEIOR 127 x TZEI 10, TZEIOR 9 x TZEIOR 56, and TZEIOR 58 x TZEIOR 108 as the highest yielding and most stable across environments. The hybrids TZEIOR 60 x TZEIOR 127 and the commercial check TZEI 124 x TZE I25 were high yielding but unstable across environments.

9.11 Conclusion

Early- and extra-early maturing QPM varieties and hybrids, with biotic and abiotic stress tolerance/resistance and acceptable levels of provitamin A, are now available in SSA. They are as high yielding and agronomically acceptable as their normal endosperm counterparts. One important lesson learned in our QPM breeding program is that there is a need for periodic upgrading of the level of streak resistance in released QPM cultivars in order to maintain the recessive QPM trait in open-pollinated cultivars that can be grown by small-scale farmers who save seed from their farms after harvesting each year for planting the following season.

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Chapter 10
Breeding for *Striga* Resistance

10.1 Biology of *Striga*

Striga spp., known as witchweeds, are root parasites of important crops in Africa. The four major parasitic witchweed species that attack maize and other cereal crops are *Striga hermonthica*, *Striga asiatica* (L.) Kuntze, *Striga aspera* (Willd.) Benth., and *Striga forbesii* Benth. Among them, *Striga hermonthica* is the most widely distributed in SSA, and it causes the greatest economic damage. *Striga asiatica* is common in East and Southern Africa (ESA) but is presently restricted only to Togo in West Africa.

Striga seeds, capable of only limited seedling growth before the seed resources are exhausted, germinate in response to certain chemicals in the root exudates of host plants. Germinated seeds develop haustoria which are attached to the roots of host plants through which photosynthates and nutrients are transferred from the host to the *Striga* plant. Germinated seed must find a host and attach itself to its roots for survival. In maize, for example, *Striga* seedlings must attach to the roots within 3–7 days or else they will die. Once attached to maize roots, *Striga* depends completely on the maize plant for water and nutrients for its growth and development for 6–8 weeks when it is still underground. Most of the damage to the host occurs before *Striga* emerges from the soil. A single *S. hermonthica* plant may produce up to 200,000 seeds which can remain viable in the soil for as long as 14 years. Freshly produced seeds require a 3- to 6-month period after ripening for optimum germination. Each seed is approximately 0.38 mm in length and weighs 7.1 μg. *Striga* seeds that have undergone ripening do not germinate even in the presence of a suitable stimulant except moistened for 1–3 weeks prior to the introduction of the stimulant. This process is referred to as "conditioning" or preconditioning. Germination usually increases with the duration of conditioning up to 3 weeks, after which it decreases.

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10.2 Economic Importance and Distribution of *Striga* in Sub-Saharan Africa

Striga is a major constraint to cereal crop production in Africa, with yield losses reaching 100% when infestation occurs early. About two-thirds of the land under cereal production in the African continent is found in agroecological zones where *Striga* is a problem. The parasite threatens the livelihood of more than 300 million people in Africa. The total loss of food crops due to parasitism by *Striga* is valued at approximately $7 billion annually. Drought increases geometrically the losses caused by *Striga*.

Striga is a problem associated with low-input production systems. The *Striga* problem has been aggravated by greater use of mono-cropping in place of rotation and intercropping systems, and increasing human population pressure on available land, leading to the intensification of cropping and reduced fallow periods. Many maize farmers in WCA have abandoned their farmlands because of the difficulty associated with the management of *Striga*-infested fields and the very low productivity of such fields.

10.3 Symptoms of *Striga* Damage on Maize

In maize, *Striga* parasitism is characterized by chlorotic blotches, scorching, or "firing" of leaves particularly around the margins, wilting, stunting, spindly stems, and poorly filled ears (Plates 10.1 and 10.2). Total crop failure can result when infestation is severe.

10.4 Strategies and Methods of *Striga* Control

Eradication of *Striga* from Africa is difficult if not impossible, given that the center of origin of the parasite is in Africa and because it has several alternative hosts, which are not limited to food crops but include grasses. Feasible control options include intercropping; rotation of cereals with crops not susceptible to *S. hermonthica* like cotton, soybean, and cowpea (legumes have the additional advantage of fixing nitrogen and improving the fertility of the soil); herbicide treatments; hand-pulling; use of catch and trap crops; high nitrogen fertilization; and use of tolerant and resistant varieties. In *Striga* research, resistance refers to the ability of host plants to reduce or limit the number of *Striga* attachments, while tolerance refers to the ability of host plants to withstand the effects of the parasites already attached (Kim 1994). Under *Striga* infestation, the resistant genotype supports significantly fewer *Striga* plants and produces a higher yield than a susceptible (converse of resistance) genotype (Doggett 1988; Ejeta et al. 1992; Haussmann et al. 2000; Rodenburg et al. 2006). Contrarily, a *Striga*-tolerant genotype germinates and

Plate 10.1 *Striga*-resistant and *Striga*-susceptible genotypes

Plate 10.2 Effect of *Striga hermonthica* parasitism on maize

supports as many *Striga* plants as the intolerant or, as proposed by DeVries (2000), *sensitive* genotype but produces more grain and stover and shows fewer damage symptoms (Kim 1994). Amusan et al. (2008) reported that *Striga* on the susceptible maize genotype usually penetrates the xylem and shows substantial internal haustorial development as compared to what is observed on the resistant genotype, where the haustorial ingression is often stopped at the endoderm.

Although no single control option can achieve complete control of the parasite, the development of cultivars with tolerance and resistance is considered the most economic, practical, sustainable, effective, and environmentally friendly way to control the parasite (DeVries 2000; Badu-Apraku et al. 2004). Therefore, host plant resistance has been the major control option employed at IITA for about three decades *(*Kim 1991, 1994; Parkinson et al. 1989; Badu-Apraku et al. 2004).

10.5 Genetics of *Striga* Resistance

Genetic resistance to *Striga* has been reported in several cereal crops including rice (*Oryza sativa*; Bennetzen et al. 2000; Gurney et al. 2006), sorghum (*Sorghum bicolor*; Maiti et al. 1984; Hess et al. 1992; Volgler et al. 1996; Haussmann et al. 2004), and maize (Adetimirin et al. 2000a; Gethi and Smith 2004; Menkir 2006; Badu-Apraku et al. 2010). Many studies have been conducted on the genetics of maize resistance to *S. hermonthica* (Kim 1994; Berner et al. 1995; Akanvou et al. 1997; Badu-Apraku et al. 2006b, 2007; Badu-Apraku 2007; Yallou et al. 2009). However, there has been contradictory reports on the gene action controlling *Striga* resistance in maize, as determined by grain yield under *Striga* infestation, number of emerged *Striga* plants on the host, and host damage syndrome rating. One school of thought holds the view that the resistance is quantitatively inherited with additive gene effects being more important than nonadditive effects in regulating the host plant damage syndrome rating and grain yield under infestation (Kim 1994; Berner et al. 1995; Akanvou et al. 1997; Badu-Apraku 2007). This implies that different genes control the number of emerged *Striga* plants and the level of host plant damage (Kim 1994; Berner et al. 1995). In contrast, results of some other studies showed nonadditive gene action as being more important than additive gene action in the control of the inheritance of host plant damage, while additive gene action was more important in the control of the number of emerged *Striga* plants (Kim 1991; Kling et al. 1999; Badu-Apraku and Fakorede 2001; Gethi and Smith 2004; Badu-Apraku et al. 2007; Yallou et al. 2009).

At the initial stages of the *Striga* resistance program at IITA, maize researchers were confronted with several problems, including development of reliable artificial infestation techniques, quantification of *Striga* resistance, and identification of sources of resistance. The researchers gradually and systematically solved the problems, as reviewed in the following sections.

Development of Reliable Artificial *Striga* Infestation and Screening Techniques Screening maize under natural field infestation, which was the practice of national maize breeders before the establishment of IITA, was prone to many escapes and was, therefore, not effective. Researchers at IITA developed and standardized reliable artificial field infestation and screening techniques (Kim 1991; Kim and Winslow 1991; Adetimirin et al. 2000b). In addition, screening for resistance to *Striga* at IITA involves the use of laboratory, screenhouse, and field techniques. The artificial infestation technique involves putting about 5000 germinable *Striga* seeds per hill in holes of about 5 cm depth and 8 cm diameter followed immediately by planting maize into the same holes, thereby eliminating escape plants that is a feature of screening under natural infestation. Before dropping the *Striga* seeds into the holes, they are mixed with fine sand in a ratio of 1:99 *Striga* seed/sand. The sand serves as the carrier material and provides adequate volume for rapid and uniform infestation. The *Striga* seed/sand mixture is applied with a calibrated scoop that delivers the required number of germinable seeds. Four row plots are normally used for the evaluation of genotypes. Two rows of each entry are infested with seeds of *S. hermonthica*, while the other two rows are *Striga*-free. The two *Striga*-infested rows of each entry are arranged in such a way that they are directly opposite the two *Striga*-free rows of the same entry, separated by a 1.5 m alley. The plots are arranged in such a way that the *Striga*-infested rows are back to back in strips across the field and alternate with *Striga*-free strips so that the first range, for example, is *Striga*-free, the second and third are infested, while the fourth and fifth are *Striga*-free. This arrangement reduces the movement of *Striga* seeds into the non-infested plots. Three maize seeds are planted per hill in each trial. The *Striga* seeds used are collected from fields of sorghum [*Sorghum bicolor* (L.) Moench] at the end of the previous growing season. About 2 weeks before *Striga* infestation and planting of maize, ethylene gas is injected into the soil to stimulate suicidal germination of existing *Striga* seeds in the soil at the sites. Apart from the *Striga* seed infestation, all management practices for both *Striga*-infested and *Striga*-free plots are the same. Fertilizer application to all plots is delayed until about 30 days after planting when 30 kg ha^{-1} N, 26 kg ha^{-1} P, and 50 kg ha^{-1} K are applied. Reduced rate and delay in application of fertilizer are adopted in order to subject the maize plants to stress, a condition that favors the production of strigolactones, which stimulate germination of *Striga* seed and enhance good germination of *Striga* seeds and attachment of *Striga* plants to the roots of host plants in *Striga*-infested plots (Kim 1991). Weeds other than *Striga* are controlled manually.

Quantification of *Striga* Resistance *Striga* plants thrive on the host, with much damage occurring underground before the parasitic plants appear on top of the soil around the maize plant. Initially, screening was done on the basis of number of emerged *Striga* around individual maize plants within a genotype, and this was considered as resistance; that is, the fewer the number of emerged *Striga* plants, the higher the resistance of the maize genotype. Experience soon taught the researchers, however, that maize genotypes could carry as many *Striga* plants as a known susceptible genotype but with little or no reduction in grain yield relative to performance under *Striga*-free conditions. This was termed tolerance by the scientists. Therefore, resistance and tolerance have been identified as the two types of defense mechanisms against *Striga* infestation by the maize plant (Kim 1994). Indeed, maize genotypes exhibiting low *Striga* damage syndrome ratings and few emerged *Striga* plants, and also, genotypes combining low emerged *Striga* plants with severe *Striga* damage occur frequently in the IITA program. Host plant damage and the number of emerged *Striga* plants are negatively correlated with yield; that is, the lower their values, the higher the grain yield under *Striga* infestation. Studies by Badu-Apraku et al. (2007) showed a large positive additive genetic correlation between grain yield and EPP and moderately large negative genetic correlations of grain yield with flowering traits. Similar results were reported by other researchers (Kim and Adetimirin 1995; Akanvou et al. 1997; Menkir and Kling 2007). However, the genotypic correlation between host damage rating and emerged *Striga* plants is low, an indication that the two traits are under different genetic control, as was speculated by earlier researchers (Kim 1994; Akanvou et al. 1997). The two traits, along with high grain yield and good performance of several other agronomic traits, have been subjected to extensive studies under *Striga*-infested and *Striga*-non-infested conditions, in an effort to identify the most appropriate traits to use in breeding for *Striga* tolerance/resistance (Kim 1991, 1994; Badu-Apraku et al. 1999). While the traits are controlled predominantly by additive gene action, nonadditive gene action could also be important (Kim 1994; Kling et al. 2000; Badu-Apraku and Fakorede 2001). Based on the results of the extensive studies conducted by IITA scientists, host plant damage rating, emerged *Striga* plants, and high grain yield under *Striga* infestation have been considered as the most appropriate traits to use as selection criteria in breeding maize for *Striga* tolerance/resistance (Kim 1991; Badu-Apraku et al. 1999). The three traits are relatively easy to determine: emerged *Striga* plants are determined by counting, host plant damage is determined on a rating scale of 1–9 (Table 10.1), while grain yield is routinely recorded at the

Table 10.1 A scoring scale used at IITA for rating *Striga* host damage on maize

Rating	Description
1.	No chlorosis, no blotching, and no leaf scorching (firing) and normal plant growth
2.	Mild leaf blotching and scorching on about 10% of leaves with purplish-brown necrotic spots, almost normal plant growth. No stunting and no reduction in ear size
3.	Mild definite leaf blotching and scorching on about 20% of leaves with some purplish-brown necrotic spots. Mild stunting and reduction in ear size
4.	Some definite leaf scorching on about 30% of leaves with some purplish-brown necrotic spots; some stunting and ear and tassel size reduction
5.	Definite leaf scorching on about 40% of leaves with gray-brown necrotic spots. Some stunting and ear and tassel size reduction
6.	Definite leaf scorching on about 50% of leaves with mostly gray necrotic spots. Definite stunting and stem diameter, ear size, and tassel size reduction
7.	Definite leaf scorching on about 60% of leaves with severe gray necrotic spots and leaf wilting and rolling. Definite stunting and stem diameter, ear size, and tassel size reduction, with severe stalk lodging and husk opening at late-growing stage
8.	Definite leaf scorching on about 70% of leaves with definite gray necrotic spots. Conspicuous stunting, leaf wilting, rolling, and stem diameter, ear size, and tassel size reduction
9.	Complete leaf scorching of all leaves, causing premature death of host plant and no ear formation

end of the season in most field experiments. *Striga* emergence count and the host damage rating are done 8 and 10 weeks after planting. It must be pointed out that rating of host plant damage could be subjective, particularly when handled by early career maize breeders, but this improves with experience. In addition, the data are usually subjected to transformation before being subjected to statistical analysis.

The heritabilities of host plant damage rating and yield performance under *S. hermonthica* infestation are moderate, but heritabilities for *Striga* emergence are low (Kling et al. 2000; Badu-Apraku 2007). For example, Akanvou et al. (1997) found, in a tropical maize population, narrow-sense heritability estimates of 0.33 for host plant damage rating, 0.14 for number of emerged *Striga* plants, and 0.32 for grain yield under *Striga* infestation. After three cycles of S_1 recurrent selection in TZE-Y Pop STR C_0, Badu-Apraku et al. (2007) found that the estimates for dominance variance were larger than additive genetic variance for grain yield, plant height, ear height, number of ears at harvest, and *Striga* damage rating at 8 weeks after planting (WAP). Heritability estimates were generally low for most traits (<0.40). However, moderate-to-large additive genetic variances and wide ranges in mean values were observed for most traits, indicating the availability of adequate genetic variability in the population to facilitate further significant progress from selection.

Identification of Sources of Resistance The IITA breeding program for early and extra-early germplasm has placed emphasis on the formation of high-yielding drought and *Striga*-resistant/*Striga*-tolerant populations using drought-tolerant and *Striga*-resistant germplasm from diverse sources identified through several years of extensive testing in WCA. The source germplasm included (i) local and exotic germplasm identified from trials conducted for several years in many locations in WCA, (ii) resistant/tolerant inbred lines imported from temperate countries, (iii) African landrace pools found to possess resistance to the parasite, and (iv) backcross progenies from crosses involving *Zea diploperennis*. Sources of moderate resistance were also found in inbred lines 1368 STR and 9450 STR from IITA. The two inbred lines belong to the intermediate-late-maturity group. Therefore, crosses in which they were involved were subjected to backcross breeding to maintain the early and extra-early characteristics, along with the successful introgression of *Striga* resistance/tolerance into the maize populations and varieties.

10.6 Breeding Maize for *Striga* Resistance at IITA

The International Institute of Tropical Agriculture initiated maize breeding for *Striga* resistance in 1980 with breeding nurseries established in the northern Guinea savanna in Nigeria for the first time. The strategy is simultaneous selection for the three traits, low number of emerged *Striga* plants (resistance), low score for *Striga* damage rating (tolerance), and high grain yield, a strategy also adopted for *Striga* resistance breeding in maize by DeVries (2000) and sorghum by Haussmann et al. (2001).

The maize production and productivity constraints in much of the savanna agroecology were complicated. In addition to the *Striga* problem, varieties that would fit the relatively short rainy season were in urgent demand. In 1980, IITA started breeding specific varieties targeted to this agroecology. The genetic information generated from the research conducted by IITA indicated that *Striga* resistance was quantitatively inherited and should be amenable to recurrent selection. A breeding program for *Striga* resistance was, therefore, initiated in Côte d'Ivoire in 1994 to combat the threat posed by *S. hermonthica* to maize in the savannas. The program had the objective of developing maize populations, varieties and inbred lines with combined earliness, resistance/tolerance to *S. hermonthica*, and tolerance to drought and low soil nitrogen. Four populations, TZE-W Pop DT STR (early-maturing, white endosperm), TZE-Y Pop DT STR (early-maturing, yellow endosperm), TZEE-W Pop STR (extra-early maturing, white endosperm), and TZEE-Y Pop STR (extra-early maturing, yellow endosperm), resulting from backcrossing, inbreeding, and hybridization (introgression) of inbred lines 1368 STR and 9450 STR as sources of *Striga* resistance in the IITA-WECAMAN breeding program (Badu-Apraku et al. 1999), were subjected to the recurrent selection program, which started with the early populations in 1996 followed by the extra-early populations in 1997. In addition, four early populations, two with white endosperm (TZE-W Pop DT STR and DTE-W STR Syn Pop) and the other two with yellow endosperm (TZE-Y Pop DT STR and DTE-Y STR Syn Pop), were subjected to the recurrent selection program.

10.7 Screening Methodologies for *Striga* Resistance and Strategies for Improving Effectiveness of Selection

Special emphasis was placed on the following factors, which are very important in determining success in *Striga* resistance breeding: (i) reliable infestation technique for screening to differentiate resistant/tolerant from susceptible genotypes, (ii) availability of appropriate germplasm and good sources of *Striga* resistance, (iii) use of appropriate breeding methods for incorporating resistance genes into adapted germplasm, and (iv) extensive multilocation evaluation to identify genotypes with stable performance. Infestation is greatly influenced by environmental factors and can be erratic. It was, therefore, necessary to ensure that developed varieties did not only give good performance under infestation but also produced high yield in the absence of *Striga*. Consequently, the standard practice has been to carry out evaluation in infested and adjacent non-infested plots.

Screening maize for resistance to *Striga* was most effective under certain practices, including (i) moderate level of N fertilizer application, usually 30–50 kg/ha in the savanna where N fertilizer recommendation is 120 kg N/ha; (ii) rotation with crops such as cotton and soybean which can help induce suicidal germination of *Striga* seeds in the soil and cleanup of breeding nurseries, particularly non-infested plots; (iii) use of lattice design to reduce the error variance, particularly when a large number of genotypes are being evaluated; (iv) increasing the number of replications and locations; (v) transformation of *Striga* count data for statistical analysis; (vi) screening and selection or selfing on individual plant basis; and (vii) combination of screenhouse evaluation with field testing.

10.8 *Striga* Screening Methodology

The principal screening sites for *Striga* resistance for the populations were Ferkessédougou and Sinématiali (hereafter called Ferke and Siné, respectively) in Côte d'Ivoire and Mokwa and Abuja, in Nigeria. The screening method developed by IITA Maize Program (Kim 1991; Kim and Winslow 1991) was adopted. Three maize seeds were placed in the same hole with the *Striga* seeds. Screening of segregating materials derived from the two source populations was done using 5 m rows with susceptible checks planted at regular intervals of ten rows. Both the segregating materials and the susceptible checks were infested. The infested susceptible checks offered an opportunity to monitor the level of *Striga* infestation and to ensure effective selection for STR.

Striga infestations were carried out in moist soils thus making preconditioning unnecessary. Where the soil was dry at planting, sprinkler irrigation was applied immediately after planting. The maize plants were thinned to two plants per stand about 2 weeks after emergence to obtain a final population density of about 66,000 plants per hectare. Fertilizer application to the artificially *Striga*-infested plots was delayed until about 30 days after planting when 30–50 kg/N ha^{-1} was applied as 15-15-15 NPK. The actual quantity of NPK applied was based on the fertility of the soil as indicated by soil tests. The amount of NPK applied was monitored to minimize escapes due to high levels of fertilizer. Data collected on segregating progenies included grain yield, ear number, ear rot, husk cover, plant and ear heights, and percent root and stalk lodging. In addition, host plant damage syndrome rating (Kim 1991) and the number of emerged *Striga* plants were made at 8 and 10 weeks after planting (56 and 70 days after planting) in the *Striga*-infested rows. *Striga*-tolerant plants normally retain the green leaf and exhibit restricted mild purplish chlorosis, while ear and stalk developments are little affected by *Striga*. The highly susceptible plants on the other hand show grayish leaf color and leaf scorching after initial leaf wilting. These symptoms are usually accompanied by poor development of stalk and ear, along with root and/or stem lodging (Kim 1991). Selection was based on grain yield, *Striga* emergence counts, *Striga* damage syndrome, plant and ear heights, and ears per plant, all of which were measured under *Striga* infestation.

By 2006, four cycles of S_1 recurrent selection for improvement in *Striga* resistance and grain yield had been completed in the four populations (TZE-W Pop DT STR and TZE-Y Pop DT STR, TZEE-W Pop STR and TZEE-Y Pop STR). However, the levels of *Striga* resistance were not as high as desirable, and there appeared to still be room for improvement, especially in the extra-early maturing populations. Therefore, the recurrent selection for improved *Striga* resistance continued in the extra-early populations. During this same period, several drought- and *Striga*-tolerant early-maturing inbred lines developed in our program were used as sources of tolerance genes for introgression into the early populations. Details of the recurrent selection program are presented later in this chapter.

10.9 Critical Data to Collect for *Striga* Resistance Breeding

Data that are critical for resistance and tolerance screening include number of *Striga* plants per plant or per plot; host damage score or *Striga* damage syndrome rating usually scored on a scale of 1–9 (Table 10.1), both at 8 and 10 weeks after planting; plant height; number of ears per plot expressed as number of plants per plant; stalk and root lodging scored on a scale of 1–9; ear aspect on a scale of 1–9; and grain yield.

Materials showing tolerance and resistance to *Striga* under artificial *Striga* infestation are expected to exhibit reduced host plant damage symptoms (equal to or less than 5), reduced number of emerged *Striga* plants which is indicative of reduced *Striga* germination, attachment or development of the parasite on the host, and high number of ears and grain yield. The following traits are also considered under non-infested conditions: grain yield, husk cover, resistance to maize streak virus and ear rot, grain texture, and resistance to lodging.

10.10 S_1 Recurrent Selection Program for *Striga* Resistance

Recurrent selection is a cyclical scheme designed to increase the frequency of favorable alleles in a population. The procedure has been used effectively for the improvement of quantitatively inherited traits in maize (Sprague and Eberhart 1977; Hallauer and Miranda 1988; Kling et al. 2000; Menkir and Kling 2007; Badu-Apraku et al. 2006a, 2008; Badu-Apraku 2010), including biotic and abiotic stresses (Monneveux et al. 2006; Chapman and Edmeades 1999; Bolaños and Edmeades 1993; Badu-Apraku et al. 1997). Although *Striga* resistance or tolerance has been shown to be multigenic (Ejeta et al. 1992; Kim 1994; Lane et al. 1997), only a few studies have been conducted on the effectiveness of recurrent selection in improving the level of resistance in maize (Menkir and Kling 2007; Badu-Apraku et al. 2006a, 2008). Hypothetically, the adoption of recurrent selection methods that capitalize on additive gene action, under an effective and reliable artificial method of *Striga* infestation for the screening of progenies, should facilitate the accumulation of *Striga* resistance genes to develop germplasm with multigenic resistance that could be durable over time and effective for the control of the parasitic weed (Berner et al. 1995; Menkir and Kling 2007; Badu-Apraku et al. 2012).

10.11 Selection Procedure

Recurrent selection for *Striga* resistance was initiated in TZE-W Pop DT STR C_0 and TZE-Y Pop DT STR C_0 populations in 1996, using S_1 lines as the selection unit. That year, 196 S_1 lines were evaluated under artificial *Striga* infestation at Ferke, Siné (high-yield environment), and Kamboinse, a drought stress environment. A base index similar to that of IITA (MIP 1996) was used to select the best 25–30% of the families across locations, and their remnant S_1 seeds were intermated in 1998 to complete the first cycle (C_1). The top 7–10% of the S_1 families were also selected from each population and intermated to form the cultivars EV DT-W 98 and EV DT-Y 98, respectively. Using the procedure, each population has been taken through three additional cycles of S_1 recurrent selection, involving screening under artificial infestation with *S. hermonthica* and under non-infested conditions at Ferke or Abuja and Mokwa. The number of progenies screened in each cycle ranged from 196 to 280, and the top 25 to 30% of each population were recombined to reconstitute the population for the next cycle of improvement, while the top 10% of the S_1 families of each cycle were intermated to form *Striga*-tolerant experimental varieties (EV) for each population. The cultivars derived from C_2 and C_3 were EV DT-W 2000 STR, EV DT-Y 2000 STR, TZE-W Pop × 1368 STR, EV DT-W 99 STR, EV DT-W 98 C2, and EV DT-Y 98 C_2.

Similarly, S_1 recurrent selection was initiated in the TZEE-W Pop STR C_0 and TZEE-Y Pop STR C_0 populations during the dry season of 1997. One hundred and sixty-seven S_1 lines extracted from each population (plus two checks) were tested under *S. hermonthica*-infested and *S. hermonthica*-non-infested conditions at Sinématiali and Ferke, Côte d'Ivoire, respectively. A 13 × 13 simple lattice design with two replications was utilized for the evaluation of lines from each population. The first cycle of improvement was completed in 1998 by recombining remnant seed of the top 25–30 S_1's selected based on the performance across the two test environments, using the base index mentioned earlier. The top 7–10 best S_1 progenies from each population were recombined to form the cultivars EV 98 TZEE-W and EV 98 TZEE-Y from the TZEE-W Pop STR C_0 and TZEE-Y Pop STR C_0, respectively. Each population was advanced to cycles 2 and 3 in 1999 and 2001, respectively. The S_1 progenies from each cycle of improvement were evaluated under artificial infestation with *S. hermonthica* at Ferke and under *Striga*-free conditions at Sinématiali, as described earlier. The number of S_1 lines screened in each cycle ranged from 196 to 256, and 25 to 30% selected S_1s were intercrossed to form the population for the next cycle of selection. Two EVs (2000Syn EE-W and 99 TZEE-Y STR C_1) were formed by recombining the best ten lines of TZEE-W Pop STR C_2 and TZEE-Y Pop STR C_2, respectively. For the C_3, 355 S1 progenies derived from TZEE-W Pop STR C_3 (plus 5 checks) and 249 S_1 lines from TZEE-Y Pop STR C_3 (plus 7 checks) were evaluated under artificial infestation with *S. hermonthica* at Abuja and Mokwa, Nigeria, in 2003. Based on the across-location data, 30 S_1 lines were selected and intermated to form cycle 4 of each source population. The best ten S_1 progenies were recombined separately to form 2004 TZEE-W STR C_4

and 2004 TZEE-Y STR C_4. Each population was taken through another cycle of S_1 family selection under artificial *Striga* infestation in 2008, and the EVs 2008 TZEE-W STR C_5 and 2008 TZEE-Y STR C_5 were extracted from the white and yellow populations, respectively.

These populations and several of the derived varieties have shown superior performance under both *Striga*-infested and *Striga*-non-infested conditions and have proved to be invaluable sources of *Striga*-resistant synthetics and inbred lines. Several *Striga*-resistant and/or drought-tolerant varieties and inbred lines from the two source populations have been made available to the national maize programs and farmers of WCA (Badu-Apraku et al. 2006a, b; Badu-Apraku and Lum 2007). By 2007, TZE-W Pop DT STR and TZE-Y Pop DT STR and TZEE-W Pop STR and TZEE-Y Pop STR had each been taken through four cycles of S_1 recurrent selection for improved *Striga* resistance. The levels of drought tolerance in the two early populations were not as high as desirable, while the *Striga* resistance levels and drought tolerance in the extra-early populations were also low. Through the funding support of the DTMA project, a program was initiated in 2007 to increase the frequency of drought tolerance alleles in the early populations using S_1 family recurrent selection while continuing the recurrent selection for improved *Striga* resistance in the extra-early populations. At the same time, several drought- and *Striga*-tolerant early-maturing inbred lines developed in our program were used as sources of tolerance genes for introgression into the early populations. Further improvement of the early populations under controlled drought stress using recurrent selection has resulted in new generations of productive varieties that combine enhanced levels of drought tolerance with good levels of resistance to *Striga* and tolerance to low N.

Two new populations, DTE-W Syn Pop DT C_3 STR (white) and DTE-Y Syn Pop DT C_3 STR (yellow), were developed in 2008 through recombination of selected testcrosses involving drought- and *Striga*-resistant white inbred lines on the one hand and yellow inbred lines on the other hand. Following a cycle of recombination, each of the two new populations was taken through three cycles of S_1 recurrent selection from 2008 to 2013 for improvement in drought tolerance under managed drought stress and two cycles for *Striga* resistance under artificial *Striga* infestation. Through this program, 2009 DTE-W STR, 2009 DTE-Y STR, 2010 DTE STR-Y Syn, 2010 DTE STR-W Syn, 2012 DTE STR-W Syn, and 2012 DTE STR-Y Syn, with enhanced tolerance to both drought and *Striga* resistance, have been developed. Furthermore, the identification and introgression of drought tolerance genes into the extra-early white and yellow populations followed by recurrent selection in each population to increase the frequency of the favorable alleles have resulted in the development of populations that are tolerant of drought at the flowering and grain-filling periods. Presently, the source populations and the stages of the S_1 recurrent selection programs are as follows: early populations, TZE-W Pop DT C_5 STR C_5 (white), DTE-W Syn Pop DT C_3 STR (white), TZE-Y Pop DT C_5 STR C_5 (yellow), and DTE-Y Syn Pop DT C_3 STR (yellow), and two extra-early populations with combined tolerance/resistance to *Striga* and drought, TZEE-W Pop DT C_2 STR C_5 (white) and TZEE-Y Pop DT C_2 STR C_5 (yellow). The QPM versions of each of these normal endosperm source populations (TZE-W Pop DT STR QPM C_0, TZE-Y Pop DT STR QPM C_0, TZEE-W Pop STR QPM C_0, and TZEE-Y Pop STR QPM C_0) have also been developed and some selected varieties released and widely adopted by farmers in Ghana, Benin, Mali, and Nigeria.

10.12 Evaluation of Progress from Selection

Recurrent selection requires a lot of input, including time to complete each cycle of selection, human labor (skill), and facilities. Therefore, breeders evaluate the progress from the recurrent scheme after two or three cycles of selection to determine whether or not to continue with the program. If progress from selection is not adequate, the program may be terminated forthwith, or some other germplasm could be introgressed into the base population to broaden the genetic variability. Progress from selection in our program was evaluated in two sets of field trials: (i) the cycles of selection per se and (ii) the derived cultivars from the cycles. In each case, the original population and improved cycles of S_1 selection were included in the evaluation for the two early and two extra-early populations subjected to selection.

10.12.1 Cycles of Selection

The study involving the early group involved 13 entries: the C_0, C_2, C_3, and C_4 from TZE-W Pop DT STR; C_0, C_3, and C_4 from TZE-Y Pop DT STR; two derived *Striga*-resistant cultivars of the early white population (2004 TZE-W Pop DT STR C_4 and TZE-W Pop × 1368 S6 F_2); two varieties of the yellow population (EV DT-Y 2000 STR C_1 and 2004 TZE-Y Pop DT STR C_4); an elite *Striga*-resistant cultivar (99 Syn WEC) not from the recurrent selection program; and a *Striga*-susceptible check, TZE Comp4. The C_1 from TZE-W Pop DT STR and the C_1 and C_2 from TZE-Y Pop DT STR were excluded from the trials because they were lost when the cold room of IITA at Bouaké (Côte d'Ivoire) was looted during the civil war in 2002. The trials were established at Mokwa and Abuja during the growing seasons of 2005 and 2006.

A total of 17 entries were used in the study involving the extra-early group: the original populations (C_0) along with cycles 2, 3, and 4 of TZEE-W Pop STR and cycles 3 and 4 of TZEE-Y Pop STR, two derived varieties from the cycles of selection of the white source population (2000 Syn EE-W, 2004 TZEE-W Pop STR C_4), and two from the yellow (99 TZEE-Y STR C_0, 2004 TZEE-Y Pop STR C_4); three elite *Striga*-resistant cultivars derived from other selection programs (Siné TZEE-W STR, Ferke TZEE-W STR, 98 TZEE-W STR); and a *Striga*-susceptible check, TZEE-W SR BC_5. The 17 entries were planted under *Striga* infestation at Mokwa and Abuja and *Striga*-free conditions at Mokwa, Abuja, Ikenne, Zaria, and Bagauda, 2005–2007.

10.12.2 Analysis of Variance

In the *Striga*-infested environments, the combined ANOVA for the early populations showed significant genotype mean squares for grain yield, EPP, and the four *Striga* resistance traits. Location and year effects were also significant for grain yield and most other traits, but only 6 of the 40 interactions were significant. Under *Striga*-free conditions, genotype, year, and location mean squares were significant for 15 of the 18 cases, and 13 of the 24 interaction mean squares were also significant. For the extra-early populations, genotype, location, and year significantly influenced grain yield, days to silk, ASI, and EPP under both *Striga*-infested and *Striga*-free environments. Genotype mean squares were also significant for stalk lodging as well as *Striga* rating, but not *Striga* count at 8 and 10 WAP. Apart from year × location mean squares that were significant for seven of the ten traits, interaction effects were not significant in *Striga*-infested environments, but genotype × location and year × location were significant for four and five of the six traits.

10.12.3 Response to Selection

The four populations had significant responses to S_1 recurrent selection, although at strikingly different rates (Table 10.2). Under *Striga* infestation, the response was 70.6 kg ha^{-1} (6.3%) cycle^{-1} for TZE-Y Pop DT STR and 352.5 kg ha^{-1} (58.0%) cycle^{-1} for TZE-W Pop DT STR. Corresponding values for the two populations under *Striga*-free environments were similar: 194 kg ha^{-1} (6.6%) cycle^{-1} and 186.5 kg ha^{-1} (6.0%) cycle^{-1}, respectively.

For the extra-early populations, selection improved grain yield by about 90% cycle^{-1} in the yellow population when evaluated in *Striga*-infested environments and 18.41% cycle^{-1} when evaluated in *Striga*-free environments. For the white population, corresponding gains were 12.7% cycle^{-1} under *Striga* and 12.91% cycle^{-1} in *Striga*-free environments (Table 10.2).

Table 10.2 Response of grain yield to four cycles of S_1 recurrent selection in two early and two extra-early maize populations evaluated in *Striga*-infested and *Striga*-free environments in Nigeria, 2005 and 2006

	Striga-infested				*Striga*-free			
	Gain cycle^{-1}†				Gain cycle^{-1}			
Population	kg ha^{-1}	%	a	r^2	kg ha^{-1}	%	a	r^2
TZE-W Pop DT STR	352.5	58.0	608.0	0.559	186.5	6.0	3109.0	0.300
TZE-Y Pop DT STR	70.6	6.3	1115.0	0.179	194.0	6.6	2963.0	0.949
TZEE-W Pop DT STR	117.4	12.7	927.0	0.493	302.2	12.9	2336.0	0.977
TZEE-Y Pop DT STR	290.0	90.0	326.6	0.997	350.5	18.4	1901.0	0.998

†Gain cycle^{-1}, b-value; a intercept; and r^2 coefficient of determination from the linear regression

Table 10.3 Response of *Striga* traits to four cycles of S_1 recurrent selection in two early and two extra-early maize populations evaluated in *Striga*-infested environments in Nigeria, 2005 and 2006

	TZE-W Pop DT STR				TZE-Y Pop DT STR			
	Gain cycle^{-1}†				Gain cycle^{-1}			
Striga trait	No. of plant^{-1}	%	r^2	Prob.	No. of plant^{-1}	%	r^2	Prob.
Striga rating, 8 WAP	−0.26	−4.7	79.4	**	−0.09	−2.0	52.2	ns
Striga rating, 10 WAP	−0.22	−3.9	41.2	**	−0.25	−4.8	74.3	**
Striga count, 8 WAP	−7.22	−4.9	23.5	*	−4.75	−3.7	7.3	*
Striga count, 10 WAP	−1.93	−1.2	9.7	ns	−3.04	−1.9	10.9	ns
	TZEE-W Pop DT STR				TZEE-Y Pop DT STR			
Striga rating, 8 WAP	−0.05	−0.8	65.0	ns	−0.11	−1.8	35.0	*
Striga rating, 10 WAP	−0.09	−1.6	26.0	ns	−0.14	−2.2	48.0	ns
Striga count, 8 WAP	−11.45	−11.1	0.4	*	−0.19	−0.1	0.01	**
Striga count, 10 WAP	−7.82	−0.4	5.6	ns	−4.12	−2.4	0.05	**

WAP weeks after planting
*,**Significant regression models at 0.05 and 0.01 level of probability, respectively
†Gain cycle^{-1}, *b*-value; r^2, coefficient of determination from the linear regression

One particularly striking observation was that yield gain cycle^{-1} of selection was higher for original populations with low grain yield than those with relatively high grain yield. In other words, the higher the yield potential of the original population, the lower the yield gains attributable to selection. For example, on average, grain yield of the original populations under *Striga* infestation was about 744 kg ha^{-1} compared with 2577 kg ha^{-1} in the *Striga*-free environments. Corresponding average gain from selection was 36.75% and 10.96%, respectively.

Striga damage rating at 10 WAP and emerged *Striga* plants at 8 WAP decreased significantly in the improved cycles of selection in the two early populations (Table 10.3). In TZEE-Y Pop STR, *Striga* counts at 8 and 10 WAP, along with *Striga* rating at 8 but not 10 WAP, were also reduced by recurrent selection (Table 10.3). Only the number of emerged *Striga* plants at 8 WAP showed significant reduction in the TZEE-W Pop STR. Recurrent selection also induced changes in some agronomic traits (Table 10.4). Apart from ears per plant that showed 4–7% increase per selection cycle, changes in all other agronomic traits were not significant under *Striga* infestation in the early populations.

In the *Striga*-free environments, however, stalk lodging of the C_0 was higher than those of the improved cycles in both populations. Similarly, in TZE-Y Pop DT STR, ASI decreased in the improved cycles relative to the C_0. Changes in other traits did not show any consistent trends in this population.

Table 10.4 Response of some agronomic traits to four cycles of S_1 recurrent selection in two early and two extra-early maize populations evaluated in *Striga*-infested and *Striga*-free environments in Nigeria, 2005 and 2006

	Striga-infested				*Striga*-free			
	Gain cycle^{-1}†				Gain cycle^{-1}			
Population	ha^{-1}	%	r^2	Prob.	ha^{-1}	%	r^2	Prob.
TZE-W Pop DT STR								
Days to silk	0.2	0.35	35.7	ns	0.5	0.92	29.67	*
ASI, days	0.65	1.25	53.5	ns	0.04	1.49	1.07	*
EPP, number	0.02	4.63	29.4	*	0.01	0.66	89.54	ns
Plant height, cm	1.77	1.40	96.5	ns	−1.60	−1.02	63.26	*
Stalk lodging, %	0.11	2.29	7.7	ns	−0.33	13.86	96.69	*
TZE-Y Pop DT STR								
Days to silk	0.63	1.13	64.3	ns	0.08	0.13	3.94	ns
ASI, days	0.36	0.69	66.1	ns	−0.11	−3.02	12.29	*
EPP, number	0.04	6.60	86.8	*	0.01	1.56	20.49	*
Plant height, cm	0.21	0.16	0.7	ns	1.10	0.67	12.09	ns
Stalk lodging, %	−0.30	−5.48	55.4	ns	−0.44	−16.01	69.89	**
TZEE-W Pop DT STR								
Days to silk	0.514	0.91	77.0	ns	1.02	1.94	0.77	ns
ASI, days	−0.46	−7.62	91.0	ns	−0.26	−9.08	0.77	ns
EPP, number	0.01	1.52	2.98	**	0.02	1.98	58.16	**
Plant height, cm	−1.51	−1.11	23.0	ns	2.26	1.45	0.43	**
Stalk lodging, %	−0.62	−9.66	98.0	ns	0.28	10.14	0.46	ns
TZEE-Y Pop DT STR								
Days to silk	0.35	0.63	52.0	ns	0.81	1.55	94.0	**
ASI, days	−0.27	−9.09	94.0	ns	−0.27	−9.09	94.0	*
EPP, number	0.03	7.57	55.0	ns	4.77	3.23	96.0	ns
Plant height, cm	−1.00	−0.81	25.0	ns	0.24	6.45	74.0	**
Stalk lodging, %	0.52	11.01	81.0	ns	0.01	1.65	84.0	ns

ns not significant, *ASI* anthesis–silking interval, *EPP* number of ears per plant
*,**Significant regression models at 0.05 and 0.01 level of probability, respectively
†Gain cycle^{-1}, *b*-value; r^2, coefficient of determination from the linear regression

Under *Striga* infestation, selection failed to induce significant changes in the agronomic traits of the two extra-early populations except EPP, unlike in *Striga*-free environments where significant changes occurred for days to silk, ASI and plant height in the yellow population as well as EPP and plant height in the white population (Table 10.4).

10.13 Performance of EVs from the Selection Programs

A recurrent selection program will not be worth all the effort and expenses unless improved cultivars can be obtained from the different cycles of selection. Therefore, in addition to the periodic evaluation to determine progress from selection and the efficiency of the recurrent selection method in increasing the frequency of the favorable alleles, the performance of the derived cultivars from the two early and two extra-early populations was assessed in several field trials. For the early populations evaluated under *Striga* infestation, three varieties, ACR 94 TZE Comp5-Y (2158 kg ha^{-1}), ACR 94 TZE Comp5-W (2124 kg ha^{-1}), and Syn WEC STR Co (1954 kg ha^{-1}), which were derived from other selection programs, along with the C3 of the yellow population (TZE-Y Pop DT STR C_3, 1928 kg ha^{-1}) were the highest-yielding group (Table 10.5). The second group comprised six products of the selection program, with grain yield ranging from 1689 to 1871 kg ha^{-1}, along with a few other varieties, including the reference entry, Kamboinse 88 Pool 16 DT (RE). The third group, with grain yield of 1498–1541 kg ha^{-1}, contained mostly *Striga*-susceptible cultivars and the C_0 of a selection program.

Under *Striga*-free conditions, the performance of several cultivars from the selection program was equal to or better than ACR 94 TZE Comp5-Y and ACR 94 TZE Comp5-W, two outstanding varieties in WCA. The high-yielding cultivars under *Striga* infestation were also generally high yielding under *Striga*-free conditions. However, only two entries, EV DT-Y 2000 STR C_1 and TZE-W Pop DT STR C_3 from the selection program, along with ACR 94 TZE Comp5-W, had stable grain yield in *Striga*-infested and *Striga*-non-infested environments. The cultivars were not significantly different for *Striga* count and rating at 10 WAP, plant height, days to silk, and ear productivity under both *Striga*-infested and *Striga*-free conditions.

For the extra-early genotypes evaluated under *Striga* infestation, grain yield ranged from 772 kg ha^{-1} for 99 TZEE-Y STR C_0 to 1588 kg ha^{-1} for 99 Syn EE-W (Table 10.6). The susceptible check, TZEE-W SR BC_5, suffered about 66% yield loss under *Striga* infestation compared with yield when *Striga*-free (783 vs 2266 kg ha^{-1}). It also sustained the worst *Striga* damage and was among the genotypes that supported the highest number of emerged *Striga* plants (Table 10.6), indicating the severe level of infestation in the evaluation trials. Here also, the highest-yielding cultivars under *Striga* infestation were highest yielding under *Striga*-free conditions. At both 8 and 10 WAP, the cultivars were significantly different for *Striga* rating but not for emerged *Striga* plants.

The mean grain yields of the base populations, TZEE-W Pop STR C_0 and TZEE-Y Pop STR C_0, were not significantly different from that of the susceptible check, TZEE-W SR BC_5, under *Striga* infestation. The most promising white-grained genotypes in terms of grain yield, host damage, and level of *Striga* emergence were 99 Syn EE-W and 98 TZEE-W STR from other selection programs and TZEE-W Pop STR C_4, TZEE-W Pop STR C_3, and 2004 TZEE-W Pop STR from the recurrent selection program. The experimental cultivar 99 Syn EE-W outyielded the susceptible check by 51% and TZEE-W Pop STR C_4 by 47%. However, there were no significant differences in grain yield among these top-ranking white endosperm genotypes. The highest-yielding yellow-grained genotype was 2004 TZEE-Y Pop STR C_4 (3366 ha^{-1}) and was not significantly different in terms of grain-yield performance from the derived cultivars, 99 TZEE-Y STR (derived from TZEE-Y Pop STR C_2) and 2004 TZEE-Y STR C_4 (derived from TZEE-Y Pop STR C_4). TZEE-Y Pop STR C_4 was also comparable to the top-ranking white endosperm cultivars in terms of grain yield, *Striga* damage, and number of emerged *Striga*

Table 10.5 Grain yield and other agronomic characters of cultivars derived from S_1 recurrent selection in TZE-Y Pop DT STR and TZE-W Pop DT STR maize populations evaluated under *Striga*-free (non-inf.) and *Striga*-infested (inf.) conditions averaged across six locations in West Africa in 2002

	Yield (kg ha^{-1})		Days to silk		Plant height (cm)		*Striga* 10 WAP		Ears harvested	
Cultivar	Inf.	Non-inf.	Non-inf.	Inf.	Non-inf.	Inf.	Count	Rating	Non-inf.	Inf.
ACR 94 TZE COMP5-Y	2158	2033	52	53	163	137	60	4	24	21
ACR 94 TZE COMP5-W	2124	2052	52	53	166	144	67	4	24	20
98 Syn WEC STR Co	1954	2228	52	54	168	143	68	5	25	18
TZE-Y POP DT STR C3 †	1928	2081	53	55	172	137	64	5	24	16
TZE-W POP DT STR C3†	1871	2099	53	54	173	140	67	5	24	18
EV DT-Y 2000 STR C1 †	1831	2203	53	54	171	139	66	5	24	18
2000 Syn WEC †	1826	2048	52	54	169	140	66	5	25	17
Kamboinse 88 Pool 16 DT (RE)	1806	1881	52	54	169	137	65	5	23	17
EV DT-W 99 STR Co †	1806	1803	52	53	159	125	60	5	24	18
EV DT 97 STR C1	1759	2110	53	54	166	136	63	4	22	17
ACR 94 POOL 16 DT STR	1735	1867	53	55	166	137	68	5	24	15
TZE-W POP × 1368 STR S6 F2	1721	1847	53	55	175	133	58	4	23	16
TZE-W POP × 1368 STR C1 †	1689	1950	51	53	162	130	59	5	25	17
99 Syn WEC	1541	1811	55	56	171	187	64	5	24	17
EV DT-W 2000 STR Co †	1498	1521	53	52	158	135	67	5	24	15
Grand mean	1826	1988	53	54	167	140	64	5	24	17
Coefficient of variation	26	24	5	9	13	42	15	20	15	22
LSD ($P < 0.05$)	269	271	2	3	14	37	6	1	2	2
Standard error of differences	1367	1378	0.8	1.5	7.1	18.6	3.0	0.3	1.1	1.1
P stat-test for cv	*	* y	*	ns	ns	ns	ns	ns	ns	**
P stat-test for environment × cv	**	***	ns	ns	ns	ns	*	***	ns	**

WAP weeks after planting

LSD least significant difference

*, **, and ns indicate significant at $P < 0.05$ and $P < 0.01$ and not significant, respectively

†Products from the S_1 recurrent selection program

Table 10.6 Grain yield (kg ha^{-1}) and other traits of maize cultivars derived from four cycles of S_1 recurrent selection in TZEE-Y Pop DT STR and TZEE-W Pop DT STR maize populations under *Striga*-infested and *Striga*-free environments in Nigeria, 2005–2007

Entry	Grain yield (kg ha^{-1})	Days to silk	ASI^y	EPP	Plant height (cm)	Stalk lodging (%)	*Striga* rating		*Striga* count	
							8 WAP	10 WAP	8 WAP	10 WAP
Striga-infested										
99 Syn EE-W	1588	56	3	0.6	131.2	5.4	4.7	4.6	136	167
98 TZEE-W STR	1345	56	4	0.6	128.5	5.8	5.1	4.6	118	154
2004 TZEE-W Pop STR C_4 †	1235	57	4	0.5	131.5	5.1	5.4	5.2	111	134
Ferke TZEE-W STR	1106	57	4	0.5	122.7	4.9	5.5	5.2	119	150
99 TZEE-Y STR	1089	52	4	0.5	113.5	3.9	5.6	5.7	120	126
2000 Syn EE-W †	1049	56	5	0.5	123.8	5.2	5.6	5.4	120	143
Siné TZEE-W STR	1031	57	4	0.6	122.7	4.2	5.3	5.2	118	143
2004 TZEE-Y Pop STR C_4 †	956	57	5	0.5	130.0	6.2	5.3	5.4	133	170
TZEE-W SR BC5 (RE)	783	52	5	0.4	115.4	5.1	5.9	6.3	189	182
99 TZEE-Y STR C_0 †	772	54	3	0.5	121.2	5.5	5.5	6.0	163	173
LSD^y ($P < 0.05$)	534.9	2.33	1.93	0.2	15.33	1.9	0.8	1.01	69	68
P stat-test for genotypes	**^{y}	**	*	**	ns	*	**	**	ns	ns
Striga-free										
2004 TZEE-W Pop STR C_4 †	3366	56	2	0.9	165	3.4				
99 Syn EE-W	3254	56	2	0.9	162	3.3				
2000 Syn EE-W †	3128	54	2	0.9	156	4.0				
Ferke TZEE-W STR	3002	57	2	0.8	163	3.1				
2004 TZEE-Y Pop STR C_4 †	2934	55	2	0.8	164	5.6				
98 TZEE-W STR	2861	56	2	0.9	157	2.8				
99 TZEE-Y STR	2366	52	2	0.8	146	3.9				
TZEE-W SR BC5 (RE)	2266	51	2	0.8	152	5.3				
Siné TZEE-W STR	2134	56	3	0.8	149	2.8				
9 TZEE-Y STR C_0 †	2067	54	3	0.8	154	4.8				
LSD ($P < 0.05$)	329.7	0.82	0.54	0.06	7.77	2.00				
P stat-test for genotypes	**	**	*	**	**	**				

plants. The improved yield of the derived cultivars from the advanced cycles of selection in TZEE-Y Pop STR was associated with decreased number of emerged *Striga* plants at 8 and 10 WAP and *Striga* damage at 8 WAP, while that of the white population was accompanied by increased days to silking and EPP as well as decreased *Striga* emergence at 8 WAP. Changes in all other traits associated with recurrent selection in both populations were not significant.

10.13.1 Residual Variances, Heritability, and Genetic Correlation

Investigation into the changes induced by selection and possibly genetic drift in population improvement programs is invaluable in determining the modifications in the breeding methodology and strategies that should be employed to ensure continued progress in future cycles of selection. Estimates of genetic variances, heritability, and genetic correlations are useful parameters for determining whether or not to continue with the selection scheme.

Several studies were conducted specifically to (i) determine the relative changes in the mean performance, genetic variances, heritabilities, and genetic correlation coefficients for grain yield, *Striga* resistance, and other agronomic traits under *Striga*-infested and *Striga*-free environments; (ii) estimate the realized gains from the recurrent selection program based on S_1 progenies; and (iii) predict possible future gains from S_1 family selection in the populations.

In one study, 300 full-sib families were extracted from the C_3 of the early populations, TZE-W Pop DT STR and TZE-Y Pop DT STR, and evaluated in separate experiments. The full-sib families were produced using the cross-classification (or nested) genetic design (North Carolina Design I) of Comstock and Robinson (1948). The full-sib families from TZE-W Pop DT STR were evaluated under *Striga* infestation in Ferke in 2002 and Mokwa in 2003, while those from TZE-Y Pop DT STR were evaluated in Abuja and Mokwa. In addition, 50 S_1 families extracted by self-pollinating random noninbred (S_0) plants from C_0, C_2, C_3, and C_4 of TZE-Y Pop DT STR were evaluated in Abuja and Mokwa under *Striga* infestation and in Mokwa and Ikenne under *Striga*-free conditions in 2005 and 2007. Similarly, 50 S_1 families each were extracted from C_0, C_2, C_3, and C_4 of TZEE-W Pop STR and TZEE-Y Pop STR. The resulting 200 S_1 families were evaluated for 2 years (2006 and 2007) in Abuja and Mokwa under *Striga* infestation and in Mokwa and Ikenne under *Striga*-free conditions. Crop management practices for the trials and field observations were as earlier described.

Analyses of variance (ANOVA) combined over environments for each population were performed separately for the *Striga*-infested and *Striga*-free environments, using PROC GLM of the Statistical Analysis Systems (SAS). The *Striga* emergence count was transformed to normality using the log transformation (y+1) before the ANOVA. Genetic variance estimates of the population were obtained for each cycle of selection from the combined ANOVA by equating observed mean squares with expected mean squares. Heritability (h^2) was calculated as the ratio of the genetic variance (σ^2_g) to the phenotypic variance (σ^2_p) on a progeny mean basis. Standard errors for σ^2_g and h^2 estimates were computed using the method of Hallauer and Miranda (1988). Genotypic correlations between pairs of agronomic traits and the standard errors were estimated with the restricted maximum likelihood (REML) method (Holland 2006) using Proc MIXED of SAS. A genetic correlation was declared significant when the standard error was more than twice as large as the genetic correlation.

The Early Populations For the TZE-W Pop DT STR, additive genetic variances (σ_a^2) were moderately large and much larger than the dominance variances (σ_d^2) for most traits (Table 10.7). However, *Striga* emergence count was under the control of σ_d^2. The dominance variance for number of emerged *Striga* plants was about twice as large as additive genetic variance at 8 WAP and about four times as large at 10 WAP. Narrow-sense heritability (h^2) estimate was 24.5% for grain yield and ranged from 0% to 90 % for 12 other traits. Low dominance variance and moderately large additive genetic variances and narrow-sense heritability were obtained for *Striga* damage scores. Grain yield had a positive additive genetic correlation ($r_a = 0.81$) with EPP, a negative correlation with *Striga* damage ratings at 8 WAP ($r_a = -0.85$) and 10 WAP ($r_a = -0.83$), a negative r_a with flowering traits ($r_a = -0.48$, -0.65, and -0.73 for anthesis, silking, and ASI, respectively), and the number of emerged *Striga* plants at 10 WAP ($r_a = -0.56$) (data not shown). Data for grain yield and other traits of 50 S_1 families extracted from the cycles C_0 and C_4 of the white population were subjected to analysis of variance from which genetic variances and heritability estimates were computed. Results revealed that the genetic variances of grain yield and traits such as days to anthesis and silking, ear aspect, ear height, and number of emerged *Striga* plants at 8 WAP were larger in the C_4 compared with the values obtained at C_0 under *Striga* infestation (Table 10.8). However, the genetic variance for number of emerged *Striga* plants at 10 WAP decreased with selection. The heritability estimates followed similar trends as those of the genetic variances. Under *Striga*-free environments, the genetic variances of grain yield and ear aspect increased, while the variances for days to anthesis and silking decreased as selection progressed (Table 10.8). For the TZE-Y Pop DT STR, estimates of dominance variances were larger than additive genetic variances for grain yield, plant height, ear height, number of ears at harvest, and *Striga* damage rating at 8 weeks after planting (Table 10.9). Even though h^2 estimates were generally low for most traits (<0.4), moderate-to-large additive genetic variances and wide ranges were obtained for most traits suggesting that there is adequate genetic variation for improving *Striga* resistance and grain yield in the population. Highly significant correlation coefficients were obtained between grain yield and EPP, plant height, ear height, days to anthesis and silking, anthesis–silking interval, and *Striga* damage score at 10 WAP (data not shown). It was concluded that recurrent selection methods that capitalize on both additive and dominance variances would be effective for further improvement of *Striga* resistance and grain yield in TZE-Y Pop DT STR.

Analysis of the data obtained from the 50 S_1 lines extracted from each cycle of selection in the TZE-Y Pop STR C_0 population revealed that significant improvement in grain yield and *Striga* resistance was associated with recurrent selection (Table 10.10). The advanced cycles of selection significantly outyielded the original

Table 10.7 Components of variance and heritability estimates of grain yield and agronomic traits of Design I progenies from TZE-W Pop DT STR C_3 evaluated under artificial Striga infestation in Ferkè in 2002 and Mokwa in 2003

Trait	σ^2_e	σ^2_{de}	σ^2_{ae}	σ^2_d ± S.E	σ^2_a ± S.E	σ^2_{ph}	h^2, % ± S.E
Grain yield, kg/ha	615,281	39,110,182,945	77,311,442,032	63564.75 ± 128519.12	125652.3 ± 83848.89	473248.5	24.51 ± 0.18
Plant height, cm	269.33	5615.843	29821.346	20.85 ± 60.49	110.73 ± 39.07	309.88	42.98 ± 0.13
Ear height, cm	91.09	0	3570.571	+0.00 ± 20.20	39.20 ± 13.23	95.22	47.49 ± 0.14
Root lodging, %	15.58	13.135	20.191	0.84 ± 2.62	1.30 ± 1.40	7.01	13.35 ± 0.20
Stalk lodging, %	7.86	0.377	0	0.13 ± 2.00	0.00 ± 1.14	6.27	0.00 ± 0.18
Days to anthesis	2.34	0	8.266	+0.00 ± 0.93	3.54 ± 0.79	6.12	89.55 ± 0.13
Days to silking	8.29	0	56.246	+0.00 ± 2.38	6.78 ± 1.86	12.99	68.14 ± 0.14
Anthesis–silking interval, days	5.51	3.385	6.502	0.61 ± 1.20	1.18 ± 0.77	4.64	24.64 ± 0.17
No. of ears per plant	0.03	0	0.0002	0.003 ± 0.01	0.005 ± 0.00	0.03	19.67 ± 0.12
Striga rating at 8 WAP	1.28	0.209	0.324	0.16 ± 0.24	0.25 ± 0.15	0.83	26.13 ± 0.19
Striga rating at10 WAP	1.45	0	0.664	+0.00 ± 0.26	0.46 ± 0.17	0.93	44.82 ± 0.18
Emerged *Striga* plants at 8 WAP	3706.88	2,487,607	1432603.474	671.08 ± 671.23	386.47 ± 331.41	2421.65	14.92 ± 0.14
Emerged *Striga* plants at 10 WAP	4210.99	3,608,576	893799.896	856.94 ± 727.13	212.25 ± 337.10	2325.71	7.79 ± 0.15

Table 10.8 Estimates of genetic variance (± standard error) and broad-sense heritability on an entry mean basis (± standard error) for grain yield and other traits of S_1 families derived from the C_0 and C_4 of S_1 recurrent selection in TZE-W Pop DT STR population evaluated under artificial *Striga hermonthica* infestation in Mokwa and Abuja and under *Striga*-free environments in Mokwa and Ikenne, Nigeria, 2006 and 2007

	Genetic variances		Broad-sense heritability	
Trait	C_0	C_4	C_0	C_4
Striga-infested environments				
Grain yield	2118.00 ± 6399.00	37265.00 ± 18636.00*	0.07 ± 0.21	0.37 ± 0.18*
Days to silk	0.56 ± 0.55	1.14 ± 0.57*	0.18 ± 0.17	0.37 ± 0.18*
Days to anthesis	0.40 ± 0.27	0.61 ± 0.19*	0.29 ± 0.20	0.48 ± 0.15*
Plant height	22.82 ± 14.59	17.53 ± 11.31	0.31 ± 0.20	0.28 ± 0.18
Ear aspect	0^z	0.07 ± 0.03*	0^y	0.30 ± 0.18
Anthesis–silking interval	0.283 ± 0.39	0.15 ± 0.29	0.13 ± 0.19	0.12 ± 0.23
Planted	0.004 ± 0.001*	0.005 ± 0.002*	0.44 ± 0.17*	0.47 ± 0.16*
Stalk lodging	0.19 ± 0.14	0.29 ± 0.16	0.25 ± 0.18	0.32 ± 0.18
Striga damage rating 8 WAP^x	0.08 ± 0.04	0.08 ± 0.04	0.34 ± 0.18	0.32 ± 0.18
Striga damage rating 10 WAP	0.004 ± 0.02	0.05 ± 0.04	0.02 ± 0.19	0.23 ± 0.20
Striga emergence count 8 WAP	37.35 ± 14.79*	41.87 ± 15.65*	0.39 ± 0.15*	0.43 ± 0.16*
Striga emergence count 10 WAP	56.72 ± 17.57**	52.54 ± 19.03*	0.48 ± 0.14**	0.41 ± 0.15*
Striga-free environments				
Yield	12463.00 ± 15166.00	37207.00 ± 18281.00*	0.16 ± 0.18	0.37 ± 0.17*
Days to silking	0.61 ± 0.20*	0.47 ± 0.17**	0.43 ± 0.15*	0.47 ± 0.17*
Days to anthesis	0.56 ± 0.19*	0.27 ± 0.12*	0.45 ± 0.15*	0.37 ± 0.18*
Anthesis–silking interval	0.025 ± 0.04	0.030 ± 0.03	0.11 ± 0.18	0.15 ± 0.19

(continued)

Table 10.8 (continued)

Trait	Genetic variances		Broad-sense heritability	
	C_0	C_4	C_0	C_4
Plant height	16.58 ± 14.75	5.97 ± 14.39	0.21 ± 0.18	0.08 ± 0.20
Ear height	2.85 ± 5.29	3.08 ± 6.83	0.10 ± 0.18	0.10 ± 0.22
Stalk lodging	0.08 ± 0.10	0.03 ± 0.07	0.17 ± 0.21	0.07 ± 0.23
Plant aspect	0.001 ± 0.010	0.0001 ± 0.001	0.04 ± 0.18	0.03 ± 0.21
Ear aspect	0.001 ± 0.001	0.0210 ± 0.010*	0.26 ± 0.17	0.39 ± 0.19*
Ears/plant	0.0015 ± 0.002	0.0010 ± 0.002	0.12 ± 0.19	0.16 ± 0.20

* and ** are significantly different at 0.05 and 0.01 levels of probability, respectively

[z] Negative estimates of genetic variances were equated to zero

[y] Heritability was not computed because of negative estimates of genetic variances

[x] *WAP* weeks after planting

Table 10.9 Component of variance and heritability estimates of grain yield and agronomic traits of Design I progenies from TZE-Y Pop DT STR C_3 evaluated under artificial *Striga* infestation in Abuja and Mokwa in 2003

Trait	σ^2_e	σ^2_{de}	σ^2_{ae}	σ^2_d ± S.E	σ^2_a ± S.E	σ^2_{ph}	h^2, % ± S.E
Grain yield, kg/ha	366405.3	26,274,511,857	17,182,549,063	71708.88 ± 24185.51	46894.00 ± 19026.27	274662.5	17.07 ± 0.14
Plant height, cm	398.83	54328.438	25965.03	136.22 ± 31.36	63.10 ± 23.14	374.62	17.38 ± 0.12
Ear height, cm	132.39	4176.79	3321.64	31.55 ± 6.95	25.09 ± 7.99	128.53	19.52 ± 0.12
Root lodging, %	12.5	1.239	35.61	0.10 ± 0.60	2.85 ± 0.77	10.21	27.90 ± 0.15
Stalk lodging, %	4.59	0	2.85	0 ± 0.31	0.62 ± 0.20	1.68	37.01 ± 0.24
Days to anthesis	4.06	0	25.95	0	6.38 ± 0.36	11.46	55.72 ± 0.13
Days to silking	7.75	0	66.41	0	8.57 ± 0.73	13.92	61.58 ± 0.15
Anthesis–silking interval, days	5.23	0	0.58	0 ± 0.43	0.11 ± 0.32	1.35	8.22 ± 0.48
No. of ears per plant	0.04	0.0007	4.88	0.016 ± 0.00	0.001 ± 0.00	0.03	3.65 ± 0.14
Striga rating at 8 WAP	0.7	0.062	0.05	0.088 ± 0.04	0.07 ± 0.04	0.47	14.63 ± 0.16
Striga rating at10 WAP	0.92	0	0.15	0 ± 0.06	0.16 ± 0.05	0.39	41.90 ± 0.23
Emerged *Striga* plants at 8 WAP	1016.58	0	94950.19	0 ± 66.53	93.40 ± 50.86	451.73	20.68 ± 0.26
Emerged *Striga* plants at 10 WAP	1023.85	0	98948.73	0 ± 65.40	96.64 ± 52.63	521.49	18.53 ± 0.20

Table 10.10 Estimates of genetic variance (± SE) and broad-sense heritability (± SE) for measured traits of 50 S_1 lines derived from four cycles of selection in the TZE-Y Pop STR maize population evaluated under artificial *Striga* infestation at Mokwa and Abuja and *Striga*-free environments at Ikenne and Mokwa, Nigeria, in 2005 and 2007

	Genetic variance		Broad-sense heritability	
Trait	C_0	C_4	C_0	C_4
Striga-infested environment				
Yield (kg ha^{-1})	12810.4 ± 4184.32	48816.70 ± 12709	49.88 ± 0.16	62.88 ± 0.16
Days to silking	4.66 ± 1.06	4.37 ± 1.17	69.20 ± 0.16	70.70 ± 0.19
Days to anthesis	1.90 ± 0.45	2.76 ± 0.60	69.53 ± 0.17	78.75 ± 0.17
Anthesis–silking interval	3.13 ± 0.6917	2.31 ± 0.70	72.11 ± 0.16	60.17 ± 0.18
Plant height (cm)	59.60 ± 22.0725	89.72 ± 25.93	50.44 ± 0.19	58.97 ± 0.17
Ear per plant	0.01 ± 0.0022	0.01 ± 0.003	50.94 ± 0.18	68.14 ± 0.18
Ear aspect	0.08 ± 0.0338	0.13 ± 0.046	41.08 ± 0.17	49.20 ± 0.17
Striga rating 8	0.17 ± 0.0538	0.39 ± 0.102	59.46 ± 0.18	71.28 ± 0.18
Striga rating 10	0.14 ± 0.0484	0.26 ± 0.082	51.89 ± 0.18	55.15 ± 0.17
Striga count 8	172.91 ± 35.6703	108.74 ± 27.45	74.92 ± 0.18	64.96 ± 0.16
Striga count 10	291.61 ± 58.9121	137.74 ± 35.54	76.74 ± 0.16	64.90 ± 0.17
Striga-free environment				
Yield (kg ha^{-1})	43430.00 ± 12566.19**^{z}	36139.00 ± 15672.83**	58.92 ± 0.17	43.23 ± 0.19
Days to anthesis	0.94 ± 0.27**	0.13 ± 0.13	54.08 ± 0 .16	17.49 ± 0.17
Days to silking	1.16 ± 0.32*	0.31 ± 0.17	52.65 ± 0 .15	29.53 ± 0.16
Anthesis–silking interval	0.06 ± 0.06	+	18.75 ± 0.17	++

Plant height (cm)	8.86 ± 10.71	25.24 ± 15.37	14.31 ± 0.17	32.85 ± 0.20
Ear height (cm)	3.36 ± 5.00	14.72 ± 7.70	12.52 ± 0.19	37.57 ± 0.20
Ear per plant	+	0.004 ± 0.02	++[x]	4.80 ± 0.22
Stalk lodging (%)	+	0.23 ± 0.15	++	31.06 ± 0.20
Plant aspect	0.01 ± 0.006*	0.01 ± 0.006	13.12 ± 0.20	27.08 ± 0.22
Ear aspect	0.01 ± 0.01	0.01 ± 0.01*	21.13 ± 0.19	7.86 ± 0.19

[z] * and ** are significantly different from zero at 0.05 and 0.01 levels of probability, respectively

[y] +Negative estimates of genetic variances were equated to zero

[x] ++Heritability was not computed because of negative estimates of genetic variances

cycle in both research environments. However, realized gains from selection for grain yield under *Striga*-infested (68 kg $ha^{-1}cycle^{-1}$) and *Striga*-free conditions (169 kg ha^{-1} $cycle^{-1}$) were significantly lower than the predicted gains (350 and 250 kg ha^{-1} $cycle^{-1}$, respectively) (data not shown). Under *Striga* infestation, estimates of genetic variances for grain yield, EPP, days to anthesis, plant height, and *Striga* damage generally increased in the C_4 relative to the C_0 of selection (Table 10.10). In contrast, the genetic variances for days to silk, ASI, ear aspect, and number of emerged *Striga* plants decreased with selection. Heritability for grain yield, *Striga* damage, and number of emerged *Striga* plants is significantly greater than zero. Under *Striga*-free conditions, the genetic variances for grain yield, days to anthesis, silking, ASI, and ear aspect generally decreased as selection progressed. On the other hand, increases were generally detected for plant height, EPP, and stalk lodging. Genetic variances for the traits were generally higher when *Striga*-infested than when *Striga*-free. Changes in the broad-sense heritability for grain yield and other traits with selection followed trends similar to that of the genetic variances and were all significantly greater than zero in both research environments (Table 10.10). In general, heritability estimates of measured traits were higher when *Striga*-infested than when *Striga*-free. Genetic correlation between grain yield and most other traits was not significant under *Striga*-free conditions (Table 10.11). Under *Striga* infestation, grain yield had highly significant genetic correlation with ear $plant^{-1}$, ear aspect, and *Striga* damage at 8 and 10 WAP for all or most cycles of selection. Results of this study confirmed that adequate genetic variability exists in cycle 4 of the scheme to ensure future gains from selection.

The Extra-Early Populations Results of the analysis of the 50 S_1 families extracted from each of C_0, C_2, C_3, and C_4 of TZEE-W Pop STR population revealed gain in grain yield was 26% $cycle^{-1}$ under *Striga* infestation and 16.4% ha^{-1} when *Striga*-free (Table 10.12). Under *Striga* infestation, genetic variances decreased with selection for emerged *Striga* plants and EPP (Table 10.12). Under *Striga*-free conditions, genetic variability also decreased for flowering traits. Genetic variances were significant for the number of emerged *Striga* plants in all cycles and for EPP, in C_0 and C_4. Response to selection for improved *Striga* emergence, EPP, and grain yield is expected in subsequent cycles.

When *Striga*-free, the genetic correlations between the primary selection traits, grain yield, and days to silking, plant height, EPP, and ASI of the four cycles of selection were nonsignificant (Table 10.12). Under *Striga* infestation, none of the four possible genetic correlation coefficients between *Striga* traits and grain yield were significant at the C_0, increasing to one, two, and three at C_2, C_3, and C_4, respectively. In all cases, the significant coefficients were negative. The implication was that high-yielding families had low number of emerged *Striga* plants and *Striga* damage. Hence, there were more resistant families at the C_4 than the C_0 of the selection program in this population. For most other traits, there were also more significant genetic correlation coefficients at the C_4 than the earlier selection cycles of this population. Based on the results of the studies, it was concluded that (1) recurrent selection was effective for improving *Striga* resistance traits and grain yield which

Table 10.11 Genetic correlations between selected pairs of traits of S_1 lines derived from four cycles of selection in TZE-Y Pop STR tested under *Striga*-free environments at Ikenne and Mokwa and *Striga*-infested environments at Mokwa and Abuja, Nigeria, in 2005 and 2007

	Genetic correlation			
Trait	C_0	C_2	C_3	C_4
Striga-free environments				
Grain yield vs days to silk	−0.30 ± 0.30	0.44 ± 0.47	−0.06 ± 0.86	−0.31 ± 0.50
Grain yield vs plant height	+^{z}	1.00 ± 0.98	0.3 ± 0.75	0.52 ± 0.31
Grain yield vs ear height	1.00 ± 1.16	1.00 ± 1.16	1.00 ± 1.16	0.73 ± 0.30*
Grain yield vs plant aspect	−0.73 ± 0.53	−0.88 ± 0.37*	−1 ± 1.24	−0.57 ± 0.26*
Grain yield vs ears per plant	1.00 ± 5.15	0.87 ± 0.32*	−0.03 ± 0.91	0.75 ± 1.17
Grain yield vs ear aspect	−0.40 ± 0.48	−1.00 ± 1.30	−0.76 ± 1.02	−1.00 ± 1.05
Grain yield vs anthesis–silking interval (ASI)	−1.00 ± 2.70	−1.00 ± 2.72	−0.34 ± 0.97	+
Plant height vs ear height	0.78 ± 0.96	0.83 ± 0.19**	−1.00 ± 1.99	0.89 ± 0.89
Striga-infested environments				
Grain yield vs days to silk	−0.39 ± 0.26	−0.43 ± 0.31	−0.46 ± 0.35	−0.35 ± 0.19
Grain yield vs plant height	−0.11 ± 0.36	0.57 ± 0.43	0.58 ± 0.45	0.18 ± 0.24
Grain yield vs *Striga* rating at 8 WAP^{y}	−0.64 ± 0.21**	0.79 ± 0.23**	−0.56 ± 0.04**	−1.00 ± 0.06**
Grain yield vs *Striga* rating at 10 WAP	−0.78 ± 0.19**	0.81 ± 0.21**	−0.22 ± 0.78	−0.99 ± 0.08**
Grain yield vs *Striga* count at 8 WAP	0.47 ± 0.76	0.47 ± 0.76	−0.68 ± 0.60	−0.33 ± 0.37
Grain yield vs *Striga* count at 10 WAP	0.47 ± 0.63	0.47 ± 0.62	−0.36 ± 0.64	−0.47 ± 0.38
Grain yield vs ears per plant	± 0.21**	1.00 ± 0.27**	−0.002 ± 0.78	0.93 ± 0.08**
Grain yield vs ear aspect	−0.93 ± 0.15**	−0.99 ± 0.22**	0.79 ± 0.24**	−0.89 ± 0.09**
Grain yield vs anthesis–silking interval	−0.04 ± 0.28	−0.05 ± 0.37	−0.79 ± 0.37*	−0.24 ± 0.24
Ears per plant vs plant height	−0.09 ± 0.43	−0.09 ± 0.43	1.00 ± 2.69	1.00 ± 0.62
Ears per plant vs *Striga* rating at 8 WAP	−0.96 ± 0.19	0.96 ± 0.18**	−1.00 ± 0.42*	−0.73 ± 0.22**
Ears per plant vs *Striga* rating at 10 WAP	+	+	0.54 ± 0.04**	−0.88 ± 0.17**
Ears per plant vs *Striga* count at 8 WAP	−0.39 ± 0.50	−0.003 ± 0.45	+	−0.43 ± 0.29

(continued)

Table 10.11 (continued)

Trait	Genetic correlation			
	C_0	C_2	C_3	C_4
Ears per plant vs *Striga* count at 10 WAP	0.01 ± 0.36	0.01 ± 0.38	+	−0.46 ± 0.31
Striga rating at 8 WAP vs *Striga* rating at 10 WAP	0.89 ± 0.08**	1.00 ± 0.08**	1.00 ± 0.26**	0.95 ± 0.06**
Striga rating at 8 WAP vs *Striga* count at 8 WAP	−0.11 ± 0.24	0.31 ± 0.22	0.05 ± 0.29	0.42 ± 0.19**
Striga rating at 8 WAP vs *Striga* count at 10 WAP	0.01 ± 0.23	0.19 ± 0.23	−0.08 ± 0.29	0.26 ± 0.21
Striga count at 8 WAP vs *Striga* count at 10 WAP	1.00 ± 0.02**	1.00 ± 0.03**	0.98 ± 0.05**	1.00 ± 0.03**
Striga rating at 10 WAP vs *Striga* count at 8 WAP	−0.05 ± 0.26	0.51 ± 0.24*	−0.06 ± 0.46	0.49 ± 0.23*
Striga rating at 10 WAP vs *Striga* count at 10 WAP	0.17 ± 0.26	0.35 ± 0.26	−0.22 ± 0.47	0.32 ± 0.25
Ear aspect vs *Striga* rating at 8 WAP	0.89 ± 0.19**	0.76 ± 0.17**	0.32 ± 0.32	1.00 ± 0.08**
Ear aspect vs *Striga* rating at 10 WAP	1.00 ± 0.18**	0.66 ± 0.23*	0.22 ± 0.54	0.92 ± 0.098*
ASI vs *Striga* rating at 8 WAP	0.47 ± 0.20*	0.31 ± 0.23	0.43 ± 0.27	0.17 ± 0.22
ASI vs *Striga* rating at 10 WAP	0.45 ± 0.23	0.37 ± 0.28	0.57 ± 0.43	0.04 ± 0.26

WAP weeks after planting

* and ** are significantly different at 0.05 and 0.01 levels of probability, respectively

$^{z+}$Correlations not estimable because one or both variances involved were estimated to be zero

Table 10.12 Genetic correlations between selected pairs of traits of S_1 lines derived from four cycles of selection in TZEE-W Pop STR under *Striga*-free (Mokwa and Ikenne) and *Striga*-infested environments (Abuja and Mokwa) in 2006 and 2007

Trait pair	C_0	C_2	C_3	C_4
Striga-free environment				
Days to silk vs grain yield	0.28 ± 1.15	−0.51 ± 0.42	0.33 ± 0.10**	0.71 ± 0.26**
Plant height vs grain yield	0.45 ± 0.39	0.78 ± 0.55	0.37 ± 0.97	1.00 ± 2.31
Ears per plant vs grain yield	0.68 ± 1.17	0.24 ± 0.29	0.91 ± 0.43*	0.005 ± 0.01*
Ear aspect vs grain yield	−1.00 ± 0.001**	−0.29 ± 0.001**	−0.39 ± 0.17*	−0.58 ± 0.69
Anthesis–silking interval (ASI) vs grain yield	−0.80 ± 0.001**	†[z]	−0.89 ± 0.89	−0.20 ± 0.14
Ear height vs grain yield	0.89 ± 0.001**	1.00 ± 0.7	†	0.90 ± 0.85
Root lodging vs grain yield	0.59 ± 0.001**	0.06 ± 0.03	−0.15 ± 0.83	−0.39 ± 0.82
Stalk lodging vs grain yield	−0.79 ± 0.16**	0.03 ± 0.02	−1.00 ± 3.45	−0.56 ± 0.81
Plant aspect vs grain yield	−0.72 ± 0.001**	−0.86 ± 0.001**	−0.11 ± 0.59	−0.65 ± 0.85
Striga-infested environment				
Days to silk vs grain yield	−1.00 ± 1.02	−0.38 ± 0.57	−0.26 ± 0.46	0.14 ± 0.45
Plant height vs grain yield	0.08 ± 0.55	−0.09 ± 0.59	0.51 ± 0.49	1.00 ± 0.48*
Ears per plant vs grain yield	−0.13 ± 0.63	1.00 ± 0.25**	1.00 ± 7.91	0.94 ± 0.12**
Ear aspect vs grain yield	†	−0.76 ± 0.36*	−0.84 ± 0.40*	−0.81 ± 0.27*
ASI vs grain yield	−1.00 ± 0.93	−0.02 ± 0.85	−0.15 ± 0.85	−0.10 ± 0.44
Stalk lodging vs grain yield	−0.11 ± 0.85	0.49 ± 0.77	0.09 ± 0.59	−1.00 ± 0.52
Striga rating at 8 WAP[y] vs grain yield	−0.59 ± 0.43	−1.00 ± 1.25	−0.30 ± 0.51	−0.87 ± 0.23**
Striga rating at 10 WAP vs grain yield	1.00 ± 2.19	−0.86 ± 0.54	−0.58 ± 0.35	−0.94 ± 0.24**
Striga count at 8 WAP vs grain yield	0.59 ± 0.71	−0.87 ± 0.02**	−0.65 ± 0.02**	−0.39 ± 0.39
Striga count at 10 WAP vs grain yield	0.43 ± 0.57	−0.90 ± 0.84	−0.36 ± 0.01**	−0.41 ± 0.01**
Striga rating at 8 WAP vs *Striga* rating at 10 WAP	1.00 ± 0.25**	1.00 ± 7.83	0.96 ± 0.13**	1.00 ± 0.18**
Striga rating at 8 WAP vs *Striga* count at 8 WAP	−0.14 ± 0.52	−1.00 ± 3.77	0.61 ± 0.52	0.29 ± 0.42
Striga rating at 8 WAP vs *Striga* count at 10 WAP	−0.12 ± 0.44	−1.00 ± 7.54	0.50 ± 0.56	0.31 ± 0.45

(continued)

Table 10.12 (continued)

Trait pair	C_0	C_2	C_3	C_4
Striga rating at 8 WAP vs ears per plant	−0.96 ± 0.18**	−1.00 ± 0.36*	†	−0.73 ± 0.21**
Striga rating at 8 WAP vs ear aspect	†	−1.00 ± 6.23	0.79 ± 0.38*	0.79 ± 0.36*
Striga rating at 8 WAP vs ASI	0.94 ± 0.70	†	−0.12 ± 0.78	1.00 ± 0.19**
Striga rating at10 WAP vs *Striga* count at 8 WAP	−0.59 ± 0.43	−1.00 ± 0.92	0.98 ± 0.50	0.69 ± 0.30*
Striga rating at 10 WAP vs *Striga* count at 10 WAP	−1.00 ± 1.34	−1.00 ± 1.01	0.81 ± 0.41	0.70 ± 0.34*
Striga rating at 10 WAP vs ear aspect	†	−0.38 ± 1.03	1.00 ± 0.43*	1.00 ± 0.25**
Striga rating at 10 WAP vs ears per plant	†	−0.74 ± 0.46	−1.00 ± 0.42*	−0.88 ± 0.17**
Striga rating at 10 WAP vs ASI	†	0.44 ± 1.02	−0.36 ± 0.74	1.00 ± 0.43*
Ear aspect vs ASI	†	0.04 ± 0.82	−0.87 ± 0.72	1.00 ± 0.82
ASI vs ears per plant	−0.91 ± 0.62	−1.00 ± 0.67	†	1.00 ± 0.35*
Striga count 8 WAP vs *Striga* count 10 WAP	1.00 ± 0.03**	1.00 ± 0.03**	0.98 ± 0.05**	1.00 ± 0.03**

WAP weeks after planting

* and ** are significantly different at 0.05 and 0.01 levels of probability, respectively

^{z}†Genetic correlations could not be estimated because variance estimate was less than or equal to zero were characterized by low to medium heritability estimates in two early and two extra-early maize populations; (2) residual genetic variances were significant for *Striga* emergence and *Striga* damage, grain yield, EPP, and several other traits of the populations; and (3) response to selection for improved *Striga* emergence, EPP, and grain yield is expected in future cycles of selection in these populations.

10.14 Cultivar Evaluation and Trait Analysis of Tropical Early-Maturing Maize Under *Striga*-Infested and *Striga*-Free Environments

In maize *Striga* research, *Striga* damage rating is used as the index of tolerance, while the number of emerged *Striga* plants is used as the index of resistance. Tolerance to *Striga* is quantified by a host damage rating score on a scale of 1–9, where 1 is most tolerant and 9 is highly intolerant or sensitive. Different measures of tolerance have been proposed, ranging from host plant damage scores to high yield, yield loss, or relative yield loss under *Striga* infestation (Kim 1994; Adetimirin et al. 2000b; Gurney et al. 2006). However, none of these measures account for the difference in resistance among genotypes, and therefore they fail to recognize the fact that the observed damage is due to both *Striga* infection level (resistance) and the extent to which the specific genotype endures these infections (tolerance). Therefore, differences among genotypes in level of yield reduction cannot be attributed to only tolerance. A maize genotype that combines superior levels of resistance and tolerance is a promising breeding strategy and has been proposed for *Striga* resistance breeding in many studies (Kim 1991; DeVries 2000; Kling et al. 2000; Haussmann et al. 2001; Rodenburg et al. 2006). The ultimate goal of the IITA maize breeding program for biotic and abiotic stress tolerance is improved grain yield under three specific stress factors, that is, low soil nitrogen, drought, and *S. hermonthica* infestation. Maize cultivars that combine improved grain yield with *Striga* resistance are desirable in SSA to ensure food security. Breeding for high-yielding maize varieties with effective resistance and/or tolerance to the hemiparasitic weed *S. hermonthica* requires suitable selection measures for both characteristics.

In breeding maize for tolerance or resistance to *Striga*, appropriate tolerance or resistance indicator traits can improve the precision with which resistant genotypes are identified. For the stress tolerance aspect of its research activities, the IITA Maize Program focuses on four maize maturity groups: late, intermediate, early, and extra-early. At the initial stages of the stress tolerance/resistance research work, the program concentrated on late- and intermediate-maturity groups and used a base index, which combines grain yield under *Striga* infestation, *Striga* damage rating, emerged *Striga* plant*s*, and ears per plant (EPP) to select for high grain yield measured under *Striga*-infested and *Striga*-non-infested conditions (MIP 1996; Menkir and Kling 2007). At the time research on improvement of the breeding populations in the extra-early and early maturity groups started in 1994, the early-maturity component of the maize program adopted the base index used for the improvement of the late/intermediate-maturity groups but found inconsistent results, depending on traits used and type of germplasm subjected to selection. A few examples will suffice. The primary traits of interest in selecting for tolerance or resistance and high grain yield under *Striga* infestation are host plant damage rating (*Striga* damage) and *Striga* emergence count (number of emerged *Striga* plants). There are contradictory reports on the importance of *Striga* emergence count as a reliable trait for selecting for *Striga* resistance and improved grain yield under artificial *Striga* infestation. For instance, contrary to the results obtained for the late- and intermediate-maturity groups (Kim and Adetimirin 1995; Gethi and Smith 2004; Menkir and Kling 2007; Yallou et al. 2009), Badu-Apraku et al. (2006a, 2007) reported weak phenotypic and genotypic correlations between grain yield and *Striga* emergence count in early germplasm. In contrast, Badu-Apraku (2010) studied the relative changes in genetic variances, heritabilities, and genetic correlations following four cycles of S_1 family selection in the extra-early white population and reported that under *Striga* infestation, yield was not correlated with other traits at C_0 but was significantly correlated with ears per plant, *Striga* damage, and emerged *Striga* plants in advanced cycles. It was therefore concluded that the value of the traits that are used in the base index by IITA Maize Program for selecting for *Striga*-tolerant and *Striga*-resistant genotypes required assessment and confirmation in order to determine whether or not they were appropriate for the selection of resistant/tolerant early and extra-early maize.

From the foregoing, the traits to use in selecting for *S. hermonthica* resistance or tolerance in early and extra-early maize populations need to be clearly identified. Such traits would have to be combined with grain yield in a base index to maximize yield performance of selected genotypes.

The genotype-by-trait (GT) biplot proposed by Yan and Kang (2003) is a powerful statistical tool for evaluating cultivars based on multiple traits and for identifying those that are superior in certain traits and hence could be candidates for use as parents in a breeding program or directly released for commercial production. An important advantage of the GT biplot is that it can be used to identify redundant traits in an effort to reduce cost in measuring traits in field experiments without sacrificing precision. The GT biplot was therefore used to (i) examine the performance of early-maturing cultivars based on multiple traits to identify superior genotypes for release for commercial production in WCA and (ii) analyze the interrelationship between grain yield and other traits with a view to identifying traits that are most appropriate for indirect selection for improved grain yield under *Striga*-infested and *Striga*-free environments. A field study involving 15 varieties was conducted to examine the interrelationship among traits under *Striga*-free conditions. A biplot was generated to display the association among measured traits in the study. Results revealed that YLD was positively correlated with PLHT, EHT, EPP, and SLG but negatively correlated with EASP, ASI, PASP, DYA, DYS, HUSK, EROT, and RL. EASP and ASI were identified as the most reliable traits for selecting for improved grain yield under *Striga*-free conditions at $P < 0.01$ and R-square value of 25.54%. Under *Striga* infestation, there was a high positive correlation between

SLG and ASI suggesting that either of the parameters will be sufficient as a selection criterion. Similarly, there was a high correlation between STRA1 and STRA2 suggesting that either of the two traits will suffice as a selection criterion. EPP, STRA1, STRA2, and EASP were identified as the most reliable of the 11 measured traits for selecting for *Striga* resistance and improved grain yield under artificial *Striga* infestation at $P < 0.01$ and R-square value of $\geq 43.61\%$.

A base index which combines grain yield under *Striga* infestation, *Striga* damage rating, *Striga* emergence, PASP, and EPP is used for selecting for high grain yield measured under *Striga*-infested and *Striga*-non-infested conditions (MIP 1996; Menkir and Kling 2007; Badu-Apraku et al. 2010). Therefore, a study was conducted to assess the appropriateness of the traits in the base index. Based on the GT biplot, EPP, STRA1, STRA2, and EASP were identified as the most reliable of the 11 measured traits for selection for *Striga* resistance, thus justifying the use of EPP, STRA1, and STRA2 in the base index. It is not surprising that EPP was identified as one of the most reliable traits for selection for *Striga* resistance. Badu-Apraku et al. (2008) reported EPP to be a major component of the increased grain yield associated with recurrent selection programs under drought stress and *Striga* infestation. Similar results were also reported under drought stress by Bolaños and Edmeades (1993), Chapman and Edmeades (1999), and Monneveux et al. (2006). This result therefore justifies the inclusion of EPP in the selection index for yield improvement in *Striga*-prone environments as earlier reported by Adetimirin et al. (2000a), Badu-Apraku (2007), and Badu-Apraku et al. (2008). Similarly, Badu-Apraku et al. (2007) reported high negative genetic and phenotypic correlations between grain yield and host plant damage rating and concluded that *Striga* damage rating is an appropriate trait for the assessment of tolerance under *Striga* infestation (Kim and Adetimirin 1995). In contrast, STC1 and STC2 were among the traits that had weak correlation with yield, suggesting that they do not qualify to be included in the base index. This finding is supported by Badu-Apraku et al. (2007) who reported weak phenotypic and genotypic correlations between grain yield and *Striga* emergence count, indicating that it is not a reliable trait for detecting *Striga* resistance. However, it was argued that the result could also mean that grain yield and *Striga* emergence count were genetically independent (no linkage, pleiotropy) and may be effectively selected for simultaneously using an appropriate index. Contrary to this result, Badu-Apraku (2007) in a study of the genetic variances and correlations in an early white maize population reported a moderately large negative genetic correlation ($rg = -0.56$) between grain yield and *Striga* emergence count at 10 WAP. This result is further supported by Badu-Apraku (2010) who reported that under *Striga* infestation, yield was not correlated with other traits at C_0 but was strongly correlated with ears per plant, *Striga* damage, and emerged *Striga* plants in advanced cycles of the extra-early white population. Similar results were also reported by Menkir and Kling (2007) for *Striga* emergence count at 8 ($rp = -0.78$) and 10 ($rp = -0.72$) WAP and EASP ($rp = -0.97$) under *Striga* infestation for a late-maturing tropical maize population. In this study, further analysis using the stepwise multiple regression analysis showed that *Striga* emergence count at 8 WAP was among the five traits identified as important yield determinant (data not shown).

On the contrary, Badu-Apraku and Akinwale (2011) reported ears per plant, *Striga* damage at 8 and 10 WAP, and ear aspect (EASP) were the most reliable traits for selecting for resistant genotypes. *Striga* emergence count at 8 and 10 WAP was not among the reliable traits identified for selection for improved grain yield. It was concluded that the inclusion of the traits in the base index needed to be further verified. EASP had high correlation with grain yield and was one of the most reliable traits for selection for increased grain yield under *Striga* infestation. It was therefore recommended that EASP should be included in the index. Based on the contradictory reports on the reliability of number of emerged *Striga* plants for selecting for improved yield under *Striga* infestation, Badu-Apraku et al. (2014) conducted a study to confirm the reliability of traits used for selecting maize genotypes for improved grain yield under artificial *Striga* infestation. Ten open-pollinated, *Striga*-resistant extra-early maturing maize cultivars were evaluated in a paired experiment under artificial *Striga*-infested and *Striga*-free environments in Nigeria for 2 years. GGE biplot and sequential path analysis were used to examine the relationship among grain yield and other traits. Sequential path analysis identified EASP as the only trait with significant direct effect on yield under artificial *Striga* infestation, while GGE biplot identified EASP, ASI, PLHT, EPP, and the *Striga* damage ratings as the most reliable traits. It was confirmed that EASP should be included in the base index for selecting for improved grain yield of early and extra-early maturing maize under *Striga* infestation and that the number of emerged *Striga* plants should be excluded from the index.

In summary, EPP, STRA1, STRA2, and EASP have been identified as the most reliable traits for selecting *Striga*-tolerant/*Striga*-resistant genotypes. The GT biplot analysis revealed that STC1 and STC2 had weak correlation with grain yield, implying that their inclusion in the base index for selecting for *Striga*-resistant genotypes is not justified. EASP had a consistently high correlation with grain yield under *Striga* infestation, suggesting that it should be included in the base index.

10.15 Products of IITA *Striga* Resistance Breeding

Most of the tropical maize cultivars grown in Africa before 1990 were highly susceptible to *S. hermonthica* (Kling et al. 2000). The IITA, in collaboration with National Agricultural Research Systems (NARS), has developed many inbred lines, hybrids, and open-pollinated varieties of different maturity cycles with moderate to high levels of tolerance to *Striga*. Tolerant inbred lines which have been used to develop varieties that can withstand the effects of *Striga* are 9030 STR, 1368 STR, and 9450 STR. Among the populations developed are TZEE-W Pop STR, TZEE-Y Pop STR, TZE-W Pop DT STR, TZE-Y-Pop DT STR, TZE Comp 5-W, TZE Comp 5-Y, IWD STR, and TZL Comp 1-W. Considerable progress has also been achieved in improving the developed varieties, populations, inbreds, and hybrids for resistance to *Striga*. However, many of the varieties still support considerable number of *Striga* plants, which may ultimately flower, set seed, and increase the *Striga* seed bank in the soil. A further increase in the level of resistance to *Striga* was therefore considered an important breeding goal in maize. A high level of resistance was found in perennial teosinte, *Zea diploperennis* Iltis, Doebley, and Guzman (Kling et al. 2000). Therefore, IITA in addition to exploiting the genetic variation present in cultivated maize has introgressed resistance genes from perennial teosinte *Zea diploperennis* to cultivated maize of tropical adaptation, and backcross progeny with high levels of resistance has been selected from the crosses (Kling et al. 2000). Inbred lines developed from the progeny were found to exhibit significant variation in host damage symptoms and *Striga* emergence (Berner et al. 1995; Kling et al. 2000). Information on the effectiveness of the genes for resistance to *Striga* in their new genetic background was required. Gethi and Smith (2004) reported that F_1 crosses involving three *Z. mays*–*Z. diploperennis* backcross-derived lines although unadapted to the environmental conditions in Kenya, East Africa, had significantly fewer *Striga* plants compared with susceptible checks. *Striga hermonthica* is an outcross species with strain variation between environments (Kim et al. 1994) that can exert strong influence on host plant resistance or tolerance to *Striga*. Yallou et al. (2009) determined the combining ability of resistance to *S. hermonthica* among lines containing *Zea diploperennis* and tropical germplasm. Forty-five diallel crosses of ten inbred lines were evaluated in an alpha-lattice design with and without artificial *Striga* infestation at two locations each in the Republic of Benin and Nigeria for 3 years. Results of analyses showed that only general combining ability (GCA) mean squares were significant ($P = 0.01$) for the number of emerged *Striga* plants (NESPP) while both GCA and specific combining ability (SCA) mean squares were significant for host damage score (HDS) and grain yield under *Striga* infestation. The ratio of GCA to SCA mean squares for the three traits varied from 3.5 to 57.5. Although GCA × environment interaction was significant for the three traits, two inbred lines containing *Z. diploperennis* (ZD 551) and tropical (TZL TC 87) germplasm had negative and significant GCA effects for NESPP and HDS and positive GCA effects for grain yield under *Striga* infestation in the two countries. Correlation between NESPP and HDS was strong and significant ($r = 0.87$, $P = 0.01$). The results confirmed the importance of harnessing useful genes from wild relatives to improve resistance to *S. hermonthica* in adapted maize germplasm.

10.16 Genetic Gains from Selection for High Grain Yield and *Striga* Resistance in Early-Maturing Maize Cultivars of Three Breeding Eras Under *Striga*-Infested and *Striga*-Free environments

Maize production is threatened by *Striga hermonthica* infestation. Fifty early-maturing cultivars were evaluated in 2010 and 2011 for grain yield and tolerance or resistance to *Striga* under artificial infestation with *S. hermonthica* at two locations each in the Republic of Benin and Nigeria. The objective of the study was to determine the rate of genetic improvement in grain yield of the cultivars developed during three breeding eras under *Striga*-infested and *Striga*-free conditions. Under *Striga* infestation, grain yield ranged from 2537 kg ha^{-1} for cultivars bred during 1988–2000 to 3122 kg ha^{-1} for those developed during 2007–2010 with a corresponding genetic gain of 1.93% per year. When *Striga*-free, grain yield ranged from 3646 kg ha^{-1} for cultivars bred during 1988–2000 to 4227 kg ha^{-1} for those developed during 2007–2010 with annual genetic gain of 1.0%. The average rate of increase in grain yield was 41 kg ha^{-1} per year when *Striga*-infested and 34 kg ha^{-1} per year when *Striga*-free. The increase in grain yield under *Striga* infestation was associated with significant decrease in the *Striga* damage rating and the number of emerged *Striga* plants at 8 and 10 WAP, improvement in ear aspect, and increase in the number of ears per plant from old to modern era cultivars. The *Striga* damage rating decreased from 3.3 to 2.9 for the old to modern era cultivars with a genetic gain of −0.85% at 8 WAP. At 10 WAP, the damage rating decreased from 4.6 to 4.1 for the old and modern era cultivars with genetic gain of −0.80%. For the number of emerged *Striga* plants, annual genetic gains of −0.63% for 8 WAP and −0.57% for 10 WAP were obtained for cultivars of the three breeding eras. The increase in annual genetic gains for the cultivars was 0.70% for EPP and −0.65% for ear aspect. Cultivars DTE-Y STR Syn C1, EV DT-Y 2000 STR, and 2009 DTE-Y STR Syn were the highest yielding and the most stable across *Striga*-infested environments. It was concluded that substantial progress had been made in breeding for high-yielding, *Striga*-resistant/*Striga*-tolerant early-maturing cultivars during the past three decades. The outstanding *Striga*-resistant cultivars, DTE-Y STR Syn C1, EV DT-Y 2000 STR, and 2009 DTE-Y STR Syn, developed in the program from 2007 to 2012 are being extensively tested and promoted for adoption by farmers to contribute to food security in the sub-region. It is interesting to note that EV DT-Y 2000 STR which was identified as one of the most outstanding cultivars under drought (Badu-Apraku et al. 2013) was also outstanding under *Striga* infestation. It is therefore not surprising that this cultivar was formally released in 2011 for commercialization in Nigeria.

The second study was conducted at five locations in WA to determine genetic gains in yield of 56 extra-early maturing cultivars developed during 3 eras, under *Striga*-infested and *Striga*-free conditions, 2013–2014. Under *Striga* infestation, yield ranged from 2096 kg ha^{-1} for first-generation cultivars to 2292 kg ha^{-1} for third-generation cultivars with a relative gain of 2.56% per year. Under *Striga*-free conditions, yield gain ranged from 2939 kg ha^{-1} for first-generation cultivars to 3549 kg ha^{-1} for third-generation cultivars with genetic gain of 1.3%. The average increase in yield was 42 and 54 kg ha^{-1} year^{-1} under *Striga*-infested and *Striga*-free conditions. Genetic gains in yield from first- to third-generation cultivars under *Striga* infestation were associated with decrease in anthesis and silking intervals (ASI), reduced number of emerged *Striga* plants and *Striga* damage at 8 and 10 weeks after planting, improved husk cover, and plant and ear aspects. Under *Striga*-free conditions, genetic gains in yield were associated with increase in plant and ear heights, improved husk cover, and plant and ear aspects. It was concluded that considerable improvement had been made in breeding for *Striga* resistance in WA.

10.17 Conclusion

Striga thrives well under low soil fertility conditions, especially low N. Screening and breeding for tolerance/resistance is done at 30 kg N ha^{-1}. The most effective artificial infestation technique involves putting about 5000 germinable *Striga* seeds per hill in holes of about 5 cm depth and 8 cm diameter followed immediately by planting maize into the holes. This procedure eliminates the chances of escape plants that frequently occur under natural infestation. Before dropping the *Striga* seeds into the holes, they are mixed with fine sand in a ratio of 1:99 *Striga* seed/sand. The sand serves as the carrier material and provides adequate volume for rapid and uniform infestation. About 2 weeks before artificial *Striga* infestation and planting of maize, ethylene gas is injected into the soil to stimulate suicidal germination of existing *Striga* seeds in the soil at the sites. *Striga* damage rating and number of *Striga* plants per maize plant are used for selection, and scoring is done at 8 and 10 weeks after planting. These traits are generally under polygenic inheritance with heritability on progeny mean basis ranging from low to moderate values for most measured traits. However, moderate-to-large additive genetic variances and wide ranges in mean values were observed for most traits, indicating the availability of adequate genetic variability in both early and extra-early populations to facilitate further significant progress from selection. Varieties and hybrids with tolerance/resistance to *Striga* and several other biotic and abiotic stresses have been developed and released to farmers of WCA.

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Chapter 11
Breeding Maize for Drought Tolerance

11.1 General Considerations

Drought has been a recurring feature in SSA. Climatic change resulting from global warming has been found to further increase the probability of drought even in the forest agroecology of WCA. Yield loss due to drought in maize is about 15% annually in West and Central Africa (WCA). In marginal areas where annual rainfall is below 500 mm or where soils are sandy or characterized by shallow topsoil, drought effect on maize production is much higher. In East and Southern Africa, drought leads to production losses of about 17%, equivalent to US$280 million (Diallo et al. 2004). Drought may lead to complete crop failure, reduced establishment, or reduced yield if it occurs at the seedling or flowering or grain-filling stages. Drought often leads to poverty and famine and prevents farmers from adopting improved management practices because of capital constraints and risks. One way to boost maize production and productivity in SSA is, therefore, to develop drought-tolerant varieties for the farmers. Drought stress-tolerant maize varieties offer a means of stabilizing yields at no additional cost to the farmer (Edmeades et al. 1997).

In 31–36% of the areas classified as arid and semiarid worldwide, moisture is considered a limiting factor for crop production. In the remaining 64–69% of the areas, temporary drought can occur at any time during the growing season (Shaw 1977). In addition to erratic rainfall distribution, moisture stress in SSA is aggravated in soils with low water-holding capacity and soils with plow pans that reduce rooting depth (hard pans). The level of grain-yield reduction in maize as a result of drought depends on the stage of crop development at the time of the stress and its severity (Table 11.1). The flowering period in maize is the most sensitive to drought.

Drought exerts its effects on yield through physiological processes and losses in plant stand when such stress occurs during emergence and at the seedling stage. Moisture deficit induces stomatal closure and inhibits transpiration in response to increased abscisic acid production. In contrast, drought inhibits the synthesis of

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Table 11.1 Percentage reduction in maize grain yield as a result of drought (Bänziger et al. 2000)

Stage of crop development	Yield reduction (%)
Grain filling	21
Flowering	50
Few days before tassel emergence to the beginning of grain filling	90
One to two days at the time of tasseling or pollination	22

Plate 11.1 Spotty seed set in maize as a result of drought

cytokinins and gibberellins in the roots, resulting in a reduction of overall plant growth (stunting). Continued moisture stress damages protoplasmic microstructures and plasmids. Drought inhibits net CO_2 uptake by the leaf as well as CO_2 assimilation rate, both of which result in reduced net photosynthesis. It also reduces the rate of translocation of photosynthates into the grain. Drought inhibits cell growth which can affect leaf area development during and after the stress period. The damage caused by drought to tissue and tissue components can be irreversible as exemplified by early leaf senescence during grain filling.

Drought stress affects silking much more than pollen shed; it reduces the silk elongation rate, resulting in delayed silking. In addition to the delay in time taken to silk, there is ovule abortion—a consequence of the limited assimilate translocation to the developing ear. The results of such drought stress include spotty seed set (Plate 11.1), nosing back, and complete barrenness.

11.2 Mechanisms Used by Plants to Cope with Drought

Breeding for resistance to drought is one of the strategies for stabilizing maize yields in rainfed agricultural systems. Resistance to drought manifests through one or a combination of the following mechanisms: drought escape, drought avoidance, and drought tolerance. Drought escape relates to the ability of plants to complete their life cycle before the occurrence of moisture deficit, especially that which occurs towards the end of the growing season. One drought escape mechanism is manifested as early maturity. Drought avoidance refers to the ability of plants to endure drought by maintaining high tissue water potential under conditions of moisture deficit, while drought tolerance is the ability of plants to sustain little or no reduction in physiological metabolic activities under conditions of moisture deficit in comparison to high reduction in physiological metabolic activities suffered by drought-susceptible genotypes.

11.3 Gene Action Conditioning Drought Tolerance

Information on the genetic basis of genotypes' performance under drought stress is crucial for designing appropriate breeding strategies for fruitfully exploiting these assets in the breeding programs in WCA. Reports on the gene action conditioning grain yield of tropical maize under drought stress are limited and contradictory. Guei and Wassom (1992) found in two maize populations that there was greater dominance deviation for grain yield and ears per plant (EPP) even though additive genetic variance was more important than dominance variance in the expression of flowering traits. In contrast, Badu-Apraku et al. (2004) reported moderate-to-large additive genetic variance and narrow-sense heritability estimates for grain yield and other traits of full-sib families derived from the early-maturing population, Pool 16 DT, after eight cycles of recurrent selection for improved grain yield under drought stress. They indicated, however, that dominance variance was also large and should be considered during further selection. Similar results were reported by Meseka et al. (2007) who found that both GCA and SCA effects were significant for 24 late-maturing tropical maize inbred lines, with GCA accounting for >50% of total variation for all traits under drought stress. Oyekunle and Badu-Apraku (2012) also found that GCA accounted for 64.5% and 62.3% of total genetic variation for grain yield under drought stress and well-watered conditions, respectively. Betrán et al. (2003a) produced hybrids among 17 lowland white-grained tropical maize inbred lines and evaluated the hybrids and the parental lines under optimal, drought, and low-N stress conditions to determine, among other objectives, the genetic control and modes of gene action for grain yield. The differences in grain yield between hybrids and inbreds (i.e., heterosis) increased with the intensity of drought stress. Grain yield was under additive gene action, and its importance increased with intensity of drought stress. The present level of knowledge, therefore, indicates that both additive and nonadditive gene actions condition the expression of maize traits under drought stress, but additive effects are more important than the nonadditive component. Therefore, drought tolerance in maize can be improved by recurrent selection, and drought-tolerant inbred lines with good combining ability can be extracted from each improved cycle of selection for hybrid development.

11.4 Screening for Drought Tolerance

11.4.1 Screening Germplasm Under Naturally Occurring Drought

Some locations are more prone to drought than others. Such locations can be exploited for screening for ability to withstand drought. The occurrence of such natural drought presents an opportunity to assess the reactions of different genotypes to moisture deficit. Screening under natural drought stress has the limitations of nonuniformity of drought stress in the field and lack of control over timing as well as the severity of drought stress. Therefore, high-yielding genotypes selected under such conditions are further tested in several dry-land locations or under induced drought to confirm performance.

Relating performance under managed drought stress environments with that in the naturally occurring sporadic or terminal drought stress is a challenge for maize breeders. Studies have been conducted to enlighten the breeders as to how to proceed in executing breeding programs for drought tolerance, and some results have been presented in Chap. 2 of this book. The studies have, in addition, been used to identify traits under managed stress that effectively predicted grain yield under non-stressed conditions (Fig. 11.1).

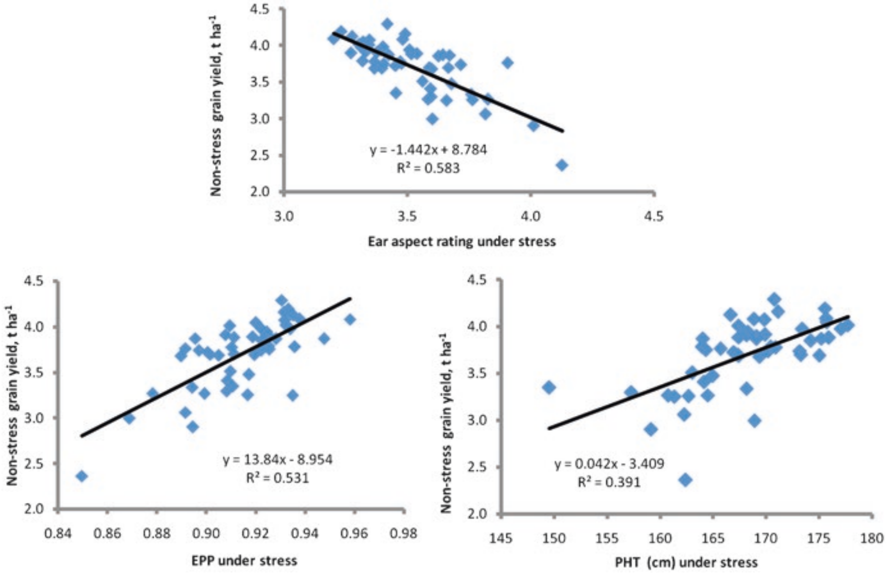

Fig. 11.1 Predicted grain yield under non-stressed environments as a function of performance of EASP, EPP, and PHT under stress environments for 50 early-maturing maize cultivars

11.4.2 Screening Germplasm Under Controlled Drought Stress

Screening for reaction to drought can also be carried out during the dry season at a site with irrigation facilities. Different genes are probably responsible for ability to withstand drought stress at various stages of maize growth and development. Irrigation water is usually withdrawn at the stage of interest to assess the level of genetic variation to moisture deficit. Breeding success is moderate to high for moisture stress induced during flowering and or grain filling. To simulate moisture stress at flowering, irrigation is withdrawn at this time, although irrigation water is provided at about 18 days after pollen shed to prevent complete yield loss. An alternative method adopted in the IITA Maize Program is to irrigate the maize plants up to 21, 25, and 28 days after planting for the extra-early, early-, and intermediate-maturing genotypes, respectively. Thereafter, irrigation water is withdrawn for the rest of the growth cycle. Effective screening for drought tolerance depends not only on removal of source of water supply but also on the aridity of the site and the soil type, texture, and depth. The topsoil of the managed drought site at Ikenne is shallow, and the screening is done during the dry season when the drought probability is highest, the relative humidity is lowest, and the harmattan is most severe during the year. The situation is even more severe at Kadawa in the Sudan savanna where natural terminal drought occurs.

11.4.3 Important Considerations in Field Screening for Drought Tolerance

1. It is important to have a leveled (non-sloping) field. This will prevent slope-induced moisture stress differences in the field and ensure greater uniformity of the stress on genotypes being screened.
2. The field should be divided into blocks and care taken to ensure the prevention of border effects.
3. The laying of pipes and sprinklers is done in such a way as to ensure uniformity of irrigation water and, in effect, drought.
4. It is useful to group the germplasm being screened on the basis of maturity so that irrigation water regime is timed to similar growth stage for all genotypes being screened.
5. Each block is irrigated to field capacity whenever irrigation is desired.
6. The pipes, sprinklers, and sprinkler heads must be kept clean as well as deliver uniform amount of water as desired by the breeder. Drip irrigation systems are particularly useful for this purpose, although they are presently not available in most parts of SSA, perhaps because of the prohibitive cost. The system is more precise and a good means to conserve irrigation water supply.
7. An appropriate experimental design must be employed for replicated experiments. For augmented designs (unreplicated experiments), it is important to have

checks planted in a systematic manner in each block. Some other designs are possible, such as alpha (0,1) lattices, depending on the number of entries being screened by the researcher.

The most useful germplasm are those with high level of tolerance to drought at different stages of growth and for which the tolerance is stable across environments. Screening should include elite and adapted genotypes, landraces—especially those grown in drought-prone environments—and introduced (possibly unadapted) genotypes with proven performance under drought. Genes for tolerance to drought in the latter are incorporated into adapted germplasm.

The choice of a breeding procedure for tolerance to drought depends on the type of products desired (OPVs or hybrids) and the human resources, budget, and infrastructure available. Consequently, various breeding methods such as recurrent selection, pedigree, and backcross breeding methods can be used. Inbreeding provides the opportunity to fix alleles for drought tolerance in inbred lines used as parents of hybrids. Although most farmers grow OPVs in WCA, hybrids, being more input and water-use efficient, are likely to be more productive under drought conditions. Therefore, hybrids are now being actively researched and promoted in the region.

Agronomic traits have been investigated for their relationships with drought tolerance. The correlation ranges from low for "stay-green" score, tassel size, leaf rolling score, and lodging to high for ASI, ears per plant, kernel weight, and kernels per ear (Table 11.2). Based on the high heritability of ASI and number of ears per plant and the high correlation of these traits with grain yield under drought, the traits have been used as secondary selection traits in drought tolerance breeding.

Table 11.2 Heritability for agronomic traits and correlation with yield under drought

Traits	Heritability under drought	Correlation with yield
Anthesis–silking interval	High	High
Stay-green score	Moderate	Low
Ears per plant	High	High
Tassel size	High	Low
Leaf rolling scores	Moderate	Low
Kernel weight	Moderate–high	Low
Kernels per ear	Moderate–high	High
Lodging	Moderate–high	Low
Rate of leaf elongation	Moderate–high	Low
Leaf chlorophyll content	Moderate–high	Low
Leaf erectness scores	High	Low
Osmotic adjustment	Moderate	Low
Canopy temperature	Low	Low

Source: Adapted from Bänziger et al. (2000)

11.5 Enhancing Drought Tolerance in Early and Extra-Early Maize Germplasm for West and Central Africa

The IITA-SAFGRAD Project initiated a research program in 1979 with the objective of developing drought-tolerant maize varieties and hybrids for the semiarid zones of WCA (Badu-Apraku et al. 1997). An important challenge was the development of an efficacious field methodology to be used in screening genetic materials for drought tolerance. Two approaches have been adopted for breeding for drought tolerance in the IITA Maize Program. The first method, which is presently being used in our breeding programs, involves growing the crop under irrigation during the dry season and imposing drought by withdrawing irrigation water from about 2 weeks before anthesis till the end of the season. Maize breeders in CIMMYT (Edmeades et al. 1995) and IITA (Menkir and Akintunde 2001) have found this method to be effective in Mexico and the rainforest agroecology of Southern Nigeria, respectively.

There has been some concern, however, that because of shallow topsoils with low organic matter content and poor soil moisture-holding capacity as well as high temperatures (≥45°C) and low relative humidity during the dry season, the method may be too severe on maize in the savanna soils of WCA. This could lead to limited progress from selection**.** Results from a study conducted in the savanna agroecology of Côte d'Ivoire using this procedure provided some evidence that justified this concern. For the study, full-sib families derived from Pool 16 DT, a tropical maize population, were evaluated in the 1995/1996 and 1997/1998 dry seasons, at two sites each season in Côte d'Ivoire (Badu-Apraku et al. 2004). In all sites, the crop was irrigated from planting to about 2 weeks before anthesis; irrigation was discontinued thereafter for the rest of the season in one site in 1995 and both sites in 1997. Irrigation was continued till maturity in the second site in 1995. The objective was to evaluate the efficacy of withdrawing irrigation water from about 2 weeks before anthesis till the end of the season as a method for screening maize for drought tolerance in the savanna ecology of WCA. Because the season was naturally dry and the probability of rain was very low, the method was flexible enough for the researcher to impose drought at any stage and for any length of time during the growth cycle of the crop. This is a merit of the method. Unfortunately, while the method has been effective in the forest agroecology of Nigeria and in Mexico where the soils have high water-holding capacity and the atmosphere is more humid, the method has several demerits in the savanna. The demerits probably arise because of the inherently poor organic matter content and low water-holding capacity of the soils coupled with the intense dry heat stress conditions in the savanna ecology. The results indicated that the stress was too severe on the maize progenies evaluated. Apart from the cumulative effect of moisture stress, the plants were subjected to the high temperatures and low relative humidity that normally characterize the savanna agroecology during the dry season. This resulted in tassel blasting for many of the progenies thus making the plant falsely protogynous. Such progenies exhibited large negative ASI, poor pollination/fertilization, and low yield resulting in an unexpected positive correlation between grain yield and ASI. Although maize normally starts shedding pollen before incipient silk extrusion, it is not unusual for the reverse to occur, especially under irrigation. However, the method studied aggravated the situation. Negative ASI occurred in both stressed and non-stressed sites but, whereas the negative ASI values were about 0.5–1.0 days for the non-stressed sites, they were mostly 2.0–3.5 days for the stressed site. In addition, the coefficients of variation (CVs) associated with the stressed environment are usually higher and the coefficients of determination (R^2) lower than those associated with the non-stressed environments. As a derived trait, ASI normally tends to have much larger CVs than the primary traits from which it is derived (anthesis and silking dates). But in this study, the CVs were extremely large thereby indicating that the screening method used in the study grossly masked the true expression of the genetic differences among the full-sib families. Results of the study contradicted those of earlier studies that found ASI as a useful secondary trait for drought tolerance in maize (Edmeades et al. 1995; Menkir and Akintunde 2001; Kamara et al. 2003). Badu-Apraku et al. (2004), therefore, concluded that the screening methodology may need to be modified if ASI is to be used as an effective secondary selection criterion for drought tolerance under the conditions of the savanna agroecology during the dry season. The results also led to the conclusion that for some traits a severe stress may be appropriate, while for traits such as grain yield, a more moderate stress level is needed. The stress level chosen for drought screening should, therefore, be the one that best exposes the genetic variation for the trait of interest. The breeder must, necessarily, experiment with the stress level that is appropriate for his germplasm and trait of interest and fine-tune crop management practices before launching into a major breeding program for drought tolerance.

Despite the demerits of the methodology, several practical implications emerged from the results. The stressed and non-stressed environments affected the full-sib families differently; that is, the much expected G × E interaction was clearly demonstrated in the study. This makes it possible to identify families that may be truly drought tolerant and should therefore be possible to obtain families that would be high yielding under terminal drought stress. Also, a variety formed from families selected in the non-stressed environment or populations produced by intercrossing the selected families were not likely to be high yielding if grown under the conditions of the stressed environment used in the study. It was therefore proposed that, for further selections, the stress conditions would have to be relaxed somewhat for several reasons. First, although WCA farmers grow maize during the dry season, the plants are not subjected to the type of induced stress evaluated in the study. In much of the savanna of WCA, availability of early and extra-early varieties (Badu-Apraku et al. 1997) has ushered in the growing of maize in hydromorphic soils supplemented with some type of irrigation, such as furrow irrigation with tied ridges and sprinkler system. There is a need to improve the drought tolerance level of the early and extra-early varieties to take maximum advantage of the dry season cropping situation. The crop is consumed as green maize to fill the hunger gap in July before the crop of the main rainy season is ready for harvest. The maize crops grown under these conditions have better access to soil moisture than those subjected to the induced stress in the study. Second, during the normal growing season, farmers are not likely to encounter drought from about 2 weeks before anthesis to the end of the season. Rather, rainfall under natural conditions may become sporadic during grain filling, and/or terminal drought may occur towards the end of the season at which time grain filling would be nearly completed. Third, a scenario of moisture stress, high temperature (heat stress), and low relative humidity leading to tassel blasting, false protogyny, negative ASI, and poor fertilization rarely occurs during the normal growing season.

The problems associated with the drought screening methodology have been observed in several other locations within the savanna agroecology of WCA including Vallée de Kou in Burkina Faso, Kaolack in Senegal, and Konni and Maradi in Niger (J. Sanou, A. Ndiaye, A. Diallo, and A. Menkir; N. Laouli, personal communications). Therefore, in order to alleviate the severity of the stressed conditions and make them closer to the normal growing conditions, irrigation could be applied once in 10 days during the period of imposed drought. An alternative and probably a more reliable method would be to irrigate whenever the maize plants start showing signs of temporary wilting such as leaf rolling early in the day, such as soon after sunrise. Leaf rolling that early will remain in that position for the rest of the day because of increased temperature and lower relative humidity as the day progresses. It is desirable to conduct further studies comparing the alternative methods of imposing drought in the WCA savanna ecology in order to identify the most effective screening method.

Bolanôs and Edmeades (1996) proposed that average yield under low N and/or drought should be 20–30% of the expected average yield in the same location under optimal management, while Bänziger et al. (2000) proposed a much more severe stress that would result in the grain yield from stressed blocks to about 15–20% of well-watered yields. Studies conducted in Niger by Laouli (unpublished 2014) demonstrated that such a level of yield reduction could not be achieved due to the harsh climatic conditions in the country. Results showed that because of the low water-holding capacity of the soils in the region of Maradi and Konni where the studies were conducted and the low relative humidity as well as the frequent windy weather conditions, most of the plants in the stressed blocks would not survive if such a yield reduction was targeted. The study showed that a moderate yield reduction of about 30–40% of the well-watered yield was more appropriate in drought experiments in Niger. It was concluded that this could be achieved by stopping the irrigation 2–3 weeks before anthesis and, thereafter, applying a rescue irrigation, 13–15 days after imposing the drought stress and resuming the irrigation 10–12 days later. This method is similar to the approach adopted by Badu-Apraku et al. (2004) in the experiment at Soumis and Ferkessédougou in Côte d'Ivoire in which the irrigation was stopped 2 weeks before flowering until maturity. The authors pointed out that the stress intensity was too severe and suggested that for such trials a "rescue irrigation" should be applied once every 10 days during the period of imposed drought or when the maize plants started showing signs of temporary wilting early in the day.

11.6 Strategies for Breeding for Drought Tolerance

The main strategy adopted for breeding for drought tolerance in the IITA Maize Program is to introgress into the intermediate, early, and extra-early cultivars genes for drought tolerance to enable them to withstand mid-season drought when it occurs during the flowering and grain-filling periods. During the past decade, the IITA Maize Program has used the S_1 recurrent selection method, improved artificial field infestation with *S. hermonthica*, and screening under drought as strategies to develop two early-maturing source populations—TZE-W Pop DT STR (white) and TZE-Y Pop DT STR (yellow)—and several early-maturing cultivars and inbred lines, which combine tolerance to drought with moderate levels of resistance to *S. hermonthica* and MSV. The extra-early populations from which the inbred lines and cultivars were developed came from crosses among local (landraces), exotic, and introduced germplasm identified through extensive multilocation trials in WCA (Badu-Apraku et al. 2001, 2007). These materials were selected on the basis of high grain yield, earliness, and resistance to the maize streak virus and above all adaptation to the heat and drought stresses characteristic of the Sudan savannas in Burkina Faso, Mali, Mauritania, Ghana, and Nigeria during both the rainy and dry seasons. The hypothesis was that, after several years of cultivation in these environments, the extra-early germplasm should have adaptive traits for tolerance to these stresses where they had survived. It was observed that some of the extra-early inbred lines in the IITA Maize Program would not only escape drought stress but also seemed to possess drought tolerance genes. The inbreds should therefore be able to withstand the drought that occurs during the flowering and grain-filling periods in the savannas of WCA as have been found in early-, intermediate-, and late-maturing cultivars. The breeding methodology employed for the development of the *Striga*-resistant and drought-tolerant populations and cultivars in the IITA Maize Program has been described in detail by Badu-Apraku et al. (2007, 2008a, b, 2009). There is a tremendous opportunity for improving the overall performance and suitability of the available varieties in the program by incorporating higher levels of tolerance to drought and *Striga*. Several alleles govern the expression of drought tolerance in maize. Therefore, a major strategy of the IITA Maize Program under the Drought-Tolerant Maize for Africa (DTMA) Project is to screen maize inbred lines with tolerance to drought from diverse sources under induced drought stress at Ikenne (6°87′N, 3°7′E, 60 m altitude, 1500 mm annual rainfall). The induced drought stress at Ikenne was obtained by withdrawing irrigation water from 21 days after planting (DAP) until maturity so that the maize plants relied on stored water in the soil for growth and development. During the first 3 weeks of growth, the plants were irrigated using a sprinkler irrigation system which provided 17 mm of water per week. The soil in the experiment station at Ikenne is eutric nitrosol (FAO classification), and the experimental fields at the station are flat and fairly uniform, with high water-holding capacity. In this case, flowering and grain filling occurred under the managed drought stress with symptoms of stress appearing after 25–30 days of induced drought stress. In the well-watered experiment at Ikenne, the plants were irrigated throughout the growth period using the same sprinkler irrigation system. The trials were planted in two adjacent blocks in the same field that received the different irrigation treatments. Two ridges each 5 m wide planted to an early-maturing maize cultivar separated the irrigated block from the adjacent nonirrigated block to minimize lateral movement of irrigation water from the well-watered to the drought stress block. The evaluations of the genotypes during the growing seasons under well-watered (rainfed) conditions at Mokwa and Zaria (high-yield non-stress environment; 11°11′N, 7°38′E, 640 m altitude, 1200 mm annual rainfall) in Nigeria were carried out to determine their yield potential. At Zaria, the plants depended on natural rainfall. At Bagauda (drought-prone environment; 12°00′N, 8°22′E, 580 m altitude, 800 mm annual rainfall), the plants were subjected to natural terminal drought stress. All management practices were similar for both well-watered and drought stress studies. Fertilizer was applied to the well-watered and drought stress plots at the rate of 60 kg ha^{-1} each of N, P, and K at planting. An additional 60 kg ha^{-1} N was topdressed at 2 WAP. The trials were kept weed-free with the application of atrazine and Gramoxone as pre- and postemergence herbicides at 5 L/ha each of Primextra and paraquat and, subsequently, by hand weeding as needed.

The promising drought-tolerant inbred lines identified in the studies were also screened for *Striga* resistance under artificial infestation at Mokwa (9°18′N, 5°4′E, 457 m altitude, 1100 mm annual rainfall) and Abuja (9°16′N, 7°20′E, 300 m altitude, and 1500 mm annual rainfall), both of which are located in the *Striga* endemic southern Guinea savanna (SGS) agroecological zone of Nigeria. In our program, our strategy is to screen the inbred lines per se for drought tolerance rather than topcross hybrids of those same lines on a common tester because we are interested in the reactions of the lines per se to drought. We then use a base index that combines superior grain yield under drought with low value, that is, desirable trait expression, for plant aspect, ear aspect, and leaf senescence, short ASI, and increased number of ears per plant to select top performers (Oyekunle and Badu-Apraku 2012). To minimize the effect of different scales, each parameter is standardized with a mean of 0 and standard deviation of 1. Hence, a positive value is considered an indicator of tolerance to drought while a negative value signified susceptibility to drought. Details are presented in Chaps. 16 and 18 in this book.

The selected drought-tolerant and *Striga*-resistant inbreds were then evaluated in hybrid combinations for tolerance to drought as well as adaptive traits in selected screening sites including Ikenne and Bagauda and under well-watered conditions (rainfed) at Ikenne, Mokwa, and Zaria. These inbred lines serve as parents for developing three-way, double-cross, and topcross hybrids. The selected drought-tolerant and/or *Striga*-resistant inbreds have also been used as sources of tolerance genes for introgression into early and extra-early breeding populations undergoing S_1 family recurrent selection for improvement in grain yield and *Striga* resistance in our program. Further improvement of the early populations under controlled drought stress using recurrent selection has facilitated the development of new productive varieties and hybrids that combine enhanced levels of drought tolerance with good levels of resistance to *Striga*. Drought-tolerant and *Striga*-resistant open-pollinated varieties and hybrids identified in the program are extensively evaluated in regional and farmer participatory on-farm trials using the mother–baby approach at several contrasting environments in WCA in collaboration with national maize programs and then released for production by farmers.

11.7 Performance of Early and Extra-Early Germplasm Developed and Evaluated Under Drought Stress

Many studies have been conducted to monitor the progress in breeding early and extra-early maize germplasm for drought tolerance in WCA. One of the earliest drought tolerance trials of the early-maturing cultivars derived from Pool 16 DT was conducted at five environments in 1995 with 16 DT varieties and two susceptible checks (Badu-Apraku et al. 1997). The environments included Sinématiali, Côte d'Ivoire (9°37′N, 305 masl, with 517 mm rainfall, which was below annual average); Ferkessédougou, Côte d'Ivoire (9°35′N, 325 masl, with a below-average rainfall of 594 mm); and Kamboinse, Burkina Faso (12°28′N, 296 masl, with a slightly below-average rainfall of 491 mm). The fourth and fifth trials were planted in the dry season of 1995–1996 (November–March) at Ferkessédougou. The fourth was the control, which was irrigated throughout the season, while the fifth was irrigated from planting till about 2 weeks before flowering when irrigation was withdrawn for the rest of the season. Varieties derived from cycles 0, 1, 2, 4, and 8 of the full-sib recurrent selection program were among the drought-tolerant entries, thereby providing an opportunity to evaluate the progress from selection for drought tolerance in the population. Mean grain yield under induced stress was 1.2 t/ha with a range of 0.9–1.6 t/ha ($LSD_{0.05}$ = 0.48), whereas under non-stress conditions, the mean was 5.6 t/ha with a range of 5.0–6.4 t/ha ($LSD_{0.05}$ = 0.52). Under drought stress, two of the 16 DT varieties, DRT-E-Y with 1.6 t/ha and FBA 88 Pool 16 DT (HD) with 1.5 t/ha, were significantly higher yielding than the other varieties. Under non-stress conditions, however, several DT varieties yielded equally with or better than the check varieties, which are normally high yielding under non-stress conditions. Similarly under well-watered conditions, DT materials from the advanced cycles were superior to selections made in the earlier cycles. Under drought conditions, however, earlier selection cycles were about equal in yield performance with most of the later cycle selections, and this resulted in a gain of only about 2% $cycle^{-1}$. On the contrary, gains were about 10% and 5% $cycle^{-1}$ when the selections were evaluated under non-stress and combined environments, respectively. The somewhat low progress from selection was attributed to the rather "crude" and variable methods of imposing drought, such as the non-tied versus tied ridge in some cases and low versus high plant density in some others. That notwithstanding, several high-yielding drought-tolerant cultivars from the different cycles of the selection program were released to farmers in different member countries of the SAFGRAD Project (Badu-Apraku et al. 1997).

Development of early and extra-early maturing maize cultivars in WCA has been in place from 1988 to date. This period may be divided into three eras based on the base populations for improvement, the stress factors emphasized, and the methods used for the programs. The three eras corresponded to the SAFGRAD, WECAMAN, and DTMA breeding eras, respectively. A total of 50 early cultivars were developed during the 22-year period from 1988 to 2000: 15 during era 1 (1988–2000), 16 during era 2 (2001–2006), and 19 during era 3 (2007–2010). The cultivars were evaluated at 13 locations in West Africa for 2 years to determine genetic gains in yield under induced drought stress and well-watered (sprinkler irrigation) conditions during the 2010–2011 and 2011–2012 dry seasons at Ikenne, Nigeria. The cultivars were also evaluated during the growing seasons of 2010 and 2011 under natural rainfed conditions at Ikenne, Mokwa, Bagauda, Saminaka, Ile-Ife, and Zaria in Nigeria; Yendi, Nyankpala, Ejura, and Fumesua in Ghana; and Angaredebou and Ina in the Republic of Benin to determine their yield potential.

Under drought, yield ranged from 1346 kg ha^{-1} for era 1 cultivars to 1613 kg ha^{-1} for era 3 cultivars with a genetic gain of 1.1% year^{-1}. Under optimal conditions, yield gain ranged from 3363 kg ha^{-1} to 3956 kg ha^{-1} for eras 1 and 3, respectively, with genetic gain of 1.3%. The average rate of increase in yield was 14 and 40 kg ha^{-1} year^{-1} under drought and optimal conditions. Under drought stress, genetic gains in yield were associated with improved plant aspect, ear aspect, and, to a limited extent, ear number per plant (Table 11.3). Under optimal conditions, it was associated with plant and ear aspects, increased ears per plant, plant and ear heights, and improved husk cover. Although the correlation coefficients (r) with yield under drought and optimal conditions were statistically significant, the coefficients of determination (r^2 values) were too small to be of much practical value in breeding. However, r^2 values for plant and ear aspects under drought stress and ear aspect

Table 11.3 Correlation coefficients of grain yield with other agronomic traits of 50 maize cultivars from 3 breeding eras evaluated under drought stress and optimal growing conditions at 28 environments in Nigeria, Ghana, and Benin Republic between 2010 and 2012

	Correlation coefficient with grain yield under	
Trait	Induced drought	Optimal conditions
Days to anthesis	−0.23**	0.32**
Days to silk	−0.43**	0.29**
Anthesis–silking interval (ASI)	−0.07	−0.21**
Plant height, cm	0.34**	0.40**
Ear height, cm	0.24**	0.27**
Husk cover	−0.14*	−0.07
Plant aspect	−0.63**	−0.22**
Ear aspect	−0.61**	−0.37**
Ears plant^{-1}	0.25**	0.57**
Stay-green characteristic	−0.35**	na[a]

*Significant at 0.05 probability level; **significant at 0.01 probability level

[a] *na* not assayed

under optimal conditions were particularly striking ($r^2 \geq 0.6$). Cultivars TZE-W DT C2 STR, DTE-W STR Syn C1, DT-W STR Synthetic, 2009 DTE-W STR Syn, and EV DT-W 2008 STR were high yielding and stable across drought environments. It was concluded that substantial progress had been made in breeding for drought tolerance during the last three decades.

Oyekunle and Badu-Apraku (2012) produced 150 hybrids from 30 early inbred lines selected based on their reaction to moisture stress under managed drought. The inbred lines were divided into six sets of five lines each, and the sets were crossed in a NCD II scheme (Comstock and Robinson 1948). The five lines in one set were used as females and crossed with the five inbred lines in another set as males. Each inbred line was used as male parent in only one set and as female parent in another set (Ifie et al. 2014). The hybrids plus six checks were evaluated under managed drought at Ikenne during the 2008/2009 and 2009/2010 dry season, at Ikenne and Bagauda during the normal growing season of 2008 and 2009, and at Zaria during the growing season of 2009. The objectives were to determine gene action controlling grain yield under stress and non-stress conditions, predict hybrid performance from the performance of the inbred parents, and identify testers for early maize breeding programs. Overall, managed drought reduced grain yield by 48% (with a range of 59–84%) for the drought-susceptible inbred lines and only by about 4–44% for drought-tolerant inbred lines. Similarly, drought reduced hybrid yield by 61% on average, ranging from 39% to 55% for the best 20 hybrids and 65–81% for the worst 10 hybrids. Only 4 of the 30 inbred lines had statistically significant GCA effects for grain yield under drought, unlike under well-watered conditions where 17 lines had significant GCA effects as male and/or female parent. Two lines, TZEI 157 and TZEI 187, consistently had negative GCA in all environments, while the GCA for TZEI 31 was consistently positive. Narrow-sense heritability for grain yield ($h^2 = 67 \pm 3.0\%$) was significantly higher under drought than under well-watered conditions ($h^2 = 49 \pm 7.0\%$). This trend also occurred for EPP, anthesis, ASI, stalk lodging, plant aspect, and ear aspect. In contrast, h^2 for silking, plant and ear heights, and husk cover were higher under well-watered than drought environments. Correlation coefficients (r-value) between inbred parents and their hybrid were statistically significant for nearly all traits under all environments and, in most cases, were slightly higher under well-watered than drought environments. Apart from the stay-green characteristic ($r = 0.64$), the significant r-values under drought ranged between 0.20 and 0.34, a clear indication that the performance of the hybrids was poorly predicted by that of their inbred parents—only about 4–12% predictability under drought stress in this study. That notwithstanding, Oyekunle and Badu-Apraku successfully identified four inbreds—TZEI 31, TZEI 17, TZEI 129, and TZEI 157—as the best testers in the study.

In a complementary study, Oyekunle et al. (2015) used 23 microsatellite markers to assess the genetic diversity of a set of inbreds, along with the 150 hybrids and the 30 inbred lines from which they were generated. The materials were evaluated at three locations in Nigeria for 2 years to assess their performance under drought and well-watered conditions. Significant differences were observed among inbreds and hybrids for most traits under both research conditions. A total of 130 alleles were detected ranging from two for nc133 to nine for phi299852 with an average of 5.7 alleles per locus. Polymorphic information content ranged from 0.17 for phi308707 to 0.77 for phi084, with an average of 0.54. Thirty-one unique alleles were detected in 21 inbreds. Microsatellite markers classified the inbred lines into five groups. Genetic distance estimates among pairs of inbreds ranged from 0.42 (TZEI 26 vs TZEI 108) to 0.85 (TZEI 24 vs TZEI 4) with an average of 0.67. Correlation between microsatellite-based genetic distance estimates of the parental lines and their F_1 hybrids was not significant for grain yield and other traits under drought and well-watered conditions. However, significant correlations existed between F_1 hybrid grain yield and heterosis under drought and well-watered conditions. TZEI 31 × TZEI 18 was identified as the highest-yielding and most stable hybrid across environments.

In an earlier study, Badu-Apraku et al. (2011) examined the correlations between mid-parent values for agronomic traits under drought with the performance of their F_1 hybrid under drought and well-watered conditions. Regression analyses were also performed to assess the predictability of hybrid performance from performance of inbred per se under drought stress and well-watered environments, using mid-parent values of inbred per se traits as the independent variables and the corresponding hybrid yield as the dependent variable. Grain yield of inbred lines had significant correlation ($r = 0.29^*$) with F_1 hybrid yield performance under drought stress but not under well-watered environments ($r = 0.16$; Table 11.4). When evaluated under drought stress, mid-parental values for grain yield resulted in only modest prediction of hybrid grain yield; that is, 1 kg ha^{-1} increase in mid-parent grain yield resulted in only 0.317 kg ha^{-1} increase in hybrid grain yield under drought stress (Fig. 11.2). Mid-parent values for days to silk (DS) and ASI under drought stress had significant correlations ($r = -0.34^*$ and -0.45^{**}, respectively) with F_1 hybrid yield under well-watered environments (Table 11.4). Each additional day increase in mid-parent values of DS and ASI under drought stress reduced hybrid grain yield

Table 11.4 Correlation between inbred line per se performance and F_1 hybrid yield under drought stress and optimal conditions

Mid-parent value under drought stress	F_1 hybrid yield under drought	F_1 hybrid yield under optimal conditions
Days to anthesis	−0.05ns	−0.15ns
Days to silk	−0.15ns	−0.34*
Plant height, cm	0.18ns	0.04ns
Plant aspect	−0.03ns	0.06ns
Ears per plant	0.22ns	0.25ns
Ear aspect	−0.24ns	−0.16ns
Leaf senescence	0.17ns	0.15ns
Anthesis–silking interval, days	−0.25ns	−0.45**
Grain yield, kg ha^{-1}	0.29*	0.16ns
F_1 hybrid yield under drought	1.00	0.65**

*, **Significant at 0.05 and 0.01 level of probability, respectively

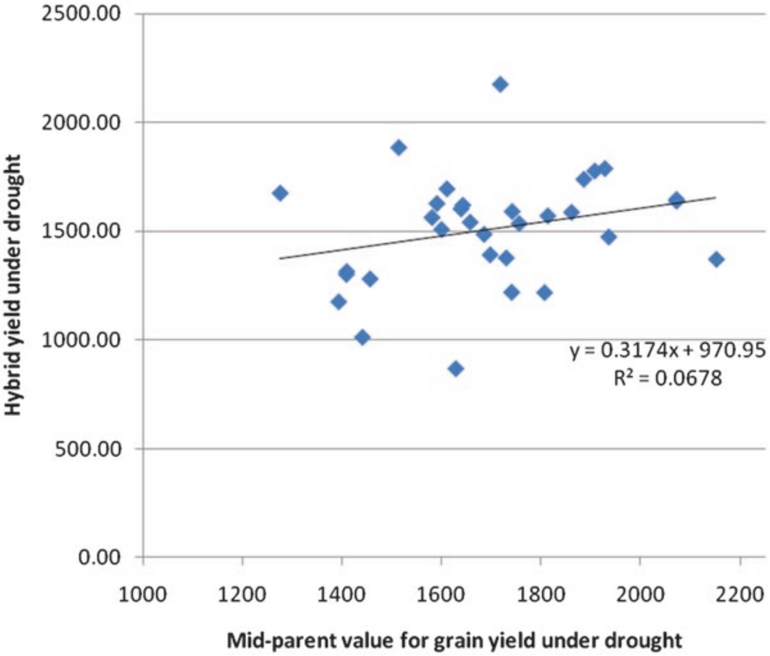

Fig. 11.2 Regression of hybrid grain yield on mid-parent grain yield under managed drought stress environments

in well-watered environments by 182 and 485 kg ha^{-1}, respectively (Fig.11.3). Inbred performance under well-watered environments had no significant correlation with hybrid yield performance either under well-watered or drought stress environments, but hybrid yield under drought had significant positive correlation with hybrid yield under well-watered conditions. Regression models showed that high-yielding hybrids under drought stress will be high yielding under well-watered environments (b-value = 1.32, r^2 = 42%; Fig. 11.4) but to a limited extent if vice versa. This suggested that hybrid yield under drought stress adequately predicted the performance of the hybrid under well-watered environments. The highly significant positive correlation of the inbred per se yield performance with F_1 hybrid yield performance under drought stress suggested the presence of additive gene action in the inbreds (Betrán et al. 2003b; Gethi and Smith 2004). The implication is that the inbred lines should transmit their yield potentials to their hybrids. However, caution should be exercised in the interpretation of this set of data since the r^2 value from the regression analysis is relatively small. Despite the positive correlations between the inbreds and hybrids in drought stress environments, field evaluation of the hybrids will still be necessary, especially because of the fact that inbred performance under well-watered environments had nonsignificant correlation with hybrid yield performance under well-watered or drought stress environments.

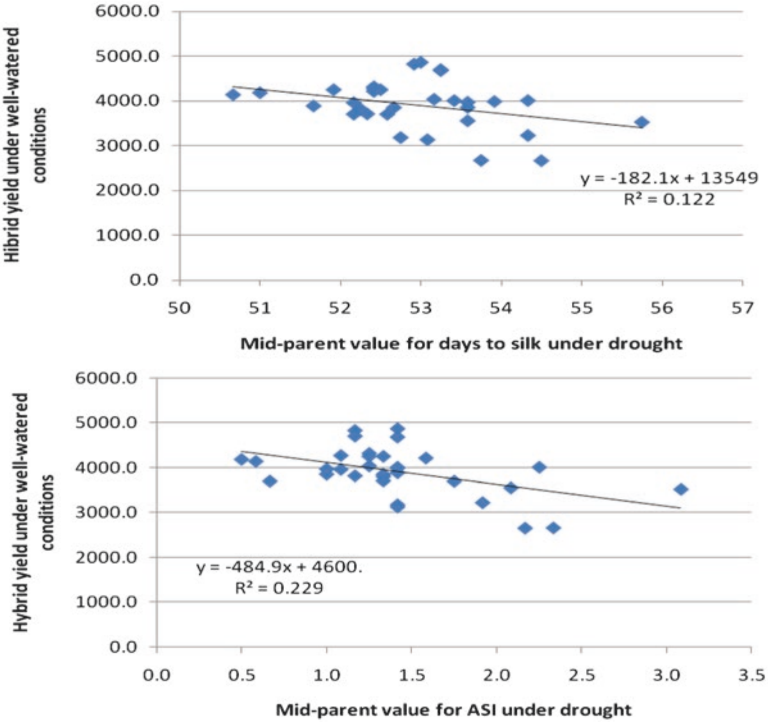

Fig. 11.3 Regression of hybrid grain yield under well-watered conditions on mid-parent values for days to silk (*top*) and anthesis–silking interval (*bottom*) under managed drought stress environments

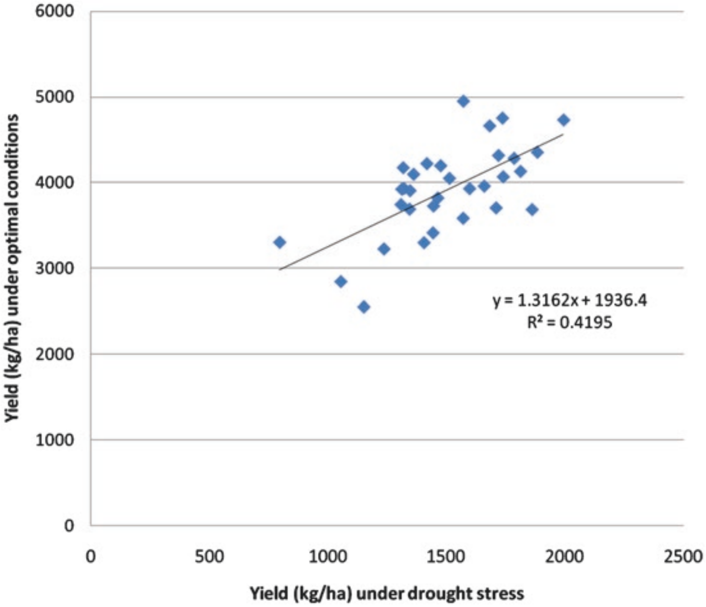

Fig. 11.4 Regression of hybrid yield performance under optimal conditions on yield performance under drought stress

The outcome of the efforts to genetically enhance maize for drought tolerance in WCA has led to several lessons to guide the breeder in future breeding efforts. The efforts have resulted in availability of drought-tolerant early and extra-early populations, open-pollinated varieties, inbred lines, and hybrids. The studies show clearly that materials in these two maturity groups are not only drought escaping by maturing before terminal drought sets in but are also genuinely drought tolerant and can withstand, to a reasonable extent, the occurrence of sporadic drought during the growing season. Using flowering as the index of maturity, there is wide genetic variability for days to anthesis and silking within each maturity group, and both traits are heritable and consistently demonstrate significant negative phenotypic and genetic correlation with grain yield. Therefore, earliness and extra-earliness are also under genetic control and do respond to selection and several other breeding methods. Referring to the response of these two maturity groups as drought escape seems misleading. In our view, a drought-escaping material is one that has an inherent mechanism to “sense” unfavorable environmental conditions and “speed up” its process of maturity with little or no reduction in yield performance relative to favorable conditions where there will be no need to speed up the maturity process. In our extensive studies, early and extra-early materials characteristically matured about the same time under stress and non-stress conditions. This is contrary to what occurs when late materials are planted in the late cropping season characterized by the occurrence of terminal drought. Under such conditions, the late material tends to speed up the completion of the growth cycle but with a trade-off in kernel weight due to poor or incomplete grain filling, leading ultimately to reduction in grain yield. The concept of drought escape in maize breeding needs further research.

11.8 Genetic Gains in Grain Yield of Early and Extra-Early Maturing Varieties Under Managed/Natural Drought Stress and Well-Watered or Optimal Growing (Rainfed/Overhead Irrigation) Environments

The first study was conducted at 13 locations in WA for 2 years to determine genetic gains in grain yield of cultivars developed during the 3 eras under managed/natural drought stress and well-watered or optimal growing (rainfed/overhead irrigation) environments. Results revealed a substantial increase in the grain yield of the third generation of early maize cultivars (2007–2010) compared to those developed during the first two generations of early cultivars (1998–2000 and 2001–2006) under drought stress and optimal growing environments. The average rate of increase in grain yield was 13.5 kg ha^{-1} $year^{-1}$ corresponding to 1.1% annual genetic gain under drought stress. Similarly, grain yield under optimum growing conditions ranged from 3363 kg ha^{-1} for the first generation of early cultivars to 3956 kg ha^{-1} for the third generation of early cultivars (Table 11.5). The average rate of increase in grain yield under this growing condition was 40 kg ha^{-1} $year^{-1}$ with a genetic gain of

Table 11.5 Grain yield and other agronomic traits of early-maturing maize cultivars of three breeding eras evaluated under managed drought stress at Ikenne and natural drought stress at Samaru between 2010 and 2012 and optimum conditions at 24 environments in Nigeria, Benin, and Ghana in 2010 and 2011

Trait	Era	Number of cultivar	Drought stress	Well-watered conditions
Grain yield, kg ha^{-1}	1988–2000	15	1345 ± 52.2	3363 ± 52.5
	2001–2006	16	1305 ± 49.2	3605 ± 46.7
	2007–2010	19	1613 ± 48.8	3956 ± 42.3
Anthesis–silking interval	1988–2000	15	4 ± 0.1	1.8 ± 0.03
	2001–2006	16	4 ± 0.1	1.9 ± 0.03
	2007–2010	19	4 ± 0.1	1.8 ± 0.03
Plant height, cm	1988–2000	15	136 ± 3.0	163 ± 0.8
	2001–2006	16	138 ± 3.0	169 ± 0.7
	2007–2010	19	139 ± 2.7	171 ± 0.7
Plant aspect	1988–2000	15	3.2 ± 0.06	2.6 ± 0.02
	2001–2006	16	3.2 ± 0.06	2.5 ± 0.02
	2007–2010	19	3.0 ± 0.05	2.4 ± 0.03
Ear aspect	1988–2000	15	2.9 ± 0.05	2.7 ± 0.02
	2001–2006	16	2.9 ± 0.05	2.5 ± 0.02
	2007–2010	19	2.8 ± 0.05	2.4 ± 0.02
Ears per plant	1988–2000	15	0.9 ± 0.02	0.9 ± 0.005
	2001–2006	16	0.8 ± 0.02	0.9 ± 0.005
	2007–2010	19	0.8 ± 0.01	0.9 ± 0.004
Stay-green characteristic	1988–2000	15	4.4 ± 0.09	–
	2001–2006	16	4.6 ± 0.09	–
	2007–2010	19	4.4 ± 0.07	–

1.33% year^{-1}. The genetic gains in grain yield under drought stress were not associated with changes in agronomic traits except improved plant aspect and husk cover. Plant aspect had a genetic gain of −0.31%, whereas husk cover had genetic gain of −0.39%. Genetic gains in yield from first- to third-generation cultivars under drought were associated with improved plant aspect and husk cover, while under optimum conditions, it was associated with plant and ear aspects, increased ears per plant, plant and ear heights, and improved husk cover.

The genetic gain of 1.1% and 1.3% year^{-1} in grain yield observed under drought stress and optimal growing environments, respectively, is substantially greater than that reported by Kamara et al. (2004) for late-maturing varieties. The authors reported genetic gain of 0.41% year^{-1} which was associated with increased total biomass production and kernel weight and reductions in plant height and days to flowering of the maize cultivars developed from 1970 to 1999 in the West African savannas. The genetic gains obtained in this study are also higher than those reported by Russell (1984) for US Corn Belt cultivars (0.68% year^{-1}) from the 1930s to the 1980s but lower than the 1.7% year^{-1} reported by Tollenaar (1989) for commercially important maize hybrids in Central Ontario from the late 1950s to the late 1980s.

The high genetic gains in grain yield under both drought stress and optimum environments in the present study are not surprising because the first generation of early cultivars was only tolerant to drought and resistant to MSV but largely susceptible to *Striga* which constitutes a major constraint in the savannas of WCA and is endemic to many testing sites where the cultivars in the present study were evaluated. During the development of the second generation of early cultivars, the major breeding emphasis was on recurrent selection for improved *Striga* resistance in the early white and yellow source populations developed from the best drought- and *Striga*-resistant materials identified based on extensive testing in WCA without a major effort on selection for drought tolerance. Starting from 2007, the source populations were subjected to the improvement for tolerance to drought and low N as well as resistance to *Striga* resulting in the development of several cultivars with combined resistance and/or tolerance to the three stresses. These improvements were reflected in the superior performance of the third generation of early cultivars over those of the first generation of early cultivars. The use of a selection index that kept days to anthesis and silking constant to identify progenies for recombination resulted in the development of early cultivars with little change in the two traits during the recurrent selection program. The selection index was also effective in keeping plant and ear heights constant despite improvements in yield potential of the second and third generations of early cultivars.

The cultivars TZE-W DT C2 STR, DTE-W STR Syn C_1, EV DT-W 2008 STR, EV DT-W 99 STR QPM, DT-W STR Synthetic, EV DT 97 STR C_1, 2009 DTE-W STR Syn, TZE-Y DT C2 STR, TZE-W DT STR C4, EV DT-Y 2000 STR, and EV DT-W 99 STR C_0 were identified as high yielding and stable across drought environments. The outstanding performance of TZE-W DT STR C4, TZE-Y DT STR C_4, EV DT-W 99 STR QPM, EV DT-W 99 STR C_0, EV DT-Y 2000 STR, and EV DT 97 STR C_1 is not surprising since these cultivars are tolerant and/or resistant to both *Striga* and drought stress. The outstanding performance of these cultivars has been confirmed in several other studies. For example, Badu-Apraku and Yallou (2009), in multilocation trials in Benin and Nigeria, 2006 and 2007, showed that TZE-W DT STR C_4 outyielded the *Striga*-susceptible check, TZE Comp 4, by 44%, when *Striga* infested and 12% when *Striga*-free. In another study in Nigeria from 2006 to 2008 to identify stable and high-yielding cultivars under *Striga* infestation and when *Striga*-free, TZE-W DT STR C_4 outyielded the *Striga*-susceptible QPM check DMRESR-W QPM by 55% when *Striga* infested and 10% when *Striga*-free. The drought tolerance and *Striga* resistance of these cultivars are of special interest as drought, and *Striga* do occur simultaneously under field conditions in WCA, and when this happens, the combined effects can be devastating. The superior performance of the cultivars is therefore of special interest and desirable because maize varieties targeted to the drought-prone areas of WCA must also be resistant to *Striga*. Based on the outstanding performance in multilocation and on-farm trials, EV DT-W 99 QPM C_0 was released in Ghana in 2009 (Obeng-Antwi 2009, personal communication), while TZE-W DT STR C_4 and TZE-Y DT STR C_4 were released in Ghana in 2012. Similarly, EV DT-W 99 STR C_0 was released in Nigeria in 2007 and EV DT-Y 2000 STR in 2011 and are being commercialized by the seed companies in the country. EV DT-W 99 STR C_0 is presently the most widely marketed open-pollinated variety by the largest seed company in Nigeria, Premier Seed Company Limited (Ogunbile, 2012, personal communication). Also, the drought-tolerant and *Striga*-resistant early variety, EV DT 97 STR C_1, has been released and commercialized in Mali and Benin.

The second study was conducted at 6 drought and 17 optimal environments in West and Central Africa (WCA) from 2013 to 2016, to determine genetic gains in grain yield of extra-early maize cultivars developed during 3 breeding eras, 1995–2000, 2001–2006, and 2007–2012, under drought and optimal environments. Grain yield ranged from 1190 kg ha^{-1} for the first-generation cultivars to 1538 kg ha^{-1} for the third-generation cultivars under drought with a corresponding genetic gain of 3.28% per year. Under optimal environments, grain yield ranged from 3296 kg ha^{-1} for first-generation cultivars to 4056 kg ha^{-1} for third-generation cultivars with an annual genetic gain of 2.25%. The average rate of increase in yield was 34 and 68 kg ha^{-1} $year^{-1}$ under drought and optimal environments, respectively. The significant increase in grain yield under drought and optimal environments was associated with delayed flowering, increased ear and plant height, reduced stalk lodging, and improved ear and plant aspect. Additional traits associated with significant yield improvement under drought were improved stay-green characteristic and increased number of ears per plant. Cultivars TZEE-Y Pop STR C_4, TZEE-W POP STR BC_2 C_0, TZEE-W STR 105, and TZEE-W STR 108 were identified as high yielding and stable across drought and optimal environments. It was concluded that substantial progress has been made in breeding for drought tolerance during the last decade.

11.9 Conclusions

In studies conducted in WCA, imposed or managed drought stress from about 2 weeks before flowering till the maturity stage reduced grain yield by 50–90% in susceptible varieties. The stress appeared too severe; therefore, other methods are being investigated. Both additive and nonadditive gene actions condition the expression of maize traits under drought stress, but additive effects are more important than the nonadditive component. Therefore, drought tolerance in maize can be improved by recurrent selection, and drought-tolerant inbred lines with good combining ability can be extracted from each improved cycle of selection for hybrid development. Several cycles of recurrent selection were effective for drought tolerance and high-yielding cultivars, such as TZE-W DT C_2 STR, DTE-W STR Syn C_1, DT-W STR Synthetic, 2009 DTE-W STR Syn, and EV DT-W 2008 STR, and several drought-tolerant hybrids were developed from the program and released in WCA. An important lesson learned from the drought-tolerant studies covering three decades is that traits have differential response to levels of stress severity. Therefore, breeders must determine the level of stress most appropriate for their germplasm and trait of interest before initiating a breeding program for drought tolerance.

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Chapter 12
Improvement of Early and Extra-Early Maize for Combined Tolerance to Drought and Heat Stress in Sub-Saharan Africa

12.1 Introduction

Drought and high temperature (heat) stress are considered to be the two major environmental factors limiting crop growth and yield (Prasad et al. 2008). These two stress factors induce many biochemical and physiological changes that influence various cellular and metabolic processes that affect crop yield and quality. Heat stress induces complex morphophysiological changes in plants and reduces productivity (Nachit et al. 1998; Kosina et al. 2007). In addition, heat stress can reduce carbohydrate production and translocation, as well as increase carbohydrate starvation throughout the periods of high respiration, especially during high night temperature (Snider et al. 2010). Stomatal closure during high temperature and limited water availability results in increased leaf temperature, especially when ambient temperature increased. This increases in leaf temperature resulted in heat stress effect on the photosynthetic apparatus relationships between grain yield and physiological traits of durum wheat varieties under drought and high temperature stress in Mediterranean environments (Carmo-Silva et al. 2012). Heat stress is also one of the environmental factors limiting maize production and productivity in SSA but has received very limited research attention in the sub-region. Climate change resulting from global warming has greatly aggravated the adverse effects of heat stress and further increased the probability of occurrence of drought and heat stress owing to irregular rainfall patterns during the growth cycle of maize in SSA (Fakorede and Akinyemiju 2003). Drought could occur at any stage of crop growth and development. However, its effect is most devastating when it occurs during flowering, the most sensitive/vulnerable crop growth stage in maize (Jäger et al. 2008). Heat stress occurs when the incident temperature in the crop environment

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rises above the critical maximum required for crop growth and development (Bita and Gerats 2013). High-temperature damage can occur at any growth stage of maize, and it almost always occurs in conjunction with drought stress, rarely by itself. For example, exposure of plants grown at 25–35 °C for 20 min in the dark led to a transient inhibition (by about 50%) of the rate of photosynthesis, which recovered within 4 h. However, treatments at temperatures above 45 °C led to permanent damage; the plants did not recover within 96 h (Sinsawat et al. 2004). Because drought and heat stresses tend to occur together, heat stress is likely to be most devastating to maize during flowering. Excessive heat kills the pollen and denatures the receptivity of silks.

Result of some field studies conducted on heat stress effects on maize has been reported in the literature. Badu-Apraku et al. (1983) obtained a yield loss of 42% when average daily temperatures were increased by 6 °C. An increase in temperature from 22 to 28 °C during the grain-filling period resulted in grain yield loss of 10% in the US Corn Belt (Thompson 1975). Lobell et al. (2011) analyzed the yields of over 20,000 historical maize trials in Southern Africa and observed a linear decrease in maize production with every degree rise in temperature above 30 °C per day. Furthermore, Lobell and Burke (2010) demonstrated that a 2 °C increase in temperature resulted in a greater reduction in maize yields than a 20% decrease in precipitation. Rowhani et al. (2011) reported greater reduction in maize yields due to increased temperature than increased intra-seasonal variability in precipitation. In the study, a 2 °C increase in temperature reduced maize yields by 13% compared to 4.2% yield loss due to 20% increase in intra-seasonal rain variability.

In an effort to contribute to increased food security and improved livelihood of resource poor farmers in SSA, the IITA Maize Program has been developing drought-tolerant maize varieties and hybrids during the past two decades. However, results from studies conducted with model species suggested that tolerance to combined heat and drought stress is under a distinctively different genetic control as compared to tolerance to either drought or heat stress (Cairns et al. 2013). Hence, the development of maize varieties with combined tolerance to drought and heat stress is crucial for achieving food security and sustained maize-based farming in the sub-region. In view of this, the IITA Maize Program has been involved in screening of drought-tolerant inbred lines and hybrids for heat tolerance, with the hope that genetic materials with combined drought and heat tolerance will be developed from the program. The activities include (1) evaluation of early and extra-early maize hybrids for drought tolerance and combined tolerance to drought and heat stress, (2) improvement of extra-early white and yellow *Striga*-resistant populations for combined heat–drought stress tolerance, and (3) screening of elite drought-tolerant and *Striga*-resistant inbred lines for combined tolerance to drought and heat stress.

12.2 Evaluation of Early and Extra-Early Maize Hybrids for Drought Tolerance and Tolerance to Combined Drought and Heat Stress

12.2.1 Genetic Materials

Four drought-tolerant (DT) hybrid trials were evaluated under managed drought stress at Ikenne, combined heat and drought stress at Kadawa, and under optimal conditions at 17 environments in Nigeria, 2012–2014. Details of entries in the trials are as follows:

(i) Trial 1—Twenty-three early white maize hybrids plus one each of OPV and hybrid check
(ii) Trial 2—Twenty-three early yellow maize hybrids plus one each of OPV and hybrid check
(iii) Trial 3—Seventeen extra-early white maize hybrids plus one each of OPV and hybrid check
(iv) Trial 4—Twenty-three extra-early yellow maize hybrids plus one each of OPV and hybrid check

The trials were conducted to (a) compare the performance of the hybrids, the OPV, and hybrid checks, estimate genetic variances and heritabilities, as well as examine the stability of the hybrids across environments; (b) investigate the dependence of yields of hybrids under combined drought and heat stress as well as under optimal growing environments on the corresponding yield performance of the hybrids under managed drought stress; and (c) identify and categorize traits accounting for the variation in grain yield into decreasing order of importance under the contrasting research conditions.

12.2.2 Field Evaluations and Statistical Analysis

The hybrids in the four separate trials were evaluated under managed drought stress at Ikenne (lat. 3°7′E, long. 6°87′N, 30 m ASL, 1200 mm annual rainfall) during the dry seasons of 2012/2013, 2013/2014, and 2014/2015 and combined heat and drought stress at Kadawa (11º45′N, 8º45′E, 468.5 m ASL, 884 mm annual rainfall) between February and June for 3 years (2012–2014), which is the dry season with the highest temperatures of the year. Furthermore, the set of hybrids were evaluated under optimal growing conditions at 17 environments for 3 years. A randomized complete block design with three replicates was used for all trials. The experimental units were 4 m long, two-row plots at a spacing of 0.75 m between rows and 0.40 m within rows. Three seeds were planted per hill, and the seedlings were thinned to two per stand at about 2 weeks after emergence resulting in a final population density of about 66,667 plants ha^{-1}. Fertilizer was applied to combined heat and drought stress trials at the rate of 60 kg each of N, P_2O_5, and K_2O ha^{-1} at 2 weeks after planting (WAP) and 60 kg of N ha^{-1} at 4 WAP. However, using the same fertilizer application rate as above, basal fertilizer was applied at planting, while top-dressing was done at 3 and 4 WAP for extra-early and early hybrid trials, respectively, managing drought stress, using the same fertilizer application rate as indicated earlier.

12.3 Procedures for Achieving Managed Drought and Combined Heat and Drought Stress

The trials for combined heat and drought stress were irrigated twice every week for the first 21 and 28 days after planting for the extra-early and early-maturing maize, respectively. The plants were then subjected to severe drought and heat stress for 3 weeks during the month of April when day temperatures varied from 35 to 39 °C and night temperature ranged from 22 to 27 °C. Irrigation water was supplied only once a week during grain filling till harvesting of the crop (with day temperature ranging from 33 to 40 °C and night temperature from 24 to 28 °C). Managed drought stress at Ikenne was achieved by planting at the end of November and supplying water to the plants through a sprinkler irrigation system that provided 17 mm water per week. The extra-early and early trials were irrigated for the first 3 and 4 WAP, respectively, after which irrigation was withdrawn till physiological maturity so that the plants relied on stored soil moisture for growth and development.

For each trial, data were recorded on days to 50% anthesis (DA) and silking (DS), and anthesis–silking interval (ASI) was computed as the difference between DS and DA. Other data recorded were plant and ear heights, root and stalk lodging, plant aspect, ear aspect, husk cover, and ears per plant (EPP) at harvest. Additional data obtained for the managed drought and combined heat and drought stress experiments at about 70 DAP was the stay-green characteristic. Leaf firing and tassel blasting were rated only under combined heat and drought stress during flowering. Leaf firing was recorded on a scale of 1–9 as the percentage of plants in a plot with leaf firing symptoms: 1, no plant with leaf firing in the plot and 9, over 90 percent of plants with leaf firing. Tassel blasting was recorded as no tassel blast (tassels with normal pollen production) or blasted tassels (tassels which were white, dry, and without any pollen). Grain yield (kg ha^{-1}) under managed drought and combined heat and drought stress was computed from shelled grain weight per plot and adjusted to 15% moisture content. However, under optimal conditions, grain yield (kg ha^{-1}) was estimated from ear weight per plot, based on 80% shelling percentage also adjusted to 15% moisture content.

Data collected on grain yield and other agronomic traits for each trial were subjected to combined analysis of variance (ANOVA) across each research condition (managed drought, combined drought and heat, and optimal environments) using PROC GLM in Statistical Analysis System (SAS) version 9.3 (SAS Inc. 2011).

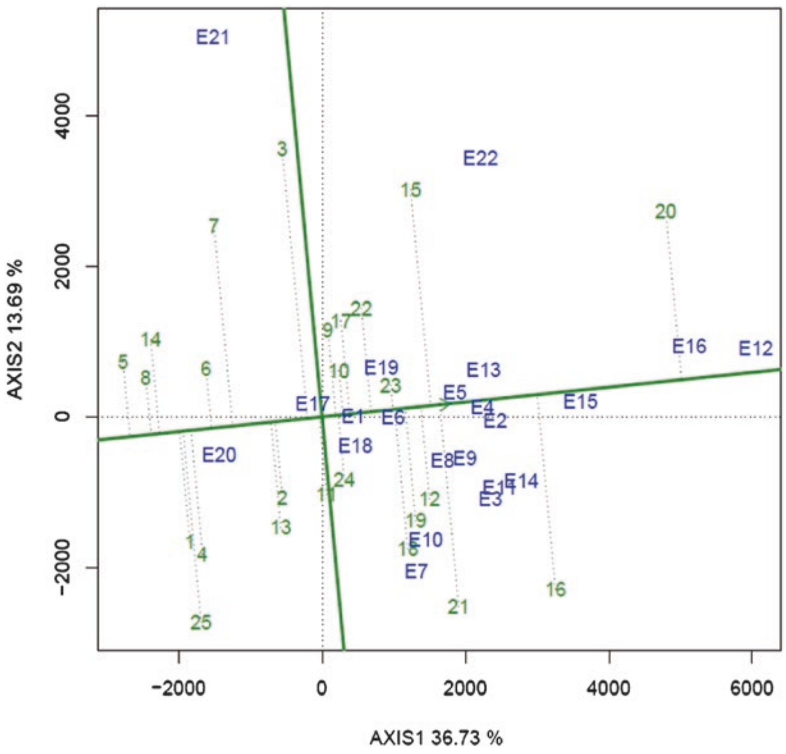
Location–year combinations were considered environments in the combined analysis. The LSD was used for separation of means among the hybrids under each research condition. Yield reduction due to any of the stress factors was estimated as [(yield under optimal − yield under stress)/yield under optimal] × 100. Yield of hybrid expressed as percentage of yield of OPV or hybrid check was computed as (yield of hybrid/yield of OPV or hybrid check) × 100. Variance components were estimated by equating the observed mean squares to their expectations and solving for the desired component (genotypic variance). Broad-sense heritability (H) estimates of the traits (Falconer and Mackay 1996) under the contrasting environments were computed on hybrid–mean basis as follows:

$$H = \sigma_g^2 / \left(\sigma_g^2 + \sigma_{g \times e}^2 / e + \sigma_e^2 / re \right)$$

where σ_g^2 is the genotypic variance, $\sigma_{g \times e}^2$ is the genotype × environment, and σ_e^2 is the residual variance. e is the number of environments, and r is the number of replicates per environment. A genetic variance or heritability estimate was considered statistically significant at 0.05 and 0.01 levels of probability if the value was greater than 2 and three times the standard error values, respectively.

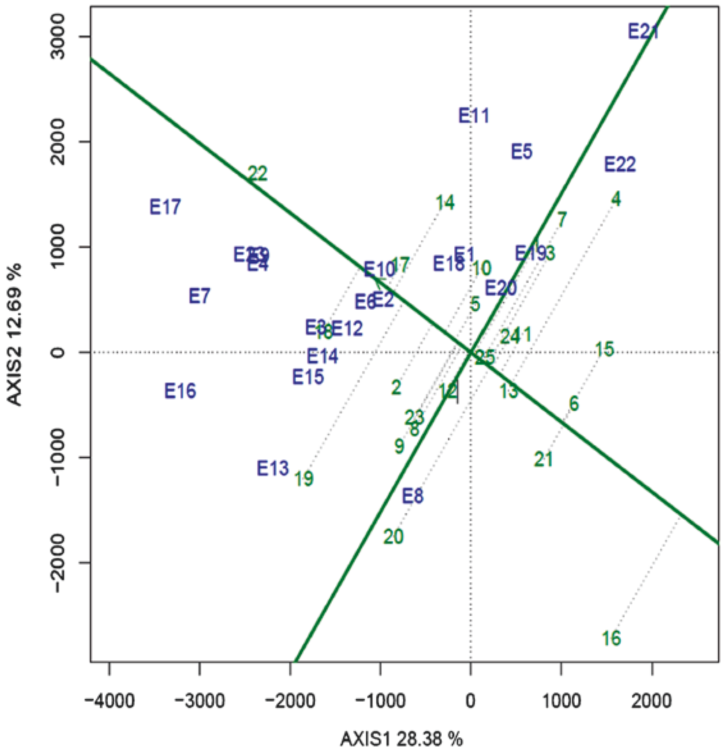
The PROC REG procedure of SAS was used for regression analysis of grain yield on other independent variables under each research condition. Sequential stepwise multiple regression analysis proposed by Mohammadi et al. (2003) was used to minimize multicollinearity. In addition, hybrid–mean yields under combined heat and drought as well as under optimal environments were regressed on corresponding yields under managed drought environments using Microsoft Office Excel (2007). The Statistical Package for the Social Sciences (SPSS) version 17.0 (SPSS 2007) was used to perform the stepwise regression analyses. The cause-and-effect relationship among traits under each research condition was investigated using the procedure proposed by Mohammadi et al. (2003). The first step in this approach identifies the predictor traits that make the largest contribution to the dependent variable, grain yield in this case. Traits belonging to this group are referred to as first-order traits. The procedure is repeated to determine the second-order traits explaining the largest portion of the residual variation and so on until the remaining traits made no significant contribution to the dependent variable at $P \leq 0.05$ (Badu-Apraku et al. 2012, 2014; Talabi et al. 2017). The standardized *b*-values from the output of the stepwise regression analysis were the path coefficients (Mohammadi et al. 2003; Badu-Apraku et al. 2012, 2014; Talabi et al. 2017). The path coefficients were subjected to *t*-test at 0.05 level of probability, and only traits with significant path coefficients were retained, indicating the percentage of the variation the traits accounted for in the dependent variable.

The GGE biplot analysis (Yan et al. 2000) was performed to provide information on the mean performance and stability of the hybrids (Figs. 12.1, 12.2, 12.3, and 12.4). The thick single-arrow black line that passed through the biplot origin (intercept of the vertical and horizontal axis) and the average tester (center of the innermost concentric circle with an arrow) was referred to as the average tester coordinate



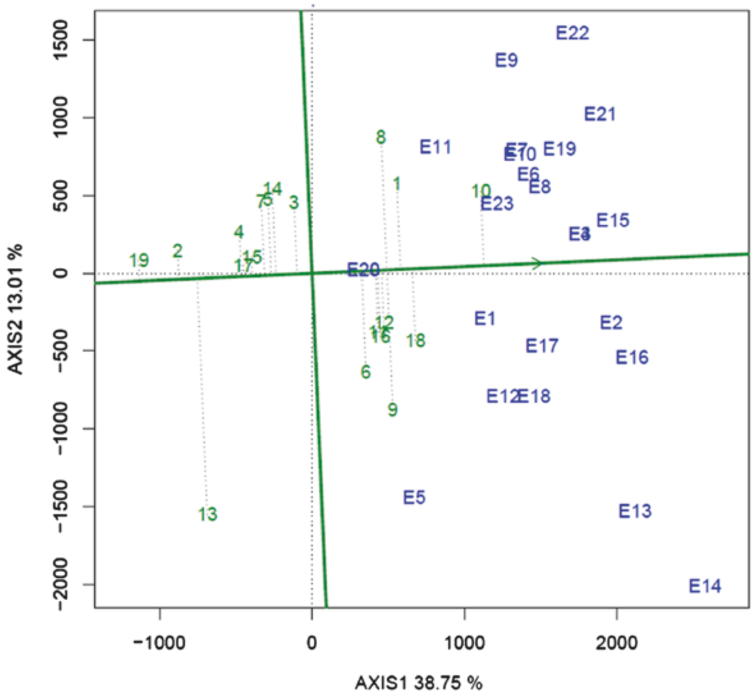
Code	Pedigree
1	(TZEI 2 x TZEI 108) x TZEI 63
2	(TZEI 59 x TZEI 108) x TZEI 63
3	(TZEI 63 x TZEI 87) x TZEI 59
4	(TZEI 63 x TZEI 108) x (TZEI 59 x TZEI 87)
5	(TZEI 63 x TZEI 59) x (TZEI 108 x TZEI 87)
6	(TZEI 63 x TZEI 87) x (TZEI 59 x TZEI 108)
7	(TZEI 2 x TZEI 63) x (TZEI 108 x TZEI 87)
8	(TZEI 2 x TZEI 63) x (TZEI 59 x TZEI 87)
9	TZE-W Pop DT STR C4 x TZEI 22
10	TZE-W Pop DT STR C4 x TZEI 7
11	TZE-W Pop DT STR C4 x TZEI 19
12	TZEI 5 x TZEI 98
13	TZEI 4 x TZEI 7
14	TZEI 1 x TZEI 3
15	TZEI 188 x TZEI 98
16	TZEI 5 x TZEI 60
17	TZEI 31 x TZEI 18
18	TZEI 60 x TZEI 86 (hybrid check)
19	TZEI 83 x TZEI 60
20	SC529
21	ENT 12 x TZEI 48
22	ENT 10 x TZEI 82
23	ENT 3 x TZEI 65
24	ENT 7 x TZEI 60
25	TZE COMP3 DT C1 F2 (OPV check)

Fig. 12.1 GGE biplot of 25 early white maize hybrids evaluated under drought, combined heat and drought, and optimal conditions at 23 environments in Nigeria, 2012–2014



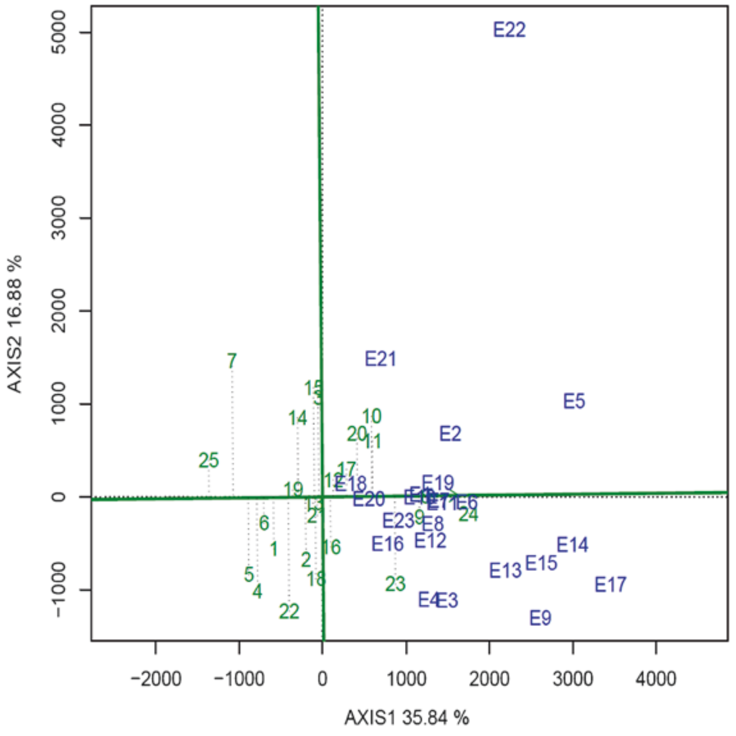
Code	Pedigree
1	(TZEI 135 x TZEI 157) x TZEI 17
2	(TZEI 16 x TZEI 157) x TZEI 129
3	(TZEI 135 x TZEI 129) x TZEI 17
4	(TZEI 135 x TZEI 157) x (TZEI 17 x TZEI 16)
5	(TZEI 135 x TZEI 17) x (TZEI 129 x TZEI 157)
6	(TZEI 129 x TZEI 17) x (TZEI 16 x TZEI 157)
7	(TZEI 135 x TZEI 129) x (TZEI 16 x TZEI 157)
8	TZE-Y Pop DT STR C4 x TZEI 17
9	TZE-Y Pop DT STR C4 x TZEI 11
10	TZE-Y Pop DT STR x TZEI 23
11	TZE-Y Pop DT STR x TZEI 9
12	TZE-Y Pop DT STR x TZEI 13 (Hybrid check)
13	TZEI 16 x TZEI 8
14	TZEI 24 x TZEI 17
15	TZEI 8 x TZEI 17
16	TZEI 23 x TZEI 13
18	TZEI 9 x TZEI 6
19	TZEI 11 x TZEI 25
20	TZEI 14 x TZEI 25
21	TZEI 136 x TZEI 14
22	TZEI 136 x TZEI 11
23	TZEI 124 x TZEI 25
24	ENT 8 x TZEI 123
25	ENT 8 x TZEI 23
26	EV DT-Y 2000 STR (OPV check)

Fig. 12.2 GGE biplot of 26 early yellow maize hybrids evaluated under drought, combined heat and drought, and optimal conditions at 23 environments in Nigeria, 2012–2014



Code	Pedigree
1	(TZEEI 21 x TZEEI 14) X TZEEI 29
2	(TZEEI 29 x TZEEI 49) X TZEEI 21
3	(TZEEI 29 x TZEEI 21) X (TZEEI 4 x TZEEI 14)
4	(TZEEI 21 x TZEEI 14) X (TZEEI 29 x TZEEI 49)
5	(TZEEI 4 x TZEEI 14) X (TZEEI 29 x TZEEI 49)
6	TZEE -W Pop STR C5 xTZEEI 29
7	TZEE -W Pop STR C5 x TZEEI 6 (Hybrid check)
8	TZEE -W Pop STR C5 x TZEEI 15
9	TZEE -W Pop STR C5 x TZEEI 21
10	TZEEI 112 x TZEEI 29
11	TZEEI 29 x TZEEI 49
12	TZEEI 29 x TZEEI 21
13	TZEEI 48 x TZEEI 29
14	TZEEI 29 x TZEEI 90
15	TZEEI 6 x TZEEI 14
16	TZEEI 110 x TZEEI 29
17	TZEEI 4 x TZEEI 14
18	TZEEI 14 x TZEEI 29
19	2008 Syn EE-W DT STR (OPV check)

Fig. 12.3 GGE biplot of 19 extra-early white maize hybrids evaluated under drought, combined heat and drought, and optimal conditions at 23 environments in Nigeria, 2012–2014



Entry	Pedigree
1	(TZEEI 82 x TZEEI 79) X TZEEI 95
2	(TZEEI 79 x TZEEI 58) X TZEEI 95
3	(TZEEI 95 x TZEEI 63) X TZEEI 79
4	(TZEEI 79 x TZEEI 63) X TZEEI 78
5	(TZEEI 79 x TZEEI 58) X TZEEI 78
6	(TZEEI 95 x TZEEI 63) X (TZEEI 79 x TZEEI 58)
7	(TZEEI 82 x TZEEI 58) X (TZEEI 79 x TZEEI 63)
8	TZEE-Y Pop STR C5 x TZEEI 95
9	TZEE-Y Pop STR C5 x TZEEI 67
10	TZEE-Y Pop STR C5 x TZEEI 82
11	TZEE-Y Pop STR C5 x TZEEI 58 (Hybrid check)
12	TZEE-Y Pop STR C5 x TZEEI 63
13	TZEEI 79 x TZEEI 58
14	TZEEI 82 x TZEEI 95
15	TZEEI 95 x TZEEI 63
16	TZEEI 95 x TZEEI 58
17	TZEEI 79 x TZEEI 76
18	TZEEI 95 x TZEEI 78
19	TZEEI 82 x TZEEI 79
20	TZEEI 9 x TZEEI 79
21	TZEEI 64 x TZEEI 79
22	TZEEI 68 x TZEEI 79
23	TZEEI 71 x TZEEI 79
24	TZEEI 87 x TZEEI 76
25	2008 Syn EE-Y DT STR (OPV check)

Fig. 12.4 GGE biplot of 25 extra-early yellow maize hybrids evaluated under drought, combined heat and drought, and optimal conditions at 23 environments in Nigeria, 2012–2014

(ATC) axis. The double-headed arrow line (ATC ordinate) separated entries with below-average means (one side of the line) from those with above-average means. A set of lines, parallel to the double-headed arrow line, spanned the whole range of the entries, grouping them based on their mean performance. The average performance of a genotype was approximated by the projection of its marker on the ATC. The stability of the genotypes was measured by their projections onto the average tester coordinate y-axis single-arrow line (ATC abscissa). The greater the absolute length of the projection of a genotype, the less stable the genotype.

12.4 Performance, Variability, and Stability of Early White and Yellow DT Hybrids Evaluated in the Regional Trials Under Managed Drought Stress at Ikenne, Combined Heat + Drought Stress at Kadawa, and Optimal Growing Conditions at 17 Environments in Nigeria, 2012–2014

Mean grain yield for Trial 1 ranged from 1665 kg ha^{-1} for the hybrid check, TZEI 60 × TZEI 86 to 2509 kg ha^{-1} for TZE-W Pop DT STR C4 × TZEI 7 under managed drought stress. Under combined heat + drought stress, mean grain yield varied from 1559 kg ha^{-1} for the OPV check, TZE COMP3 DT C1 F2, to 4072 kg ha^{-1} for TZEI 188 × TZEI 98 and under optimal environments from 3786 kg ha^{-1} for (TZEI 63 × TZEI 59) × (TZEI 108 × TZEI 87) to 5575 kg ha^{-1} for the hybrid SC529 (Table 12.1). Mean values for grain yield of the early yellow hybrids ranged from 1248 to 2477 kg ha^{-1} under managed drought, 1920 to 4188 kg ha^{-1}under heat + drought stress, and 4229 to 5872 kg ha^{-1} under optimal conditions (Table 12.2). For the extra-early white hybrids, the ranges were 1564 to 2690, 1762 to 3780, and 3676 to 4995 kg ha^{-1} under managed drought, heat + drought stress, and optimal conditions, respectively (Table 12.3). In the case of extra-early yellow hybrids, the values were 839 to 1800, 1660 to 3554, and 3020 to 4631 kg ha^{-1}for the three research conditions (Table 12.4). On average, managed drought stress reduced grain yield (50.5–63.0%) more than heat + drought stress (26.0–39.5%), and the trend was similar for nearly all of the individual hybrids (Tables 12.1, 12.2, 12.3, and 12.4). For the early yellow hybrid trial, the highest grain yield was produced by TZEI 135 × TZEI 157) × (TZEI 17 × TZEI 16) under managed drought, TZEI 24 × TZEI 17 under heat + drought stress, and TZEI 124 × TZEI 25 under optimal growing environments (Table 12.2). In the extra-early white hybrid trial, the highest grain yield was produced by TZEEI 112 × TZEEI 29 for each of the three research conditions (Table 12.3), while in the extra-early yellow hybrid trial, TZEE-Y Pop STR C5 × TZEEI 95, TZEEI 9 × TZEEI 79, and TZEEI 87 × TZEEI 76 produced the highest grain yield under the three research conditions, respectively (Table 12.4).

For the early white hybrid trial, the hybrid checks showed the highest yield reduction of 67% under managed drought stress, while the OPV checks had a yield

Table 12.1 Evaluation of early white maize hybrids under drought (3 environments), combined heat and drought (3 environments), and optimal conditions (17 environments) in Nigeria, 2012–2014

Entry	Drought stress (DS)	Combined heat and drought stress (HDS)	Optimal conditions (OPT)	Yield reduction due to DS (%)	Yield reduction due to HDS (%)	Yield expressed as % of yield of OPV check—DS	Yield expressed as % of yield of hybrid check—DS	Yield expressed as % of yield of OPV check—HDS	Yield expressed as % of yield of hybrid check—HS	Yield expressed as % of yield of OPV check—OPT	Yield expressed as % of yield of hybrid check—OPT
TZE-W Pop DT STR C4 × TZEI 7	2509	2929	4660	46	37	146	151	188	152	112	91
TZEI 83 × TZEI 60	2457	2648	5092	52	48	143	148	170	137	123	100
TZEI 31 × TZEI 18	2312	2745	4703	51	42	135	139	176	142	113	92
ENT 12 × TZEI 48	2244	2723	5279	57	48	131	135	175	141	127	103
TZEI 188 × TZEI 98	2236	4072	4944	55	18	130	134	261	211	119	97
ENT 3 × TZEI 65	2102	3367	4826	56	30	123	126	216	174	116	94
(TZEI 2 × TZEI 108) × TZEI 63	2053	2674	4084	50	35	120	123	172	138	98	80
(TZEI 59 × TZEI 108) × TZEI 63	2042	2763	4410	54	37	119	123	177	143	106	86

(continued)

Table 12.1 (continued)

Entry	Drought stress (DS)	Combined heat and drought stress (HDS)	Optimal conditions (OPT)	Yield reduction due to DS (%)	Yield reduction due to HDS (%)	Yield expressed as % of yield of OPV check—DS	Yield expressed as % of yield of hybrid check—DS	Yield expressed as % of yield of OPV check—HDS	Yield expressed as % of yield of hybrid check—HS	Yield expressed as % of yield of OPV check—OPT	Yield expressed as % of yield of hybrid check—OPT
SC529	2032	3154	5575	64	43	119	122	202	163	134	109
TZE-W Pop DT STR C4 × TZEI 22	2008	2895	4508	55	36	117	121	186	150	108	88
TZEI 5 × TZEI 98	1985	2729	5127	61	47	116	119	175	141	123	100
ENT 10 × TZEI 82	1980	3286	4810	59	32	116	119	211	170	116	94
(TZEI 2 × TZEI 63) × (TZEI 59× TZEI 87)	1965	2982	4010	51	26	115	118	191	154	96	79
(TZEI 2 × TZEI 63) × (TZEI 108× TZEI 87)	1924	3684	4167	54	12	112	116	236	191	100	82
TZEI 5 × TZEI 60	1900	1666	5572	66	70	111	114	107	86	134	109
TZEI 4 × TZEI 7	1869	1955	4387	57	55	109	112	125	101	106	86

TZE-W Pop DT STR C4 × TZEI 19	1849	2514	4729	61	47	108	111	161	130	114	93
TZEI 1 × TZEI 3	1847	3029	3896	53	22	108	111	194	157	94	76
(TZEI 63 × TZEI 87) × (TZEI 59 × TZEI 108)	1845	3415	4125	55	17	108	111	219	177	99	81
(TZEI 63 × TZEI 108) × (TZEI 59 × TZEI 87)	1837	2362	4049	55	42	107	110	152	122	97	79
(TZEI 63 × TZEI 87) × TZEI 59	1831	3885	4299	57	10	107	110	249	201	103	84
ENT 7 × TZEI 60	1758	2307	4584	62	50	103	106	148	119	110	90
TZE COMP3 DT C1 F2 (OPV check)	1714	1559	4156	59	62	100	103	100	81	100	81
(TZEI 63 × TZEI 59) × (TZEI 108 × TZEI 87)	1690	3015	3786	55	20	99	102	193	156	91	74

(continued)

Table 12.1 (continued)

Entry	Drought stress (DS)	Combined heat and drought stress (HDS)	Optimal conditions (OPT)	Yield reduction due to DS (%)	Yield reduction due to HDS (%)	Yield expressed as % of yield of OPV check—DS	Yield expressed as % of yield of hybrid check—DS	Yield expressed as % of yield of OPV check—HDS	Yield expressed as % of yield of hybrid check—HS	Yield expressed as % of yield of OPV check—OPT	Yield expressed as % of yield of hybrid check—OPT
TZEI 60 × TZEI 86 (hybrid check)	1665	1932	5108	67	62	97	100	124	100	123	100
Mean	**1986**	**2812**	**4595**	56.5 ± 1.01	37.9 ± 3.21	116.0 ± 2.59	119.4 ± 2.69	180.3 ± 8.12	145.5 ± 6.58	110.5 ± 2.47	89.9 ± 1.99
LSD	**372**	**1250**	**309**								
CV	**20**	**39**	**17**								
R squared	**0.84**	**0.78**	**0.88**								

Table 12.2 Evaluation of early yellow maize hybrids evaluated under drought (3 environments), combined heat and drought (3 environments), and optimal conditions (17 environments) in Nigeria, 2012–2014

Entry	Drought stress (DS)	Combined heat and drought stress (HDS)	Optimal conditions (OPT)	Yield reduction due to DS (%)	Yield reduction due to HDS (%)	Yield expressed as % of yield of OPV check—DS	Yield expressed as % of yield of hybrid check—DS	Yield expressed as % of yield of OPV check—HDS	Yield expressed as % of yield of hybrid check—HS	Yield expressed as % of yield of OPV check—OPT	Yield expressed as % of yield of hybrid check—OPT
(TZEI 135 × TZEI 157) × (TZEI 17 × TZEI 16)	2477	4013	4436	44	10	135	155	118	120	94	90
TZEI 9 × TZEI 6	2418	3699	5103	53	28	132	151	109	111	108	103
TZEI 24 × TZEI 17	2399	4188	5057	53	17	131	150	124	125	107	102
(TZEI 135 × TZEI 157) × TZEI 17	2386	3467	4872	51	29	130	149	102	104	103	98
TZEI 16 × TZEI 8	2223	3468	4626	52	25	121	139	102	104	98	94
TZEI 8 × TZEI 17	2221	3282	4473	50	27	121	139	97	98	95	90
TZEI 11 × TZEI 25	2196	3778	5228	58	28	120	137	111	113	111	106

(continued)

Table 12.2 (continued)

Entry	Drought stress (DS)	Combined heat and drought stress (HDS)	Optimal conditions (OPT)	Yield reduction due to DS (%)	Yield reduction due to HDS (%)	Yield expressed as % of yield of OPV check—DS	Yield expressed as % of yield of hybrid check—DS	Yield expressed as % of yield of OPV check—HDS	Yield expressed as % of yield of hybrid check—HS	Yield expressed as % of yield of OPV check—OPT	Yield expressed as % of yield of hybrid check—OPT
(TZEI 135 × TZEI 129) × (TZEI 16 × TZEI 157)	2142	3606	4596	53	22	117	134	106	108	97	93
ENT 8 × TZEI 123	2107	3370	4908	57	31	115	131	99	101	104	99
(TZEI 135 × TZEI 17) × (TZEI 129 × TZEI 157)	2096	3517	4724	56	26	114	131	104	105	100	95
ENT 8 × TZEI 23	1991	3381	4883	59	31	108	124	100	101	104	99
TZE-Y Pop DT STR × TZEI 23	1987	4035	4970	60	19	108	124	119	121	105	100
(TZEI 129 × TZEI 17) × (TZEI 16 × TZEI 157)	1985	3356	4398	55	24	108	124	99	101	93	89

(TZEI 135 × TZEI 129) × TZEI 17	1940	4091	4649	58	12	106	121	121	123	99	94
TZE-Y Pop DT STR C4 × TZEI 11	1933	1920	5147	62	63	105	121	57	58	109	104
TZEI 136 × TZEI 14	1911	2667	4862	61	45	104	119	79	80	103	98
TZEI 136 × TZEI 11	1900	2933	4592	59	36	103	119	87	88	97	93
(TZEI 16 × TZEI 157) × TZEI 129	1895	3000	5005	62	40	103	118	88	90	106	101
TZE-Y Pop DT STR × TZEI 9	1866	3811	4675	60	18	102	116	112	114	99	94
TZEI 124 × TZEI 25	1841	3741	5872	69	36	100	115	110	112	125	119
EV DT-Y 2000 STR (OPV check)	1836	3391	4714	61	28	100	115	100	102	100	95

(continued)

Table 12.2 (continued)

Entry	Drought stress (DS)	Combined heat and drought stress (HDS)	Optimal conditions (OPT)	Yield reduction due to DS (%)	Yield reduction due to HDS (%)	Yield expressed as % of yield of OPV check—DS	Yield expressed as % of yield of hybrid check—DS	Yield expressed as % of yield of OPV check—HDS	Yield expressed as % of yield of hybrid check—HS	Yield expressed as % of yield of OPV check—OPT	Yield expressed as % of yield of hybrid check—OPT
TZEI 14 × TZEI 25	1770	3081	5258	66	41	96	110	91	92	112	106
TZE-Y Pop DT STR × TZEI 13 (hybrid check)	1603	3337	4947	68	33	87	100	98	100	105	100
TZEI 23 × TZEI 13	1545	2834	4229	63	33	84	96	84	85	90	85
TZE-Y Pop DT STR C4 × TZEI 17	1428	2816	5025	72	44	78	89	83	84	107	102
Mean	2004	3391	4850	58.5 ± 1.28	29.8 ± 2.29	109.1 ± 2.96	125.1 ± 3.39	100.0 ± 3.01	101.6 ± 3.07	102.8 ± 1.07	98.0 ± 1.40
LSD	**447**	**1201**	**344**								
CV	**24**	**31**	**18**								
R squared	**0.77**	**0.60**	**0.86**								

Table 12.3 Evaluation of extra-early white maize hybrids under drought (3 environments), combined heat and drought (3 environments), and optimal conditions (17 environments) in Nigeria, 2012–2014

Entry	Drought stress (DS)	Combined heat and drought stress (HDS)	Optimal conditions (OPT)	Yield reduction due to DS (%)	Yield reduction due to HDS (%)	Yield expressed as % of yield of OPV check—DS	Yield expressed as % of yield of hybrid check—DS	Yield expressed as % of yield of OPV check—HDS	Yield expressed as % of yield of hybrid check—HS	Yield expressed as % of yield of OPV check—OPT	Yield expressed as % of yield of hybrid check—OPT
TZEEI 112 × TZEEI 29	2690	3780	4995	46	24	172	158	174	157	136	117
TZEEI 14 × TZEEI 29	2490	3038	4808	48	37	159	146	139	126	131	113
TZEEI 110 × TZEEI 29	2415	3070	4628	48	34	154	142	141	127	126	108
TZEEI 29 × TZEEI 49	2394	3223	4632	48	30	153	141	148	134	126	108
(TZEEI 21 × TZEEI 14) × TZEEI 29	2373	3359	4665	49	28	152	140	154	139	127	109
TZEE -W Pop STR C5 × TZEEI 15	2348	3041	4624	49	34	150	138	140	126	126	108
TZEE -W Pop STR C5 × TZEEI 29	2203	2281	4772	54	52	141	130	105	95	130	112
(TZEEI 4 × TZEEI 14) × (TZEEI 29 × TZEEI 49)	2119	2573	4249	50	39	136	125	118	107	116	99

(continued)

Table 12.3 (continued)

Entry	Drought stress (DS)	Combined heat and drought stress (HDS)	Optimal conditions (OPT)	Yield reduction due to DS (%)	Yield reduction due to HDS (%)	Yield expressed as % of yield of OPV check—DS	Yield expressed as % of yield of hybrid check—DS	Yield expressed as % of yield of OPV check—HDS	Yield expressed as % of yield of hybrid check—HS	Yield expressed as % of yield of OPV check—OPT	Yield expressed as % of yield of hybrid check—OPT
TZEEI 29 × TZEEI 21	2109	2606	4728	55	45	135	124	120	108	129	111
(TZEEI 21 × TZEEI 14) × (TZEEI 29 × TZEEI 49)	2101	2697	4005	48	33	134	124	124	112	109	94
TZEE -W Pop STR C5 × TZEEI 21	2069	2331	4798	57	51	132	122	107	97	131	112
TZEEI 4 × TZEEI 14	1979	2295	4189	53	45	127	116	105	95	114	98
TZEEI 6 × TZEEI 14	1893	2311	4167	55	45	121	111	106	96	113	98
(TZEEI 29 × TZEEI 21) × (TZEEI 4 × TZEEI 14)	1837	2788	4380	58	36	117	108	128	116	119	103
TZEEI 48 × TZEEI 29	1822	1762	3971	54	56	116	107	81	73	108	93
(TZEEI 29 × TZEEI 49) × TZEEI 21	1822	2096	3837	53	45	116	107	96	87	104	90

TZEE -W Pop STR C5 × TZEEI 6 (hybrid check)	1701	2409	4272	60	44	109	100	111	100	116	100
TZEEI 29 × TZEEI 90	1677	2913	4207	60	31	107	99	134	121	114	98
2008 Syn EE-W DT STR (OPV check)	1564	2178	3676	57	41	100	92	100	90	100	86
Mean	**2084**	**2671**	**4400**	52.7 ± 1.02	39.5 ± 2.00	133.2 ± 4.56	122.6 ± 4.19	122.7 ± 5.30	110.8 ± 4.78	119.7 ± 2.36	103.0 ± 2.00
LSD	**408**	**1387**	**255**								
CV	**21**	**45**	**14**								
R squared	**0.88**	**0.75**	**0.86**								

Table 12.4 Evaluation of extra-early yellow maize hybrids evaluated under drought (3 environments), combined heat and drought (3 environments), and optimal conditions (17 environments) in Nigeria, 2012–2014

Entry	Drought stress (DS)	Combined heat and drought stress (HDS)	Optimal conditions (OPT)	Yield reduction due to DS (%)	Yield reduction due to HDS (%)	Yield expressed as % of yield of OPV check—DS	Yield expressed as % of yield of hybrid check—DS	Yield expressed as % of yield of OPV check—HDS	Yield expressed as % of yield of hybrid check—HS	Yield expressed as % of yield of OPV check—OPT	Yield expressed as % of yield of hybrid check—OPT
TZEE-Y Pop STR C5 × TZEEI 95	1800	3150	4320	58	27	151	113	125	97	143	110
TZEEI 95 × TZEEI 63	1787	3300	3602	50	8	150	112	131	101	119	91
(TZEEI 79 × TZEEI 58) × TZEEI 95	1753	2322	3644	52	36	147	110	92	71	120	92
TZEEI 87 × TZEEI 76	1712	3256	4631	63	30	143	108	129	100	153	117
TZEE-Y Pop STR C5 × TZEEI 67	1696	3018	4331	61	30	142	107	119	92	143	110
TZEEI 79 × TZEEI 76	1602	3190	3898	59	18	134	101	126	98	129	99

TZEE-Y Pop STR C5 × TZEEI 58 (Hybrid check)	1589	3264	3942	60	17	133	100	129	100	130	100
(TZEEI 95 × TZEEI 63) × TZEEI 79	1518	3552	3573	58	1	127	95	141	109	118	91
(TZEEI 82 × TZEEI 79) × TZEEI 95	1509	2710	3495	57	22	126	95	107	83	116	89
TZEE-Y Pop STR C5 × TZEEI 63	1451	2713	3825	62	29	121	91	107	83	126	97
TZEEI 68 × TZEEI 79	1449	1979	3643	60	46	121	91	78	61	120	92
TZEEI 82 × TZEEI 95	1444	3077	3456	58	11	121	91	122	94	114	88
TZEEI 95 × TZEEI 78	1410	2358	3755	62	37	118	89	93	72	124	95
TZEEI 9 × TZEEI 79	1352	3554	3898	65	9	113	85	141	109	129	99

(continued)

Table 12.4 (continued)

Entry	Drought stress (DS)	Combined heat and drought stress (HDS)	Optimal conditions (OPT)	Yield reduction due to DS (%)	Yield reduction due to HDS (%)	Yield expressed as % of yield of OPV check—DS	Yield expressed as % of yield of hybrid check—DS	Yield expressed as % of yield of OPV check—HDS	Yield expressed as % of yield of hybrid check—HS	Yield expressed as % of yield of OPV check—OPT	Yield expressed as % of yield of hybrid check—OPT
(TZEEI 95 × TZEEI 63) × (TZEEI 79 × TZEEI 58)	1347	2223	3407	60	35	113	85	88	68	113	86
TZEEI 95 × TZEEI 58	1337	2578	3809	65	32	112	84	102	79	126	97
TZEEI 71 × TZEEI 79	1300	2752	4340	70	37	109	82	109	84	143	110
TZEEI 64 × TZEEI 79	1297	3043	3736	65	19	109	82	120	93	123	95
2008 Syn EE-Y DT STR (OPV check)	1194	2526	3026	61	17	100	75	100	77	100	77
TZEEI 79 × TZEEI 58	1157	2799	3680	69	24	97	73	111	86	122	93

TZEE-Y Pop STR C5 × TZEEI 82	1021	3223	3948	74	18	86	64	128	99	130	100
(TZEEI 79 × TZEEI 58) × TZEEI 78	993	1660	3391	71	51	83	62	66	51	112	86
(TZEEI 82 × TZEEI 58) × (TZEEI 79 × TZEEI 63)	985	2432	3020	67	19	82	62	96	75	100	77
TZEEI 82 × TZEEI 79	984	2568	3607	73	29	82	62	102	79	119	92
(TZEEI 79 × TZEEI 63) × TZEEI 78	839	1739	3432	76	49	70	53	69	53	113	87
Mean	**1381**	**2514**	**3736**	63.0 ± 1.30	26.0 ± 2.56	115.6 ± 4.62	86.9 ± 3.46	109.2 ± 4.16	84.6 ± 3.22	123.4 ± 2.54	94.8 ± 1.95
LSD	**364**	**1102**	**269**								
CV	**28**	**41**	**19**								
R squared	**0.80**	**0.76**	**0.80**								

reduction of 62%. Under managed drought stress, only two hybrids showed higher yield reduction than the OPV checks. It is striking that the OPV and hybrid checks showed the highest yield reduction of 62% due to combined heat + drought stress. About 92% of the hybrids under managed drought stress, all the hybrids under combined heat + drought stress, and 67% of the hybrids under optimal growing environments showed higher yields when the yield of the hybrids was expressed as percentage of the OPV check. Similarly, all hybrids under managed drought stress, 96% of the hybrids under combined heat + drought, and 9% of the hybrids under optimal environments produced higher grain yield relative to the hybrid check. The early yellow hybrids showed trends similar to those of the early white hybrids when the yields were expressed as percentages of the OPV (EV DT-Y 2000 STR) and hybrid (TZE-Y Pop DT STR × TZEI 13) checks. Generally, yield of most early hybrids, when expressed as percentages of the OPV and hybrid checks, was more than 100% under drought and/or heat + drought but less than 100% of the yield of the hybrid check. Similarly, yield reductions in the extra-early hybrids due to managed drought stress were generally higher than the corresponding reduction due to the combined heat + drought stress (Tables 12.3 and 12.4). Greater gains were also obtained over the OPV than the hybrid check when the yields of the extra-early hybrids were expressed as percentages of the means of the hybrid and OPV checks.

Results of the GGE biplot analysis further facilitated the identification of the best hybrids for the SSA farmer. For the white early hybrids, the analysis identified the SC529 as the highest yielding but less stable across environments (Fig. 12.1). However, ENT 3 × TZEI 65 yielded higher than the grand mean and was identified as the most stable across test environments. The hybrid was further tested in farm trials and released for commercialization in Nigeria in 2016. For the early yellow hybrids, TZEI 124 × TZEI 25 was the highest yielding and most stable hybrids across test environments (Fig. 12.2). This hybrid has also been released for commercialization in Mali, Nigeria, and Ghana to contribute to food security and improved livelihood in the sub-region. The extra-early hybrids TZEEI 112 × TZEEI 29 (white) and TZEEI 87 × TZEEI 76 (yellow) were also identified in this study as the highest yielding and most stable hybrids across the test environments for the maturity group (Figs. 12.3 and 12.4). The hybrids will be further tested, particularly on farm, with a view to releasing them for commercialization in the WCA sub-region.

The implication of these results is that the managed drought stress was more severe than the combined heat and drought stress. A plausible explanation for this is that having withdrawn irrigation at 21 and 28 days after planting from extra-early and early hybrid trials conducted under managed drought as well as combined heat and drought stress, irrigation was resupplied to trials conducted under combined drought and heat stress during the grain-filling periods. The results obtained from this study demonstrated that breeding efforts have minimized yield reduction due to drought and/or combined heat and drought in the evaluated hybrids as compared to the commercial hybrid and OPV checks in the trials. Higher gains were obtained in the yield of the hybrids over the OPV checks than was obtained over the hybrid checks.

Table 12.5 Genetic variances and heritability estimates of 25 early white hybrids evaluated under 3 drought, 3 heat and drought, and 17 optimal environments in Nigeria, 2012–2014

Trait	Genetic variances			Broad-sense heritability		
	Drought	Heat	Optimal	Drought	Heat	Optimal
Yield	a	1868 ± 91,504	216,347 ± 67945**	a	0.007	0.884
DA	0.826 ± 0.399*	0.812 ± 0.3579*	0.962 ± 0.283**	0.597	0.651	0.942
DS	1.141 ± 0.515*	0.892 ± 0.365	1.049 ± 0.308	0.635	0.695	0.944
ASI	0.060 ± 0.049	0.0002 ± 0.076	0.017 ± 0.008*	0.37	0.001	0.565
PHT	22.915 ± 16.522	28.988 ± 20.922	58.434 ± 17.619**	0.417	0.417	0.92
EHT	a	7.314 ± 8.462	30.893 ± 9.495**	a	0.271	0.903
RL	0.085 ± 0.039*	0.006 ± 0.019	0.165 ± 0.056*	0.632	0.108	0.822
SL	0.224 ± 0.097*	0.082 ± 0.114	0.173 ± 0.058*	0.663	0.23	0.825
HUSK	0.029 ± 0.094	0.012 ± 0.022	0.017 ± 0.006*	0.105	0.175	0.795
PASP	0.091 ± 0.041*	0.018 ± 0.017	0.055 ± 0.016**	0.632	0.337	0.91
EASP	0.042 ± 0.0321	0.033 ± 0.060	0.024 ± 0.009*	0.397	0.18	0.749
STGR	0.216 ± 0.087*	0.124 ± 0.078	b	0.707	0.474	b
LFR	b	0.051 ± 0.094	b	b	0.177	b
EPP	0.0006 ± 0.0008	0.001 ± 0.002	0.001 ± 0.0011	0.229	0.132	0.255

*, **Significantly different from zero at 0.05 and 0.01 levels of probability

[a] Negative variances and heritability estimates treated as zero

[b] Data not applicable

Estimates of genetic variances under the research conditions for each of the four sets of genotypes are summarized in Tables 12.5, 12.6, 12.7, and 12.8. Under the optimal environments, most traits had statistically significant genetic variances, unlike the stress environments in which most traits did not. Indeed, only 17 of the 112 (about 15%) possible variance estimates for drought and heat + drought stress were statistically significant, whereas 43 of the 56 (about 77%) of the variance estimates under optimum conditions were statistically significant. Another striking observation is the consistency of some traits, including the stay-green (STGR) characteristic, leaf firing (LFR), grain yield, and several others. In most cases, the traits had nonsignificant genetic variances in none or only one of the eight possible variance estimates under drought and heat + drought stresses. In particular STGR and LFR had no significant genetic variance under the heat + drought and optimal environments for any of the genetic materials. The implication of this observation is that the stress environments masked the genetic expression of most traits of maize in this study. This is of concern, especially when one considers that grain yield, ears per plant, days to anthesis, silking, and the anthesis–silking interval are involved. Without significant genetic variance estimates, heritability estimates are meaningless, and progress from selection cannot be made. In this study, more traits had higher heritability estimates under optimal than under stress conditions, corroborating the findings of Bolanos and Edmeades (1996), Bänziger and Lafitte (1997), and Badu-Apraku et al. (2004). Variance and heritability estimates obtained in this study, however, should be interpreted cautiously. Because they were based on hybrids rather than progenies from specific base populations, the values cannot be extrapolated beyond the genetic and environmental materials in the study.

Table 12.6 Genetic variances and heritability estimates of 25 early yellow hybrids evaluated under 3 drought, 3 heat and drought, and 17 optimal environments in Nigeria, 2012–2014

Trait	Genetic variances			Broad-sense heritability		
	Drought	Heat	Optimal	Drought	Heat	Optimal
Yield	33,506 ± 21,557	a	95,159 ± 32653*	0.462	a	0.809
DA	0.726 ± 0.396	0.676 ± 0.332*	1.112 ± 0.325**	0.536	0.556	0.948
DS	1.375 ± 0.617	1.194 ± 0.529*	1.617 ± 0.467**	0.638	0.604	0.961
ASI	0.093 ± 0.076	0.160 ± 0.110	0.039 ± 0.016*	0.374	0.393	0.647
PHT	34.245 ± 17.582	92.066 ± 40.356*	87.482 ± 25.532**	0.566	0.663	0.95
EHT	12.864 ± 8.074	45.655 ± 23.022	26.800 ± 8.086**	0.473	0.552	0.919
RL	0.029 ± 0.048	a	0.095 ± 0.034*	0.194	a	0.778
SL	0.240 ± 0.095*	0.188 ± 0.203	0.106 ± 0.038*	0.713	0.235	0.784
HUSK	0.019 ± 0.009*	0.050 ± 0.034	0.024 ± 0.008**	0.613	0.42	0.866
PASP	0.034 ± 0.030	0.108 ± 0.064	0.038 ± 0.012**	0.349	0.517	0.902
EASP	0.162 ± 0.070*	0.004 ± 0.040	0.018 ± 0.008*	0.658	0.032	0.671
STGR	0.052 ± 0.027	0.089 ± 0.084	b	0.57	0.395	b
LFR	b	a	b	b	a	b
EPP	0.001 ± 0.0001*	0.006 ± 0.002*	0.001 ± 0.0002*	0.599	0.806	0.748

*, **Significantly different from zero at 0.05 and 0.01 levels of probability

[a] Negative variances and heritability estimates treated as zero

[b] Data not applicable

Table 12.7 Genetic variances and heritability estimates of 19 extra-early white hybrids evaluated under 3 drought, 3 heat and drought, and 17 optimal environments in Nigeria, 2012–2014

Trait	Genetic variances			Broad-sense heritability		
	Drought	Heat	Optimal	Drought	Heat	Optimal
Yield	35,551 ± 33,572	97,298 ± 55,488	124,921 ± 44055*	0.3684	0.5797	0.897
DA	0.723 ± 0.4597	0.4816 ± 0.4194	1.4736 ± 0.483**	0.5262	0.3964	0.964
DS	0.790 ± 0.5338	0.0432 ± 0.3653	1.5710 ± 0.516**	0.4978	0.0455	0.9627
ASI	a	0.1002 ± 0.1089	0.0379 ± 0.016*	a	0.3241	0.7361
PHT	a	a	15.6494 ± 5.887*	a	a	0.8414
EHT	10.079 ± 11.2051	a	9.6217 ± 3.955*	0.3174	a	0.7708
RL	0.079 ± 0.0625	0.0246 ± 0.0388	0.0874 ± 0.035*	0.4314	0.2301	0.7886
SL	0.138 ± 0.073	0.2936 ± 0.2550	0.1587 ± 0.057*	0.6259	0.3974	0.8773
HUSK	0.016 ± 0.011	0.0228 ± 0.0194	0.0037 ± 0.002	0.4675	0.4061	0.5573
PASP	a	0.0400 ± 0.0281	0.0190 ± 0.007*	a	0.4818	0.8434
EASP	0.065 ± 0.049	0.0301 ± 0.0362	0.0326 ± 0.012*	0.4528	0.2955	0.8486
STGR	0.181 ± 0.075*	0.2091 ± 0.1506	b	0.7691	0.4703	b
LFR	b	0.0686 ± 0.0668	b	b	0.358	b
EPP	a	0.0040 ± 0.0032	0.0007 ± 0.0002**	a	0.4326	0.7728

*, **Significantly different from zero at 0.05 and 0.01 levels of probability

[a] Negative variances and heritability estimates treated as zero

[b] Data not applicable

Table 12.8 Genetic variances and heritability estimates of 25 extra-early yellow hybrids evaluated under 3 drought, 3 heat and drought, and 17 optimal environments in Nigeria, 2012–2014

Trait	Genetic variances			Broad-sense heritability		
	Drought	Heat	Optimal	Drought	Heat	Optimal
Yield	44,804 ± 21913*	44,678 ± 68,857	134,685 ± 41252**	0.591	0.207	0.906
DA	0.377 ± 0.267	0.495 ± 0.423	0.767 ± 0.227**	0.424	0.358	0.939
DS	0.580 ± 0.447	1.122 ± 0.640	0.863 ± 0.259**	0.393	0.515	0.925
ASI	a	0.107 ± 0.142	0.001 ± 0.006	a	0.238	0.045
PHT	1.745 ± 13.277	a	36.436 ± 11.220**	0.044	a	0.901
EHT	6.690 ± 7.325	a	33.238 ± 10.010**	0.285	a	0.921
RL	0.069 ± 0.046	0.024 ± 0.050	0.042 ± 0.019*	0.455	0.156	0.618
SL	0.067 ± 0.050	0.114 ± 0.093	0.100 ± 0.035*	0.405	0.373	0.799
HUSK	0.007 ± 0.008	a	0.016 ± 0.011	0.296	a	0.405
PASP	a	0.055 ± 0.047	0.032 ± 0.010**	a	0.355	0.882
EASP	0.090 ± 0.046	0.019 ± 0.021	0.043 ± 0.013**	0.575	0.271	0.893
STGR	a	0.025 ± 0.062	b	a	0.131	b
LFR	b	a	b	b	a	b
EPP	0.001 ± 0.001	0.001 ± 0.001	0.005 ± 0.0002*	0.467	0.332	0.684

*, **Significantly different from zero at 0.05 and 0.01 levels of probability

[a]Negative variances and heritability estimates treated as zero

[b]Data not applicable

Table 12.9 Correlation coefficients for grain yield of early and extra-early maize hybrids evaluated under drought stress, heat + drought stress, and optimal environments for 3 years

	Early white			Extra-early white		
Stress	DS	HS + DS	Optimum	DS	HS + DS	Optimum
Drought stress	1	0.284	0.379	1	0.749**	0.805**
Heat + drought stress		1	0.145		1	0.657**
	Early yellow			*Extra-early yellow*		
Drought stress	1	0.495*	−0.073	1	0.506**	0.512**
Heat + drought stress		1	0.011		1	0.478*

*, **Significantly different from zero at 0.05 and 0.01 probability level, respectively

12.5 Dependence of Yield of Hybrids Under Combined Heat and Drought and Optimal Environments on the Corresponding Yields Under Managed Drought Stress

Interrelationships among the stressed and optimal environments for grain yield performance of the early white hybrids were not significant, and only that of drought stress with heat + drought stress was significant for early yellow hybrids, although the coefficient of determination ($r^2 = 0.25$) was low (Table 12.9). In contrast, grain yield of both white and yellow extra-early hybrids showed highly significant

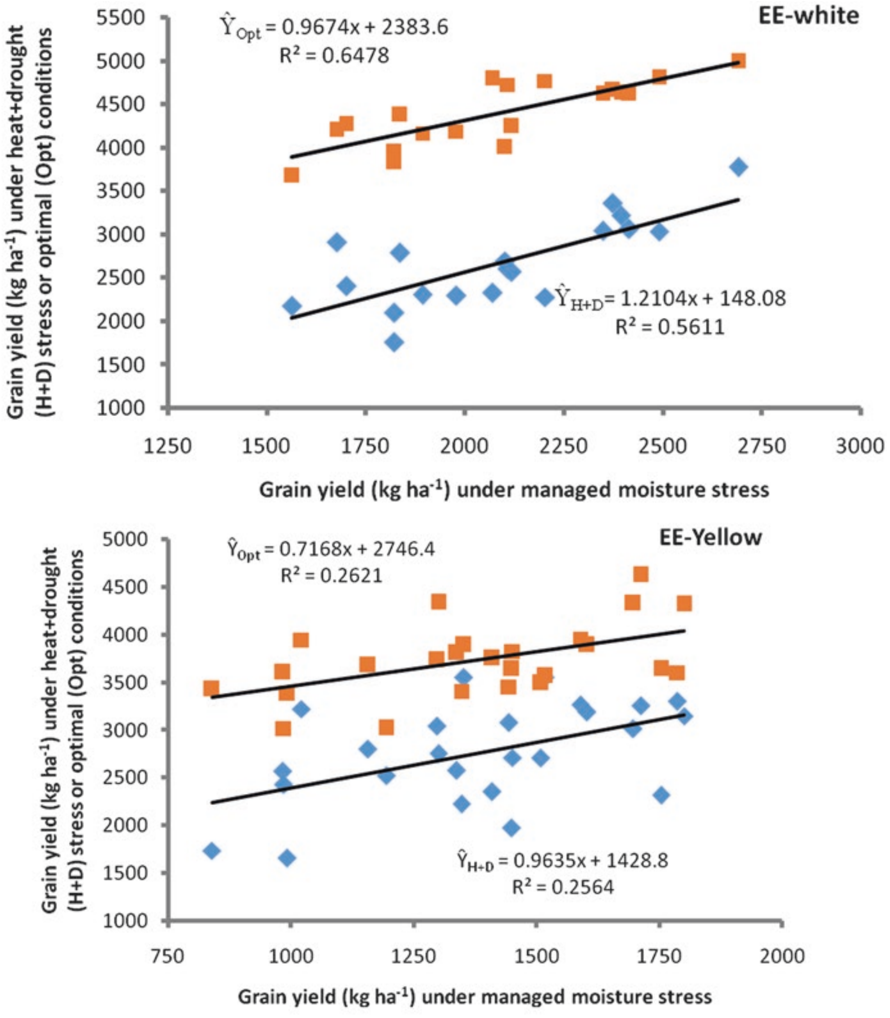


Fig. 12.5 Regression of the grain yield of extra-early white (EE-white) and yellow (EE-yellow) hybrids under heat + drought (H + D) stress and optimal (OPT) environmental conditions on the grain-yield performance of the hybrids evaluated under managed moisture stress conditions in Nigeria, 2012–2014

correlation coefficients among the three research conditions. Regression analysis showed that the observed yields of the extra-early hybrids under managed drought stress could predict the obtainable yield of the hybrids under combined heat + drought stress ($R^2 = 0.56$) and under optimal environments for the extra-early white ($R^2 = 0.56$ and 0.65, respectively) and the extra-early yellow ($R^2 = 0.26$ in each case) hybrids (Fig. 12.5). The implication is that the selected outstanding hybrids under managed drought stress should have a corresponding superior performance under combined heat and drought stress and under optimal environments. This is consistent with the findings of Badu-Apraku et al. (2013) who reported that the yields of early maize cultivars under optimal environments were dependent on the corresponding cultivar yields under managed drought stress with $R^2 = 0.58$. For the present study, however, failure of hybrid performance of heat + drought stress and optimal environments to be predictable from performance of the hybrids under managed drought stress and the lower though statistically significant R^2 values obtained in the regression involving yellow relative to white extra-early hybrids needs some further research attention. One possible explanation, though, is that the yellow germplasm is genetically and/or physiologically distinct from the white, at least for some traits, including yield. In addition, the deviation mean squares for the yellow extra-early hybrids were much larger, thereby making the residual mean squares from regression much larger than those of the white extra-early hybrids. Since the introduction of hybrids to WCA, performance of yellow hybrids has always lagged behind that of white hybrids, and results of the present study did not deviate from that pattern for the extra-early maturity group (Tables 12.3 and 12.4). One pointer to the cause of this difference in performance of the two groups of hybrids seems to be in the grain-filling characteristic, as was alluded to in Chap. 3 of this volume.

12.6 Trait Associations of Early and Extra-Early Maize Hybrids Under Managed Drought Stress, Heat + Drought Stress, and Optimal Growing Environments

Another important objective of this study was to identify traits accounting for the variation in grain yield and the relationships among the traits under managed drought stress, combined heat + drought stress, and optimal growing environments. Traits were categorized into first-, second-, and up to the sixth-order traits in descending order of the contributions to grain yield. Hence, traits which fall in the first- and second-order are reliable secondary traits for selection for improved grain yield under the respective research conditions.

Trait associations varied greatly between white vs yellow hybrids within the same maturity group, between early- and extra-early maturity groups, and among the environmental conditions within and between maturity groups. For example, under managed drought stress, ear aspect was the only trait in the first-order secondary factor affecting grain-yield performance of extra-early white hybrids (Fig. 12.6). Four other groups or factors of traits were identified following the first-order trait, with each group containing only two traits except the second to the last group that had three traits. Together, the traits accounted for 76% of the total variation in grain yield. For the same set of hybrids under heat + drought stress, however, three traits made the primary impact on grain production although ear aspect was also one of the traits (Fig. 12.7). Three other groups of traits were identified, each one containing at least

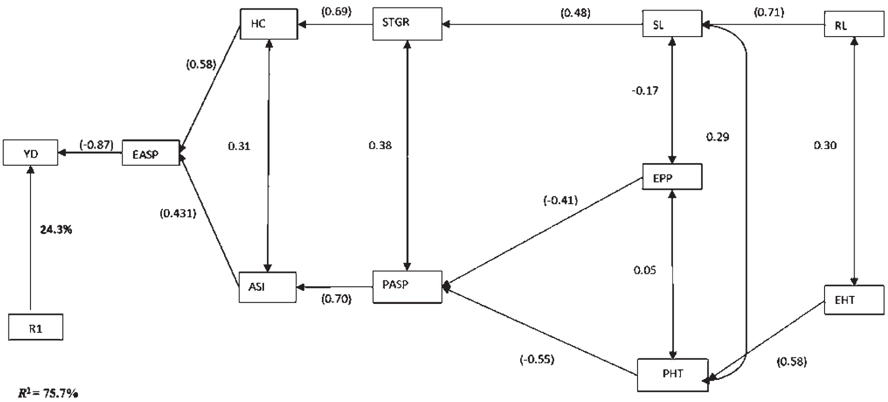


Fig. 12.6 Path analysis model diagram showing causal relationships of measured traits of extra-early maturing white hybrids evaluated under managed drought stress at Ikenne, 2012–2014. *Bold* value is the residual effect; values in parenthesis are direct path coefficients, while other values are correlation coefficients. *R1* is residual effects, *ASI* anthesis–silking interval, *EASP* ear aspect, *EPP* ears per plant, *HC* husk cover, *PASP* plant aspect, *PHT* plant height, *STGR* stay-green characteristics, *RL* root lodging, *SL* stalk lodging, and *YD* grain yield

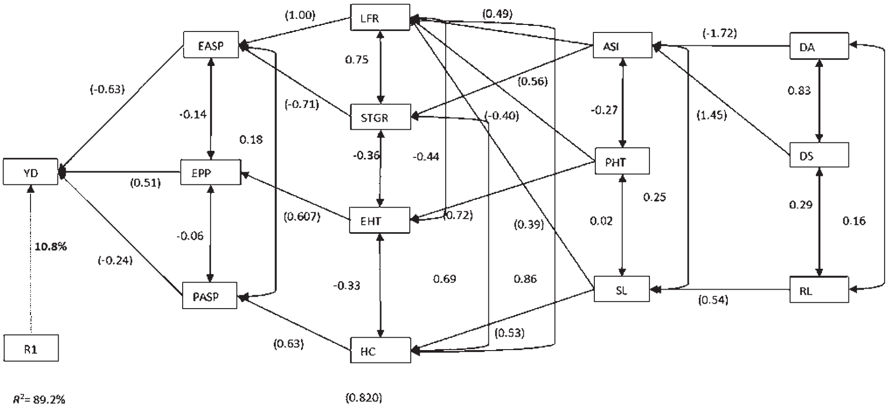


Fig. 12.7 Path analysis model diagram showing causal relationships of measured traits of extra-early maturing white hybrids evaluated under combined heat and drought stress at Kadawa, 2012–2014. *Bold* value is the residual effect; values in parenthesis are direct path coefficients, while other values are correlation coefficients. *R1* is residual effects, *ASI* anthesis–silking interval, *DA* days to 50% anthesis, *DS* days to 50% silk, *EASP* ear aspect, *EHT* ear height, *EPP* ears per plant, *HC* husk cover, *LFR* leaf firing, *PASP* plant aspect, *PHT* plant height, *STGR* stay-green characteristics, *RL* root lodging, *SL* stalk lodging, and *YD* grain yield

three traits. Together, the traits accounted for 89% of the total variance in grain yield. In the early white hybrids, PASP and EASP formed the first-order traits, while it was PASP and HUSK in the early yellow hybrids. Results of evaluation under combined heat + drought stress revealed that EASP, EPP, and PASP were the first-order traits accounting for the variation in grain yield of the extra-early white maize hybrids,

Table 12.10 Order of traits identified in the sequential stepwise regression of grain yield on agronomic traits of early white and yellow hybrids evaluated under managed moisture stress, combined heat + drought stress, and optimal environmental conditions in Nigeria, 2012–2014

	White early hybrids			Yellow early hybrids		
Order	Managed drought	Combined heat + drought	Optimal	Managed drought	Combined heat + drought	Optimal
First	PASP, EASP	EPP, SL	PASP	PASP, HC	DS, EASP, EHT	ASI, EASP, PHT, SL
Second	PHT, EPP, HC	EHT, DS	PHT, EASP	EPP, PHT	ASI, DA, LFR	DA, DS, HC, EPP, PASP, EHT, RL
Third	STGR, EHT, DS	PHT, ASI, DA	EHT, DS, HC	ASI, DA, DS	RL, EPP, STGR	
Fourth	SL, DA, ASI	PASP, EHT	DA, ASI, SL	EASP, SL		
Fifth	RL	HC, LFR	RL			
Sixth		STGR, RL				
R^2						

EPP and DS in the extra-early yellow, EPP and SL in the early white, and DS, EASP, EHT, HUSK, PASP, and PHT in the early yellow maize hybrids. Under optimal environments, first-order traits explaining the variation in grain yield included EASP, PASP, and EPP for the extra-early white maize hybrids, EASP and DA for the extra-early yellow, PASP alone for the early white, and ASI, EASP, PHT, and SL for the early yellow. Other categorization of the hybrids into orders as well as interrelationships among the traits is presented in Table 12.10 for early and Table 12.11 for the extra-early hybrids. An important trend under managed drought was that traits such as EASP, PASP, EPP, PHT, and HUSK were categorized as either first- or second-order traits in at least 75% of the time. However, under combined heat + drought stress, only EPP was categorized as first or second other traits in at least three out of the four trials, while EASP, PASP, EPP, PHT, SL, and DS were identified either as first- or second-order traits in three out of four trials under optimal environments.

12.7 Improvement of Extra-Early White and Yellow *Striga*-Resistant Populations for Combined Heat + Drought Stress Tolerance

Several strategies have been used to stabilize grain yield of early and extra-early maize in the sub-region. One approach is breeding for drought-escaping cultivars that reach maturity before the onset of drought stress. The second is to breed cultivars that possess drought tolerance genes and can withstand drought that occurs during the flowering and grain-filling periods.

Table 12.11 Order of traits identified in the sequential stepwise regression of grain yield on agronomic traits of extra-early white and yellow hybrids evaluated under managed moisture stress, combined heat + drought stress, and optimal environmental conditions in Nigeria, 2012–2014

	White extra-early hybrids			Yellow extra-early hybrids		
Order	Managed drought	Combined heat + drought	Optimal	Managed drought	Combined heat + drought	Optimal
First	EASP	EASP, EPP, PASP	EASP, PASP, EPP	EASP, HC	EPP, DS	EASP, DA
Second	HC, ASI	LFR, STGR, EHT, HC	HC, PHT, SL, DS	EPP, PASP, PHT, STGR, EHT	DA, ASI	PASP, EPP, SL, ASI, DS
Third	STGR, PASP	ASI, PHT, SL, ASI	DA, EHT, RL, ASI	RL, ASI, DS, SL	PASP, EASP	EHT, PHT, RL, HC
Fourth	PHT, EPP			DA	RL, HC	
Fifth	EHT				EHT	
Sixth					PHT	
R^2						

Following the identification of extra-early inbreds and hybrids which are not only tolerant to low N and drought escaping (characteristics of extra earliness) but that also possess genes for tolerance to drought that occurs during flowering and grain-filling periods (Badu-Apraku and Oyekunle 2012), a program was initiated in 2011 to develop extra-early white and yellow populations with combined tolerance to drought at the flowering and grain-filling periods as well as high levels of *Striga* resistance. Nineteen white and 20 yellow extra-early inbreds selected for high tolerance to drought were crossed to the extra-early white (TZEE-W Pop STR C_5) and yellow (TZEE-Y pop STR C_5) populations with enhanced *Striga* resistance due to the introgression of resistant genes from *Zea diploperennis*.

Two hundred testcrosses involving each population and selected drought-tolerant inbreds were evaluated at Ikenne under induced drought stress during the 2011/2012 dry season. The top 25% testcrosses of each population were identified and recombined to reconstitute the populations TZEE-W Pop DT C_0 STR C_5 and TZEE-Y Pop DT C_0 STR C_5. In addition, the top 10 best testcrosses of each population were recombined to form experimental varieties designated 2012 TZEE-W DT STR C_5 and 2012 TZEE-Y DT STR C_5, respectively. The two experimental varieties were made available for the DTMA regional trials in 2013. Results of the regional variety trials across six environments in WCA revealed that the varieties 2012 TZEE-W DT STR C_5 and 2012 TZEE -Y DT STR C_5 outperformed the reference variety, TZEE-W-SR BC5, by 60 and 39%, respectively, in terms of grain yield (Table 12.12).

Table 12.12 Grain yield and other agronomic characters of extra-early varieties in the 2013 RUVT—extra-early evaluated across six locations in West and Central Africa

Variety	Grain yield (kg/ha)	Days to anthesis	Days to silk	Anthesis–silking interval	Plant height (cm)	Ear height (cm)	Root lodging (%)	Stalk lodging (%)	Husk cover	Plant aspect	Ear aspect	Ear rot	Ears/plant
TZEE-W Pop STR × Z105	4129	53	54	1	168	84	1	4	2	2	3	1	0.9
TZEE-W Pop STR C5	4088	53	54	1	174	87	2	4	2	2	3	1	1.0
Local check	4020	53	55	2	176	92	3	4	3	2	3	1	0.9
2008 TZEE-W STR	4016	53	54	1	170	89	2	4	2	2	3	1	0.9
TZEE-W Pop STR × Z107	4007	54	55	1	167	84	3	4	2	2	3	1	0.9
2009 TZEE-OR1 STR	3996	53	54	1	177	87	2	5	2	2	3	1	1.0
2009 TZEE-OR2 STR QPM	3976	53	55	1	171	81	4	4	2	2	3	1	0.9
TZEE-W Pop STR × Z108	3953	53	55	1	167	83	3	6	2	2	3	1	1.0
TZEE-W Pop STR × Z104	3872	53	54	1	165	81	2	5	2	2	3	1	0.9
TZEE-W POP STR C4	3814	53	54	1	172	90	3	5	2	2	3	1	0.9
2012 TZEE-W DT STR C5	3773	52	53	1	170	83	3	5	2	3	3	1	1.0
2004 TZEE-Y Pop STR C4	3771	52	53	1	170	78	6	8	2	3	3	1	1.0
2004 TZEE-W Pop STR C4	3715	53	54	1	165	93	2	5	2	3	3	1	0.9
TZEE-Y Pop STR × Z106	3689	52	53	1	170	86	2	4	3	3	3	1	1.0
TZEE-W DT C0 STR C5	3635	51	52	1	167	82	2	5	2	3	3	1	0.9
TZEE-Y Pop STR QPM C0	3454	52	53	1	170	84	3	6	2	3	3	1	0.9
TZEE-Y Pop STR C5	3444	52	53	2	177	88	4	8	2	3	3	1	0.9
TZEE-W Pop STR QPM C0	3347	54	55	2	178	89	3	5	2	3	3	1	1.0
2012 TZEE-Y DT STR C5	3281	51	52	2	166	76	4	5	3	3	3	2	0.9
TZEE-Y DT C0 STR C5	3152	51	52	1	164	75	3	7	2	3	3	2	0.9

(continued)

Table 12.12 (continued

Variety	Grain yield (kg/ha)	Days to anthesis	Days to silk	Anthesis–silking interval	Plant height (cm)	Ear height (cm)	Root lodging (%)	Stalk lodging (%)	Husk cover	Plant aspect	Ear aspect	Ear rot	Ears/plant
2008 TZEE-Y STR	3051	52	53	2	170	81	5	7	2	3	3	2	0.9
TZEE-W-SR BC5 (RE)	2364	49	51	2	163	79	3	8	3	3	3	1	0.9
Grand mean	3661	52	54	1	170	84	3	6	2	3	3	1	0.9
LSD	297	1	1	0	8	8	2	2	0	0	0	1	0.1
CV	14	2	2	52	8	15	37	31	19	18	14	97	11
Cultivar	**	**	**	*	**	**	*	**	**	**	**	*	*
Environment	**	**	**	**	**	**	**	**	**	**	**	**	**
Cultivar × environment	**	**	**	**	**	**	**	**	**	**	**	ns	ns

Ikenne, Mokwa, Zaria, Kpeve, Pokuase_2, Kiboko

*,**Significant at 0.05 and 0.01 probability levels, respectively

Furthermore, 250 S_1 families from each of TZEE-W Pop DT C_0 STR C_5 and TZEE-W Pop DT C_0 STR C_5 generated during the minor season of 2012 plus four checks were evaluated under drought stress at Ikenne during the 2012/2013 dry season. Based on the results of the evaluation, the best 130 S_1 families of TZEE-W Pop DT C_0 STR C_5 and 70 S_1 families of the yellow population were further evaluated under heat stress at Kadawa in 2013.

The methodology used for the screening of the S_1 lines was the same as described for the hybrid trial evaluations. However, a base index that combined superior grain yield under drought with low value, that is, desirable trait expression, for plant aspect, ear aspect, leaf senescence, short ASI, and increased number of ears per plant, was used to select top performers (Oyekunle and Badu-Apraku 2012). To minimize the effect of different scales, each parameter was standardized with a mean of 0 and standard deviation of 1. Hence, a positive value was considered an indicator of tolerance to drought, while a negative value signified susceptibility to drought. The base index was computed as

Base index = [(2 × Yield) + EPP – ASI – PASP – EASP – STGR].

The top 25% testcrosses of each population were identified and recombined to reconstitute the populations TZEE-W Pop DTH C_1 STR C_5 and TZEE-Y Pop DTH C_1 STR C_5. In addition, the top 10 best S_1 families of each population were recombined to form experimental varieties designated 2013 TZEE-W DTH STR C_5 and 2013 TZEE-Y DTH STR C_5. The two experimental varieties were included in the DT regional trials in 2014 (Table 12.13).

During the 2014 growing season, 300 and 256 S_1 lines extracted from the white and yellow extra-early populations (TZEE-W Pop DTH C_1 STR C_5 and TZEE-Y Pop DTH C_1 STR C_5) were evaluated under optimal growing conditions at Bagauda. In addition, the progenies of each of the two populations were evaluated under combined heat and drought stress at Kadawa season. Based on the combined results of the evaluations under drought and heat stress and optimal conditions, the top 25% S_1 lines were recombined separately to form TZEE-W Pop DTH C_2STR C_5 and TZEE-Y Pop DTH C_2 STR C_5 during the 2014/2015 dry season. Furthermore, the top 10% performers were recombined to form experimental varieties (2014 TZEE-W DTH STR and 2014 TZEE-W DTH STR) during the 2014–2015 dry season (Tables 12.14 and 12.15). Furthermore, 256 and 239 S_1 progenies were generated from the populations TZEE-W Pop HDT C_2 STR C_5 and TZEE-Y Pop HDT C_2 STR C_5 and evaluated under induced drought stress at Ikenne during the 2015–2016 dry season and terminal drought stress at Kadawa during the 2016 growing season. Data were analyzed across drought stress environments, and the results were used to select the top 25% S_1 lines which were recombined to form TZEE-W Pop HDT C_3 STR C_5 and TZEE-Y Pop HDT C_3 STR C_5. The top 10% S_1 lines were recombined to form experimental varieties 2016 TZEE-W STR F_1 and 2016 TZEE-Y STR F_1 from the white and yellow populations, respectively.

Table 12.13 Grain yield and other agronomic traits of extra-early maize varieties in the 2014 RUVT—extra-early evaluated across eight locations in Nigeria

Variety	Grain yield (kg/ha)	Days to anthesis	Days to silk	Anthesis–silking interval	Plant height (cm)	Ear height (cm)	Root lodging (%)	Stalk lodging (%)	Husk cover	Plant aspect	Ear aspect	Ear rot	Ears/plant
2004 TZEE-W Pop STR C4	4445	54	56	2	160	76	4	14	3	4	5	3	0.9
TZEE-W STR 108 BC2	4411	54	56	2	160	77	6	17	3	5	5	3	0.9
TZEE-W STR 105 BC2	4272	56	57	2	164	78	6	19	3	5	5	3	0.8
2008 TZEE-W STR	4113	55	57	2	154	73	13	14	3	5	5	3	0.8
TZEE-W POP STR C4	4082	54	56	2	158	75	5	17	3	5	5	3	0.8
TZEE-W STR 104 BC2	4061	54	56	1	157	74	5	15	3	5	5	2	0.8
TZEE-W Pop STR × Z105	4048	56	58	2	155	71	7	16	3	5	5	3	0.8
TZEE-W Pop STR C5	4016	55	56	2	161	74	8	19	3	5	5	4	0.9
2013 TZEE-W Pop DT STR	3990	52	54	1	163	74	11	22	3	5	5	3	0.8
2012 TZEE-W DT STR C5	3971	52	54	2	164	77	6	19	3	5	5	3	0.8
TZEE-W Pop DT C1 STR C5	3872	53	55	2	157	74	5	18	3	5	5	2	0.8
TZEE-W STR 107 BC2	3841	56	58	2	167	80	7	12	3	5	5	2	0.9
2004 TZEE-Y Pop STR C4	3836	53	55	2	166	74	9	28	3	5	5	3	0.8
TZEE-W Pop DT C0 STR C5	3796	53	55	2	158	70	5	17	3	5	5	3	0.8
TZEE-Y STR 106 BC2	3756	53	55	2	159	73	6	21	3	5	5	3	0.8
2008 Syn EE-W DT STR	3659	53	56	2	159	72	6	19	3	5	5	3	0.8
TZEE-W Pop STR × Z107	3576	55	57	2	161	75	6	13	3	5	5	2	0.8
Local check	3422	53	55	2	154	76	4	18	3	5	5	4	0.8
2012 TZEE-Y DT STR C5	3234	51	53	2	159	73	7	20	3	5	5	3	0.8
2013 TZEE-Y Pop DT STR	3211	52	54	2	155	69	7	29	4	5	6	3	0.8

TZEE-Y Pop DT C0 STR C5	3170	52	54	2	161	73	7	23	3	5	5	3	0.8
TZEE-Y Pop STR C5	3152	53	55	2	156	72	8	26	3	5	6	4	0.8
TZEE-Y Pop DT C1 STR C5	3124	53	55	2	155	67	10	23	3	5	5	3	0.8
2008 TZEE-Y STR	3009	55	56	2	157	72	10	30	3	5	5	3	0.8
2008 Syn EE-Y DT STR	2442	54	56	1	145	65	9	15	4	6	6	3	0.7
Grand mean	3700	54	55	2	158	73	7	19	3	3	5	1	0.8
LSD	373	1	1	0.5	8	6	7	6	0.2	0.4	0.4	0.8	0.1
CV	18	3	3	51	9	14	49	31	13	18	13	97	15
Cultivar	**	**	**	ns	**	**	ns	**	**	**	**	*	*
Environment	**	**	**	**	**	**	**	**	**	**	**	**	**
Cultivar × environment	**	**	**	**	ns	ns	ns	ns	ns	*	**	ns	**

Abuja_IN, Mokwa_IN, Ikenne_DS, Ikenne_OPT, Zaria, Bagauda, Mokwa_OPT, and Abuja_UN

*,**Significant at 0.05 and 0.01 probability levels, respectively

Table 12.14 Grain yield and other agronomic traits of S_1 families of TZEE-W POP DT C_2 STR C_5 evaluated under drought stress at Ikenne during 2015–2016 dry season and Kadawa in 2016 growing season

Entry	Variety	Grain yield (kg/ha)	Days to anthesis	Days to silk	Anthesis–silking interval	Plant height (cm)	Ear height (cm)	Root lodging (%)	Stalk lodging (%)	Husk cover	Plant aspect	Ear aspect	Ear rot	Leaf death score	Ears/plant	Base index
175	TZEE-W Pop DT C2 STR C5 S1–175	3314	52	53	1	161	81	0	0	4	5	4	2	4	0.9	30.16
205	TZEE-W Pop DT C2 STR C5 S1–205	3146	51	52	1	123	65	1	2	4	5	5	0	5	0.9	23.95
107	TZEE-W Pop DT C2 STR C5 S1–107	2500	54	55	0	131	67	1	6	4	5	5	0	4	0.7	22.52
120	TZEE-W Pop DT C2 STR C5 S1–120	2956	53	54	1	158	85	0	7	4	5	5	0	5	0.8	21.99
109	TZEE-W Pop DT C2 STR C5 S1–109	3187	52	53	1	143	63	0	2	5	5	5	1	5	0.7	21.95
150	TZEE-W Pop DT C2 STR C5 S1–150	3069	53	54	0	143	72	1	1	4	5	5	0	5	0.7	21.92
186	TZEE-W Pop DT C2 STR C5 S1–186	2879	52	53	1	138	87	1	6	4	5	4	0	5	0.8	20.69

163	TZEE-W Pop DT C2 STR C5 S1–163	2982	55	56	1	160	92	0	5	4	5	5	0	5	0.7	20.15
111	TZEE-W Pop DT C2 STR C5 S1–111	2841	51	52	1	142	70	1	9	4	5	5	1	4	0.8	19.71
87	TZEE-W Pop DT C2 STR C5 S1–87	2467	52	52	1	168	88	0	4	4	5	5	0	5	0.7	18.43
Grand mean		**1968**	**53**	**54**	**1**	**145**	**75**	**1**	**6**	**5**	**5**	**6**	**0**	**5**	**0.6**	
LSD		**802**	**2**	**3**	**1**	**19**	**14**	**3**	**9**	**1**	**1**	**1**	**1**	**1**	**0.2**	
CV		**29**	**3**	**3**	**71**	**10**	**13**	**48**	**50**	**14**	**11**	**13**	**184**	**14**	**24**	
P for genotype		**	**	**	*	**	**	**ns**	**	**	**	**	**ns**	**	**	
P for env		**	**	**	**	**	**	**	**	**	**	**	**	**	**	
P for genotype × env		**	**ns**	**ns**	**ns**	**ns**	*	**ns**	*	**ns**	**	**	**ns**	**	**	

*,**Significant at 0.05 and 0.01 probability levels, respectively

Table 12.15 Grain yield and other agronomic traits of S_1 families of TZEE-Y POP DT C_2 STR C_5 evaluated under drought stress at Ikenne during 2015/2016 dry season and Kadawa in 2016 growing season

Entry	Variety	Grain yield (kg/ha)	Days to anthesis	Days to silk	Anthesis–silking interval	Plant height (cm)	Ear height (cm)	Root lodging (%)	Stalk lodging (%)	Husk cover	Plant aspect	Ear aspect	Ear rot	Leaf death score	Ears/plant	Base index
84	TZEE-Y Pop DT C2 STR C5 S1–84	1620	53	54	1	136	57	2	10	4	5	6	0	4	0.7	25.70
55	TZEE-Y Pop DT C2 STR C5 S1–55	1631	51	53	2	139	61	1	7	4	6	5	0	5	0.9	25.52
95	TZEE-Y Pop DT C2 STR C5 S1–95	1531	52	53	1	148	60	2	3	5	5	5	0	4	0.7	24.88
19	TZEE-Y Pop DT C2 STR C5 S1–19	1363	50	52	2	159	72	1	5	4	4	5	0	4	0.7	24.69
14	TZEE-Y Pop DT C2 STR C5 S1–14	1540	50	52	2	147	64	1	7	5	5	5	0	5	0.8	21.49
111	TZEE-Y Pop DT C2 STR C5 S1–111	1299	51	53	1	138	69	4	13	4	5	5	0	5	0.7	21.01
168	TZEE-Y Pop DT C2 STR C5 S1–168	1482	50	52	2	150	62	2	8	5	5	5	0	5	0.7	19.62

132	TZEE-Y Pop DT C2 STR C5 S1–132	1640	50	52	2	151	68	1	10	5	5	6	0	5	0.8	19.05
91	TZEE-Y Pop DT C2 STR C5 S1–91	1780	48	51	3	144	68	1	13	5	5	5	1	5	0.8	17.93
94	TZEE-Y Pop DT C2 STR C5 S1–94	1236	51	52	1	134	65	2	3	4	5	6	0	5	0.8	17.37
Grand mean		**926**	**51**	**53**	**2**	**139**	**64**	**2**	**8**	**5**	**6**	**6**	**0**	**5**	**0.5**	
LSD		**597**	**2**	**2**	**2**	**18**	**13**	**8**	**9**	**1**	**1**	**1**	**1**	**1**	**0.2**	
CV		**46**	**3**	**3**	**54**	**9**	**14**	**65**	**44**	**12**	**12**	**13**	**25**	**12**	**29**	
P for genotype		**	**	**	**	**	**	**	**	**	**	**	**	**	**	
P for env		**	**	**	**	**	**	**	**	**	**	**	*	**	**	
P for genotype × env		**	**	**	**ns**	**	**	*	*	*	*	**	*	**ns**	**	

*,**Significant at 0.05 and 0.01 probability levels, respectively

12.8 Screening of Elite Drought-Tolerant and *Striga*-Resistant Inbred Lines for Heat and Drought Stress Tolerance

The methodology used to impose combined heat and drought stress is the same as described for the S_1 family evaluation earlier. A total of 154 extra-early and 525 advanced early-maturing drought-tolerant and *Striga*-resistant inbred lines were evaluated under combined drought and heat stress at Kadawa during the dry season of 2013. Through the screening, several early- and extra-early maturing inbred lines with good levels of combined tolerance to drought and heat stress were identified for the use in genetic studies and for the development of hybrids with combined tolerance to heat and drought stress (Table 12.16).

In 2014, advanced 50 extra-early and 25 early-maturing drought-tolerant and *Striga*-resistant inbred lines were evaluated under combined drought and heat stress at Kadawa during the dry season. A total of 136 drought-tolerant white and yellow early-maturing inbred lines selected based on the 2013 dry season evaluations at Ikenne were also planted for evaluation under combined drought and heat stress at Kadawa in mid-February 2014. The results from these evaluations were also used in the identification of extra-early and early-maturing inbred lines with combined heat and drought stress tolerance (Table 12.16 and 12.17).

12.9 Conclusions

Four trials involving 23 early white (Trial 1), 23 early yellow (Trial 2), 17 extra-early white (Trial 3), and 23 extra-early yellow maize hybrids plus one OPV and one hybrid as checks for each trial were conducted under managed moisture stress, heat + drought stress, and optimal environments in Nigeria for 3 years. Most hybrids showed higher gains over the OPV than the hybrid checks in all the trials. Relative to the optimal environments, managed drought and heat + drought stress reduced yield performance of the hybrids. The reduction was more in the managed drought stress trials than the heat + drought stress, an indication that the managed drought stress was too severe due to the longer duration of the imposed dry spell on the crop. Significant estimates of genetic variance and heritability were obtained under each environmental condition but with higher number of traits and larger values occurring under optimal conditions. Yield performance under managed drought stress significantly predicted yield under heat + drought stress and optimal conditions for the white and yellow extra-early hybrids but not for the early hybrids. Therefore, for the extra-early germplasm, selection under managed stress will likely perform well under heat + drought stress and optimal conditions. Path-coefficient analyses showed that different traits may have to be used as secondary traits for indirect selection for yield improvement under the different environmental conditions. Ear aspect, plant aspect, and ears per plant were the traits selected as the primary traits

Table 12.16 Extra-early maize inbreds selected for outstanding performance under combined heat and drought stress in 2013 and 2014

S/N	Inbred designation	Pedigree	Color	Year
1	TZdEEI 2	TZEE-Y POP STR 106 S5 19/194-1/2-1/2-2/2-1/3 (33)	Yellow	2013
2	TZdEEI 4	TZEE-Y POP STR 106 S5 35/194-2/2-1/2-2/2-1/3 (40)	Yellow	2013 and 2014
3	TZdEEI 7	TZEE-Y POP STR 106 S5 189/194-1/1-1/2-4/5-7/9 (154)	Yellow	2013
4	TZdEEI 13	TZEE-Y POP STR 106 S5 35/194-2/2-1/2-1/2-1/3 (239)	Yellow	2013
5	TZdEEI 16	TZEE-W POP STR 104 S5 86/160-2/2 (272)	White	2013 and 2014
6	TZdEEI 19	TZEE-W POP STR 104 S5 20/208-1/2-1/3-2/2-1/1(595)	White	2014
7	TZdEEI 26	TZEE-W POP STR 108 S5 65/198-1/1-1/2-1/2-3/3 (454)	White	2014
8	TZdEEI 28	TZEE-W POP STR 108 S5 135/198-1/1-3/6-2/3-2/3 (472)	White	2013
9	TZdEEI 44	TZEE-W POP STR 108 S5 63/198-1/1-3/3-1/2-1/1 (847)	White	2013
10	TZdEEI 45	TZEE-W POP STR 108 S5 65/198-1/1-1/2-1/2-2/5 (853)	White	2014
11	TZdEEI 60	TZEE-W POP STR 107 S5 135/254-1/1-1/2-2/2-2/2	White	2013
12	TZdEEI 64	TZE-W POP STR 107 S5 37/254-2/2-2/2-2/3-1/3	White	2014
13	TZdEEI 87	TZEE-W POP STR 105 S5 117/253-1/3-2/3-1/8-4/4	White	2013
14	TZdEEI 89	TZEE-W POP STR 105 S5 126/253-1/2-1/2-3/3-2/4	White	2014
15	TZdEEI 90	TZEE-W POP STR 105 S5 126/253-1/2-2/2-1/1-1/3	White	2013 and 2014
16	TZdEEI 91	TZEE-W POP STR 105 S5 126/253-2/2-1/2-2/3-2/3	White	2013 and 2014
17	TZdEEI 93	TZEE-W POP STR 105 S5 170/253-1/2-1/3-1/1-1/1	White	2014
18	TZdEEI 103	TZE-W POP STR 105 S5 24/253-1/2-1/1-4/5-2/2	White	2013 and 2014
19	TZdEEI 111	TZE-W POP STR 105 S5 128/253-1/1-1/2-1/2-1/3	White	2013
20	TZEEI 3	TZEE-W SR BC5 x 1368 STR S7 Inb 76	White	2014
21	TZEEI 23	TZEE-W SR BC5 x 1368 STR S7 Inb 80	White	2013 and 2014
22	TZEEI 36	TZEE-W SR BC5 x 1368 STR S7 Inb 28	White	2013 and 2014
23	TZEEI 49	TZEE-W Pop x LD S6 (Set A) Inb 43A	White	2013
24	TZEEI 55	TZEE-W Pop x LD S6 (Set B) Inb 23-2-4	White	2013
25	TZEEI 56	TZEE-W Pop x LD S6 (Set B) Inb 21	White	2013
26	TZEEI 60	TZEE-Y SR BC1 x 9450 STR S6 Inb 3B	Yellow	2014

(continued)

Table 12.16 (continued)

S/N	Inbred designation	Pedigree	Color	Year
27	TZEEI 64	TZEE-Y SR BC1 x 9450 STR S6 Inb 8A	Yellow	2013
28	TZEEI 73	TZEF-Y SR BC1 x 9450 STR S6 Inb 3A	Yellow	2013
29	TZEEI 75	TZEF-Y SR BC1 x 9450 STR S6 Inb 7B	Yellow	2013
30	TZEEI 76	TZEF-Y SR BC1 x 9450 STR S6 Inb 8B	Yellow	2013 and 2014
31	TZEEI 83	TZEF-Y SR BC1 x 9450 STR S6 Inb 10C	Yellow	2013
32	TZEEI 87	TZEF-Y POP STR COS6 Inb 47-24B	Yellow	2013
33	TZEEI 94	TZEE-Y Pop Co S6 Inbred 47-2-4B	Yellow	2013 and 2014
34	TZEEI 100	TZEF-Y POP STR COS6 Inb 47-3-4	Yellow	2013 and 2014
35	TZEEI 105	TZEE-W POP X LDS6 Inb 43	White	2014
36	TZEEI 107	TZEE-W SR BC 5X 1368 STR S7 Inb 60	White	2014

Summary: white = 23; yellow = 13

Table 12.17 Early maize inbreds selected for outstanding performance under combined heat and drought stress in 2013 and 2014

S/N	Inbred designation	Grain Color	Pedigree	Year
1	ENT 3	White	[M37W/ZM607#bF37sr-6-2-X]-8-2-X-1-BB-B-xP84c1 F27-4-3-3-B-1-B] F29-1-2-1-6 x [KILIMA ST94A]-30/MSV-03-2-10-B-1-B-B-xP84c1 F27-4-1-6-B-5-B]3-1-2-B/CML442)-1-1	2013
2	ENT 10	White	Cuba/Guad C3 F85-3-3-1-B-B-B-B	2013
3	ENT 13	Yellow	[M37W/ZM607#bF37sr-2-3sr-6-2-X]-8-2-X-1-BB-B-xP84c1 F27-4-3-3-B-1-B] F29-1-2-2 x [KILIMA ST94A]-30/MSV-03-101-08-B-B-1xP84c1 F27-4-1-4-B-3-B] F2-1-2-1-1-1-B x CML486]-1-1	2013 and 2014
4	TZEI 7	White	WEC STR S7 Inbred 12	2014
5	TZEI 8	Yellow	TZE-Y Pop STR Co S6 Inbred 62-3-3	2013 and 2014
6	TZEI 10	Yellow	TZE-Y Pop STR Co S6 Inbred 152	2014
7	TZEI 17	Yellow	TZE Comp5-Y C6 S6 Inbred 35	2013
8	TZEI 18	White	TZE-W Pop STR Co S6 Inbred 136-3-3	2013 and 2014
9	TZEI 23	Yellow	TZE-Y Pop STR Co S6 Inbred 62-2-3	2013 and 2014
10	TZEI 31	White	TZE-W Pop x LD S6 Inbred 4	2014
11	TZEI 56	White	TZE-W Pop STR Co S6 Inbred 75-1-3	2013
12	TZEI 135	Yellow	TZE-Y Pop STR Co S6 Inbred 17-2-3	2013 and 2014
13	TZEI 177	Yellow	TZE Comp5-Y C6 S6 Inbred 62-1-2	2013 and 2014
14	TZEI 182	Yellow	TZE-Y Pop STR Co S6 Inbred 152-2-2	2013 and 2014
15	TZEI 188	White	TZE-W Pop STR Co S6 Inbred 1-1-4	2013 and 2014
16	TZEI 240	White	(TZEI 7 x TZEI 3)S6 Inb 113-1/3-2/2	2014
17	TZEI 241	White	(TZEI 7 x TZEI 3)S6 Inb 113-2/3-1/3	2014
18	TZEI 242	White	(TZEI 7 x TZEI 3)S6 Inb 113-3/3-1/1	2014

(continued)

Table 12.17 (continued)

S/N	Inbred designation	Grain Color	Pedigree	Year
19	TZEI 268	White	(TZEI 7 x TZEI 3)S6 Inb 178-3/4-3/3	2014
20	TZEI 272	White	(TZEI 7 x TZEI 3)S6 Inb 191-1/2-3/3	2014
21	TZEI 278	White	(TZEI 7 x TZEI 3)S6 Inb 2-1/2-3/3	2014
22	TZEI 281	White	(TZEI 7 x TZEI 3)S6 Inb 34-4/4-2/2	2014

Summary: white = 14; yellow = 8

influencing yield under most of the research conditions in our study. Two heat + drought-tolerant, high-yielding, and stable hybrids, ENT 3 × TZEI 65 and TZEI 124 × TZEI 25, have been released in some WCA countries, and several others, such as TZEEI 112 × TZEEI 29 (white) and TZEEI 87 × TZEEI 76 (yellow) are in the final stages of evaluation for release to seed companies in the sub-region.

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Chapter 13
Breeding for Tolerance to Low Soil Nitrogen

13.1 Introduction

One of the essential nutrients required for normal plant growth and development is nitrogen. It is an important constituent of chlorophyll, the green pigment in leaves required for photosynthesis. Consequently, nitrogen is a major micronutrient required for high yield of the maize plant but unfortunately the most limiting in tropical soils. The savannas of West and Central Africa (WCA) offer a very productive environment for maize production because of its high incoming solar radiation due to low cloud cover and reduced incidence of pests and diseases as a result of low humidity as well as low night temperature. Tropical soils, including those of the savannas, are, however, low in organic matter content and available nitrogen. The estimated annual loss of maize yield due to low soil nitrogen (low N) stress varies from 10 to 50% per year in sub-Saharan Africa (SSA) (Logrono and Lothrop 1997).

Nitrogen stress before flowering reduces leaf area development, photosynthesis rate, and the number of ear spikelets (potential grains), while occurrence of the stress during the flowering period results in kernel and ear abortion (Plate 13.1), and stress during grain-filling accelerates leaf senescence and reduces crop photosynthesis and kernel weight (Bänziger et al. 2000). In physiological context, occurrence of nitrogen stress pre-flowering would pose a limitation to the source and sink, while the stress occurrence at post-flowering stage, for example, during grain-filling would adversely affect photosynthesis and green leaf duration.

The low levels of nitrogen in tropical soils constitute a major constraint to high productivity except when organic or inorganic fertilizers are applied. Several decades of farming without the application of adequate doses of fertilizer have resulted in the depletion of essential soil nutrients required to support plant growth in SSA (Sanchez 2010). Leaching and the extensive removal of crop residues for animal feed and fuel have further compounded soil nitrogen depletion (Zambezi and Mwambula 1997). Weber et al. (1996) indicated that the maize plant requires 50–60 kg N and 30 kg P ha^{-1}

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Plate 13.1 Effect of low soil nitrogen on grain yield

in plant available forms for 1 ton of grain produced. Nitrogen uptake and biomass production are highly correlated with grain yield, suggesting a correlation between N requirement and grain yield (Greenwood 1976; Pandey et al. 2000; Bänziger et al. 2000). A fertilizer rate of 90–120 kg N ha^{-1} is recommended for maize production for increased grain yield in SSA. However, fertilizer application rates are still far below the recommended doses in the sub-region due to exorbitant prices of inorganic fertilizer, lack of credit, and the unavailability of these fertilizers to resource-poor farmers especially during the cropping seasons.

Low-nitrogen effects in SSA could be reduced through the application of organic manure and inorganic fertilizer, compost, as well as the use of legumes capable of fixing atmospheric nitrogen. Farmers could also use compost and green manure to increase the nitrogen supply in the soil. However, composting is very demanding and may require addition of some nitrogen source to ensure that it is rich in N. As a result, very few farmers can afford to produce enough good manure for application (Snapp et al. 2002; Rufino et al. 2006). Another promising alternative available is the use of nitrogen-fixing legumes in rotation. The challenge with this alternative is the length of time required to grow the legumes. A full season may be required to grow the legumes as an improved fallow, and this may not be possible in the intensive farming areas where the land is used at all times (Kaya et al. 2000). In addition, nitrogen fixation is dependent on many factors including appropriate legume species, the presence of nodulating *Rhizobia*, and favorable climatic conditions.

In SSA, recommended N fertilizer rates are often lower where there is a high risk of crop failure, especially due to drought than N rates that give maximum yields under optimal conditions (McCown et al. 1992). Poor weed management also increases the incidence of N stress. Together, these constraints result in low N being a frequent characteristic of maize-growing environments in the tropics (Bänziger and

Lafitte 1997a). Therefore, for improved maize production and productivity in SSA, a fertilizer rate of 90–120 kg N ha^{-1} is recommended for maize production in most countries. However, fertilizer application rates in the sub-region are still far below the recommended doses due to the exorbitant price and the unavailability to resource-poor farmers. Therefore, breeding for tolerance to low N offers the most economic and sustainable approach for increased maize yields by small-scale farmers who utilize low agricultural input in SSA. Low-N-tolerant cultivars are superior in the utilization of available N, either because of enhanced N-uptake capacity or more efficient use of absorbed N for grain production (Lafitte and Edmeades 1994). Factors that affect the availability of N include leaching and removal of crop residues as feed and fuel. Nitrogen stress before flowering reduces leaf area development, photosynthesis rate, and the number of ear spikelets, while stress during the flowering period results in kernel and ear abortion, while stress during grain-filling accelerates leaf senescence and reduces crop photosynthesis and kernel weight. Annual yield loss of maize due to low-N stress environments varies from 10% to 50% (Wolfe et al. 1988). Therefore, the development of maize germplasm with tolerance to low N is crucial for increased maize productivity (Lafitte and Edmeades 1994).

Bänziger et al. (1999) reported that improvement for drought tolerance also resulted in specific adaptation and improved performance under low-N conditions, suggesting that tolerance to either stress involves a common adaptive mechanism. Thus, selection for improved partitioning of assimilates to the developing ear using drought stress at flowering as the selection criterion can simultaneously improve tolerance to drought and low N. This perception is strengthened by the findings of Andrade et al. (2000) who reported that a common curve described the response of kernel number to crop growth rate around flowering whether the crop was stressed by inadequate water or by N deficiency. Selection for *Striga* resistance under low N could also result in concomitant increase in tolerance to low N. For example, Badu-Apraku et al. (2009) evaluated the S_1 progenies from two extra-early maturing populations, TZEE-W Pop STR (white) and TZEE-Y Pop STR (yellow), under low-N rate (30 kg N ha^{-1}) rather than the high dose (120 kg N ha^{-1}) recommended for maize production in the savanna agroecology of WCA. Results revealed that the gains from three cycles of selection for grain yield in the extra-early white and yellow populations under artificial *Striga*-infested and *Striga*-free environments were more pronounced in the advanced cycles under high N (157 kg ha^{-1} $cycle^{-1}$) than low N (144 kg ha^{-1} $cycle^{-1}$) in the yellow and higher under low N than high N in the white population. As a result, selection under low N has become an important strategy of the IITA Maize Improvement Program for developing low-N-tolerant cultivars.

One effective strategy available to reduce fertilizer cost is to develop maize genotypes with combined high-nitrogen use efficiency and high-yield potential. Genotypes with high-yield potential under low N are also needed to support the rapidly growing population and to provide incentives to farmers who mostly apply modest amounts of N in their maize fields. Improved maize varieties that tolerate low N will help maize farmers in stress-prone areas to obtain better harvests (Zaidi et al. 2003). In addition to improved yield under severely N-deficient conditions, these cultivars will be more responsive to the small N doses that farmers apply. The development of maize genotypes tolerant to low-N stress, therefore, is crucial to increased maize production and productivity in SSA.

Breeding for tolerance to low N offers the most appropriate and sustainable approach for increased maize yields by small-scale farmers who utilize low agricultural input in SSA. With the increasing demand for maize grain and expansion of production into marginal areas, improvement of maize germplasm using appropriate and effective breeding strategies is critical. Maize varieties and hybrids that are responsive to nitrogen fertilizer are urgently needed for improved grain production in SSA.

Low-N-tolerant cultivars are superior in the utilization of available N, either because of enhanced N-uptake capacity or more efficient use of absorbed N for grain production (Lafitte and Edmeades 1994). Factors that affect the availability of N include leaching (Bennet et al. 1989) and removal of crop residues as feed and fuel (Zambezi and Mwambula 1997). Nitrogen stress before flowering reduces leaf area development, photosynthesis rate, and the number of ear spikelets (potential grains), while stress during the flowering period results in kernel and ear abortion, and stress during grain-filling accelerates leaf senescence and reduces crop photosynthesis and kernel weight (Bänziger et al. 2000).

Several approaches have been utilized to develop improved maize cultivars for tolerance to low-N environments including selection for improved yield under N stress and for specific mechanisms expected to confer tolerance to low N (Lafitte and Bänziger 1997). In a study by Castleberry et al. (1984), higher selection gains were obtained for increased grain yield under high-N than low-N conditions. However, selection gains under low N are predicted to be higher when selection is conducted under both low and high N (Bänziger and Lafitte 1997a). Furthermore, several studies have reported good performance of tropical maize genotypes selected for drought tolerance under low-N conditions (Lafitte and Edmeades 1995; Lafitte and Bänziger 1997; Logrono and Lothrop 1997; Bänziger et al. 1999; Meseka et al. 2006).

13.2 Nitrogen Dynamics in the Soil and Mechanisms That Optimize Low-Nitrogen Tolerance

Genetic and environmental factors influence the dynamics of the amount of nitrogen in the soil and its availability to plants. The amount of nitrogen available to plants is dependent on the level of soil organic matter and clay content, given that these two fix nitrogen in the soil and can therefore release the nutrient (mineralization) under some conditions. In the soils of WCA, organic matter content is low, and the clay is largely kaolinite, the low fixation type. Nitrogen applied as fertilizers is an additional source of making the nutrient available in the soil. Available soil nitrogen is reduced by nitrogen uptake by plants, volatilization, leaching, and losses through running water, all of which are important environmental factors. Genotypic differences are also known to exist for ability of plants to take up nitrogen in the soil. Plants also differ in their ability to mobilize photosynthates produced, using absorbed nitrogen as input, into economic part, and relocation of assimilates during conditions of nitrogen stress. Although maize germplasm can be screened for each of these mechanisms using appropriate indices, screening based on yield and associated secondary traits under low nitrogen offers the prospects of identifying genotypes that owe their superiority to a combination of the mechanisms for low-nitrogen tolerance.

13.3 Screening for Low Soil Nitrogen Tolerance

Attention is presently being paid to breeding for tolerance to low soil nitrogen in SSA because genotypes that optimize grain yield under optimal soil nitrogen are not necessarily the best when soil nitrogen is limiting—an indication of genotype x environment interaction. Breeding for low-N tolerance has proved to be an economically feasible and sustainable approach because farmers in SSA either do not apply fertilizers or apply it in quantities too low to optimize the potential of the varieties that are cultivated. Reasons for low fertilizer use are (i) high cost of fertilizers and (ii) poor accessibility/availability. In addition to the low use of inorganic fertilizers, a high proportion of crop residue that could serve as sources of nitrogen and other nutrients when decomposed is fed to livestock, burnt, or consumed by termites. Consequently, the trend is one of declining soil fertility. Given the uncertainty in fertilizer application practices as a result of these factors, it is desirable to have genotypes that can show superiority under stress and optimal soil nitrogen conditions. Evaluation for tolerance to low nitrogen must, therefore, be carried out under both low-N optimal growing conditions. In WA, given the differences in soil types, solar radiation, and recommended nitrogen rates for the different agroecological zones, decision on what is low would vary with agroecological zone. For successful screening for tolerance to low N in SSA, soil nitrogen level in the soil should be well below 1.5 g/kg, the critical level above which no fertilizer is required for optimum yield. Conventionally, screening of maize genotypes for low-N tolerance is conducted on experimental plots which have been depleted of soil nitrogen by continuous planting of maize and removal of the stovers after each harvest. Soil samples from low-N plots are analyzed to ascertain the amount of available N in the soil and to estimate the additional amount of N required for the set low-N level (e.g., 30 kg of N ha^{-1}). Uniformity of screening sites is required to reduce experimental error that could be associated with identifying genotypes that truly owe their superiority to ability to excel under conditions of nitrogen stress. Measures that are used to increase precision in non-stressed environments will also improve precision in nurseries for breeding for tolerance to low nitrogen. Screening for tolerance to low N involves the exposure of the genetic materials to two levels of N fertilizer, 30 and 90 kg N ha^{-1}. The lower level is the testing rate, while the higher level serves as the control. The two levels are used for selection to ensure that selected low-N-tolerant genotypes were not necessarily mediocre in performance under high N. Soil tests are carried out and inorganic N fertilizer added to make up the two levels. Two sites are used for low-N screening: Ile-Ife in the forest agroecology and Mokwa in the southern Guinea savanna (SGS). The sites have been depleted of inherent soil N as far as possible, as indicated by soil tests. In addition to the specific low-N screening sites, the *Striga* screening sites at Mokwa and Abuja also served as indirect screening sites for low N because only 30 kg N ha^{-1} is applied to the *Striga*-infested plots, while the non-infested plots that receive optimal recommended N rate (90 kg N ha^{-1}) serve as the control. Standard agronomic practices are employed for weed, insect, and disease control. Border rows are necessary as with all trials, and two to three plants closest to alleys or walkways should be avoided since these plants are less stressed than those in the middle of the plot. For very poor soils, yield may approach zero. In such soils, some little quantity of nitrogen fertilizer (e.g., <30 kg/ha) may be applied.

13.4 Data to Collect When Screening for Tolerance to Low Soil Nitrogen

Grain yield is the main trait to consider when screening for tolerance to low N. Other agronomic traits assayed when screening for low-N tolerance include days to 50% anthesis and silking, anthesis–silking interval, plant and ear heights, plant and ear aspects, root and stalk lodging, leaf senescence, and ears per plant. Pollen shed and silking are usually delayed under nitrogen stress, with the latter exhibiting a greater delay resulting in higher ASI (anthesis–silking interval). Genotypes with low ASI values under nitrogen stress are considered tolerant to low soil nitrogen. The heritability of grain yield is usually low under these stress factors; therefore, selection for grain yield alone without other suitable secondary traits may be ineffective under low-N conditions. Desirable secondary traits are those that have high heritability and significant genotypic and phenotypic correlations with grain yield under nitrogen stress. Therefore, secondary traits such as ears per plant, delayed leaf senescence, and anthesis–silking interval are used in combination with grain yield for selecting low-N-tolerant genotypes (Bänziger and Lafitte 1997b; Bänziger et al. 1999).

13.5 Germplasm for Low Soil Nitrogen Tolerance

Germplasm from diverse sources can be screened for tolerance to low N. In WCA, open-pollinated varieties from farmers' fields are likely sources of genes for tolerance to low soil nitrogen. This is because farmers grow their maize with little or no fertilizers, and by selecting high-yielding plants under such conditions to provide them seeds for the next cropping season, they inadvertently may have increased the frequency of genes for tolerance to low N in their populations. Elite populations could also be improved for tolerance to low N through recurrent selection, while inbred lines could thereafter be developed from the improved low-N-tolerant populations.

13.6 Genetics of Tolerance to Low N in Maize

Contradictory reports are available on the type of gene action conditioning tolerance to low N in maize. Preponderance of additive gene action was obtained for tolerance of maize to low soil N (Rizzi et al. 1993; Below et al. 1997; Lafitte and Edmeades 1995; Kling et al. 1997). Similar results were reported by Mosier et al. (2005), Miti et al. (2010), Badu-Apraku et al. (2013), and Ifie (2014). Adofo-Boateng et al. (2015) examined the heterotic patterns and combining ability of grain yield of intermediate-maturing maize inbred lines under low-and high-soil-nitrogen environments determined the mode of gene action conditioning grain yield as well as the grain yield and stability of testcrosses under low-N (30 kg ha^{-1}) and high-N (90 kg ha^{-1} N) environments at three locations in Ghana in 2013 and 2014. Results revealed significant GCA and SCA effects for grain yield and most measured traits with predominance of GCA effects over SCA effects, indicating that most traits were controlled predominantly by additive gene action. On the contrary, several authors (Katsantonis et al. 1988; Betran et al. 2003; Meseka et al. 2006; Makumbi et al. 2011) reported that nonadditive genetic effects conditioned grain yield of maize hybrids under low N. De Souza et al. (2008) examined the genetic control of grain yield, nitrogen use efficiency, and its primary components and indicated that additive and nonadditive genetic effects were responsible for the genetic control of nitrogen use efficiency and grain yield under high N and that additive genetic effects were more important while only additive gene action was significant for nitrogen use efficiency for maize grown in low-N soils.

13.7 Evaluation of Progress in Breeding for Tolerance to Low Soil Nitrogen and Other Stresses

The Guinea savanna has the greatest potential for increased maize production due to high solar radiation, low night temperatures, and low incidence of diseases and pests. Unfortunately, maize is plagued by three major production constraints in the Guinea savanna, namely, drought, nitrogen deficiency, and infestation by *Striga hermonthica*. Under field conditions, drought, *Striga*, and soil nutrient deficiencies may occur simultaneously, and the combined effect could be devastating (Cechin and Press 1993; Kim and Adetimirin 1997). Therefore, maize varieties targeted to the *Striga*-prone areas of WCA must also be resistant or at least tolerant to drought and low N. Badu-Apraku et al. (2008) compared the effects of drought stress and *Striga hermonthica* on maize under field conditions. Grain yield was reduced by 53% under drought stress and 42% under *Striga* infestation. Several workers have reported that drought stress and low soil nutrient status, especially of low N, aggravates *Striga hermonthica* parasitism on maize (Cechin and Press 1993; Kim and Adetimirin 1997; Lagoke et al. 1991; Mumera and Below 1993). Therefore, in the agroecological zones such as the Sudan and northern Guinea savannas where intermittent drought occurs frequently, it is important to incorporate drought tolerance into varieties that have resistance to *Striga* and tolerance to low N because the two stresses occur concurrently. Farmers in *Striga* endemic ecologies of WCA demand varieties with combined *Striga* resistance and drought tolerance and are unwilling to adopt maize varieties which do not meet these requirements (Badu-Apraku, personal communication). Furthermore, maize productivity can be significantly improved in WCA by promoting the commercialization of cultivars that combine high resistance/tolerance to *Striga* and drought with improved N use efficiency. Kim (1991) recommended that the amount of NPK applied during screening of maize genotypes for *Striga* resistance must be monitored for effective selection to ensure that there are no escapes as a result of high levels of fertilizer. If the stress is too severe, all genotypes will succumb and be declared susceptible, and if too mild, there will be too many escapes. Consequently, during the four cycles of improvement in the extra-early source populations, 30–50 kg N ha^{-1}, 26 kg P ha^{-1}, and 50 kg K ha^{-1} was applied as 15–15–15 NPK in both the *Striga*-infested and non-infested plots. The actual quantity of N applied was determined by the fertility of the soil. It was also important to determine whether the selection under low levels of N (30–50 kg N ha^{-1}), rather than at the high dose of 120 kg N ha^{-1} recommended for maize production in Nigeria, had any effect on the performance of the different cycles of selection in the source populations and the derived cultivars. A study was conducted from 2005 to 2007 to assess the progress made in improving each of two extra-early populations for grain yield, *Striga* resistance, and other agronomic traits when the four cycles of selection were grown in artificially *Striga*-infested and *Striga*-free environments and to evaluate in *Striga*-free environments the effect of low- and high-N rates on the progress from selection in the two source populations. Results showed that the yield gain in advanced cycles of selection was more pronounced under high N (157 kg ha^{-1} cycle^{-1}) than low N (144 kg ha^{-1} cycle^{-1}) in the yellow and higher under low N than high N in the white. Selection in the yellow population was accompanied by increased days to anthesis and silking as well as plant and ear heights under low N and increased days to silking under high N. In the white population, selection induced increased days to anthesis, ear height, and decreased anthesis–silking interval.

Several workers (Bänziger et al. 1999; Badu-Apraku et al. 2011) have reported that improvement for drought tolerance also resulted in specific adaptation and improved performance under low-N conditions, suggesting that tolerance to either stress involves a common adaptive mechanism. Although there are several methods available for the control of *Striga*, drought, and low soil N in WCA, the most sustainable and economic control method is genetic enhancement of the maize germplasm. Even though the early-maturing *Striga*-resistant and drought-tolerant inbreds, hybrids, and open-pollinated cultivars developed in the IITA-MIP were not intentionally selected for tolerance to low N until 2007, selection for *Striga* resistance is normally conducted under low-N conditions. To elicit maximum genotypic differences among S_1 progenies of the IITA recurrent selection program for improved resistance/tolerance to *Striga* in two extra-early populations, TZEE-W Pop STR and TZEE-Y Pop STR, Badu-Apraku et al. (2009) evaluated the S_1 progenies under low-N rate (30–50 kg N/ha) rather than the high dose (120 kg N/ha) recommended for maize production in the savanna agroecology of WCA. Their study showed that the yield gain after three cycles of selection in the extra-early white and yellow populations for grain yield under artificially *Striga*-infested and *Striga*-free environments were more pronounced in the advanced cycles under high N (157 kg/ha/cycle) than low N (144 kg/ha/ cycle) in the yellow and higher under low N than high N in the white. Furthermore, Badu-Apraku et al. (2010) identified EVDT 97 STRC1, TZE-W DT STR C4, and TZE Comp3 C_3 as tolerant to low N even though there was no conscious effort to select for tolerance to low N in their recurrent selection for *Striga* resistance and/or drought-tolerant programs through which they were derived. It was concluded that selection of S_1 progenies for grain yield and *Striga* resistance in the two populations under *Striga* infestation at low N led to concomitant improvement in grain yield and some other traits in the advanced cycle of selection.

13.8 Gains in Grain Yield Under Low Nitrogen After Three Decades of Breeding for Drought Tolerance and *Striga* Resistance in Early Maize

Breeding for resistance to *Striga hermonthica* and tolerance to drought has been a major strategy to improve maize production and productivity in SSA during the last three decades. Thus, though the early-maturing *Striga*-resistant and drought-tolerant inbreds, hybrids, and open-pollinated varieties developed in the IITA-MIP were not intentionally selected for tolerance to low N until 2007, selection for *Striga* resistance is normally conducted under low-N conditions. To elicit maximum genotypic differences among S_1 progenies of the IITA recurrent selection program for improved resistance/tolerance to *Striga* in two extra-early populations, TZEE-W Pop STR and TZEE-Y Pop STR, Badu-Apraku et al. (2009) evaluated the S_1 progenies under low-N rate (30–50 kg N/ha) rather than the high dose (120 kg N/ha) recommended for maize production in the savanna agroecology of WCA. The study showed that the yield gain after three cycles of selection in the extra-early white and yellow populations for grain yield under artificially *Striga*-infested and *Striga*-free environments was more pronounced in the advanced cycles under high N (157 kg ha^{-1} cycle^{-1}) than low N (144 kg ha^{-1} cycle^{-1}) in the yellow and higher under low N than high N in the white. Furthermore, Badu-Apraku et al. (2010) identified EVDT 97 STRC1, TZE-W DT STR C4, and TZE Comp3 C3 as tolerant to low N even though there was no intentional selection for tolerance to low N in the recurrent selection for *Striga*-resistant and/or drought-tolerant programs through which they were derived. It was concluded that selection of S_1 progenies for grain yield and *Striga* resistance in the two populations under *Striga* infestation at low N led to concomitant improvement in grain yield and some other traits in the advanced cycle of selection. Edmeades et al. (2006) observed gains of 210 kg/ha/cycle for S_1 family selection and 86 kg/ha/cycle for full-sib selection or about the same gain per year from both methods. The authors reported similar gains under drought indicating that selection in drought environment may be the most effective for improving grain yields under low fertility conditions. They concluded that drought environments caused variation in the partitioning of nitrogen (N) to the ear at flowering and identified genotypes with higher harvest indices. Thus, selection for improved partitioning of assimilates to the developing ear using drought stress at flowering as the selection criterion can simultaneously improve tolerance to drought and low N. This perception is reinforced by the findings of Andrade et al. (2000) who reported that a common curve described the response of kernel number to crop growth rate around flowering whether the crop was stressed by inadequate water or by nitrogen deficiency.

Comparisons of performance of cultivars under contrasting N levels have been reported by several workers (Castleberry et al. 1984; O'Neill et al. 2004). For example, Castleberry et al. (1984) showed that genetic gains for grain yield under low and high soil fertility of 25 open-pollinated and hybrid maize cultivars commercialized in the USA during the period between the 1930s and 1980s were 51 and 87 kg ha^{-1} year^{-1}, respectively. In contrast to the findings of these studies, O'Neill et al. (2004) showed that the widely grown US hybrid (B73 × Mo17) grown during the 1970s produced 8% more yield under a deficit N treatment than hybrids released in the early and late 1990s, while the latter had greater yield responses at high fertilizer N levels. However, similar studies in tropical maize is limited thus making it difficult to ascertain completely the genetic gains that have been made for grain yield in relationship to N fertility in the numerous cultivars that have been released in SSA. Results of the study conducted by Badu-Apraku et al. (2015) in the early-maturing maize cultivars in WCA have shown that under low-N conditions, grain yield improved from 2280 kg ha^{-1} during the first era to 2610 kg ha^{-1} during the third era, an increase of 165 kg ha^{-1} era^{-1}. Under high N, yield increased from 3200 to 3650 kg ha^{-1}, an increase of 225 kg ha^{-1}. Relative gain per period was 30 kg ha^{-1} for the two N rates. It was concluded that selection for *Striga* resistance and drought tolerance in early-maturing maize populations enhanced low-N tolerance in the maize cultivars derived from the populations. The improvement was higher in later than earlier breeding eras.

13.9 Gains in Grain Yield Under Low Nitrogen After Three Decades of Breeding for Drought Tolerance and *Striga* Resistance in Extra-Early Maize

A study was conducted at two locations in Nigeria in 2013 and 2014 to determine the rate of genetic improvement in grain yield of extra-early cultivars developed during three breeding eras under low- and high-N environments. Results showed that under low N, mean grain yield ranged from 2690 kg ha^{-1} for cultivars bred during 1995–2000 to 3273 kg ha^{-1} for those developed during 2007–2012 with an annual genetic gain of 2.01%. Under high-N environments, grain yield ranged from 3493 kg ha^{-1} for cultivars bred during 1995–2000 to 4398 kg ha^{-1} for those developed during 2007–2012 with a genetic gain of 2.53% per year. The average rate of increase in grain yield was 50.1 kg ha^{-1} per year under low N and 79.3 kg ha^{-1} per year under high N. The increase in grain yield under low N was associated with the days to anthesis, improved root lodging, and increased ear height. Cultivars TZEE-W POP STR C4, TZEE-W STR 107 BC1, and 2009 TZEE-OR1 STR were the highest yielding and most stable across low- and high-N environments and were recommended for commercialization in SSA. It was concluded that substantial progress has been made in breeding for high-yielding, low-N-tolerant extra-early cultivars for SSA during the past three decades.

13.10 Genetic Gains from Selection for Grain Yield and Low-Nitrogen Tolerance in Extra-Early Maturing Maize Cultivars of Three Breeding Eras in Low- and High-Nitrogen Environments

Comparisons of performance of cultivars under contrasting N levels have been reported by several workers (Castleberry et al. 1984; O'Neill et al. 2004). For example, Castleberry et al. (1984) showed that genetic gains for grain yield under low and high soil fertility of 25 open-pollinated and hybrid maize cultivars commercialized in the USA during the period between the 1930s and 1980s were 51 and 87 kg ha^{-1} $year^{-1}$, respectively. In contrast to the findings of these studies, O'Neill et al. (2004) showed that the widely grown US hybrid (B73 × Mo17) grown during the 1970s produced 8% more yield under a deficit N treatment than hybrids released in the early and late 1990s, while the latter had greater yield responses at high fertilizer N levels. Genetic gains in tropical maize under drought stress are not as well documented (Edmeades et al. 1999; Beyene et al. 2015). Genetic gains for grain yield of CIMMYT's ESA early-maturing open-pollinated varieties (OPVs) have been estimated at 0.11, 0.029, 0.085, and 0.193 Mg ha^{-1} $year^{-1}$ under optimal conditions, random drought occurring naturally during the wet season, low N, and maize streak virus (MSV) (Masuka et al. 2017a). In the intermediate–late-maturity group, genetic gain under optimal conditions, random drought, low N, and MSV was 0.079, 0.042, 0.053, and 0.109 Mg ha^{-1} $year^{-1}$. No significant yield gains were made under managed drought stress for both maturity groups. Genetic gains for grain yield in CIMMYT's ESA hybrid maize breeding program have been estimated at 0.109, 0.325, 0.227, 0.209, and 0.141 Mg ha^{-1} $year^{-1}$ under optimal conditions, managed drought stress imposed by withholding irrigation during the dry season, random drought occurring naturally during the wet season, low N, and MSV, respectively, during the period 2000–2010 (Masuka et al. 2017b). In WCA, genetic gain has only been determined for OPVs. A genetic gain of 0.4% $year^{-1}$ for grain yield under optimal conditions was estimated for intermediate-maturing maize OPVs released between 1970 and 1999 in the Nigerian savannas (Kamara et al. 2004). A more recent study by Badu-Apraku et al. (2013, 2015) estimated genetic gain for early-maturing OPV grain yield at 0.040 Mg ha^{-1} $year^{-1}$ (1% $year^{-1}$) under optimal conditions and 0.014 Mg ha^{-1} $year^{-1}$ under managed drought stress between 1988 and 2010. Results of the only study conducted with early-maturing maize cultivars under low-N conditions in WCA have shown that grain yield improved from 2.28 Mg $ha\text{-}^{1}$ during the first era (1995–2000) to 2.61 Mg ha^{-1} during the third era (2007–2012) under low-N conditions, an increase of 0.165 Mg ha^{-1} era^{-1} (Badu-Apraku et al. 2015). Under high N, yield increased from 3.20 to 3.65 Mg ha^{-1}, an increase of 0.225 Mg ha^{-1} era^{-1}. However, similar studies in tropical maize are limited thus making it difficult to ascertain completely the genetic gains that have been made for grain yield in relationship to N fertility in the numerous cultivars that have been released in SSA.

For more than two decades, improved extra-early varieties have been developed during three eras: 1995–2000 (era 1), 2001–2006 (era 2), and 2007–2012 (era 3). Deliberate selection for low-N tolerance was done in era 3 but not in eras 1 and 2 when selection was for tolerance/resistance to some other stresses. A study was conducted to evaluate the rate of genetic improvement in grain yield of the extra-early cultivars developed during the three eras. The study involved 56 cultivars: 14, 17, and 25 extra-early cultivars developed in the three eras, respectively. The cultivars were evaluated under low N and high soil nitrogen (high N) at two locations in Nigeria in 2013 and 2014. A substantial increase in the grain yield was observed in the third generation of extra-early maize cultivars (era 3) compared to those developed during the first two eras under low-N and high-N environments. Under low N, grain yield increased from 2646 kg/ha during the first era to 32,743 kg/ha during the third era. Similarly, under high N, yield improved from 341,493 kg/ha during the first era to 4,400,398 kg/ha during the third era. Results of path diagrams of the causal relationships among traits under each research condition are shown in Figs 13.1 and 13.2 for the two N environments, respectively. Under low N, the stepwise regression analyses identified plant aspect, stalk lodging, days to silking, ear aspect, and plant height as traits with high direct effects on grain yield. The five traits accounted for 79.5% of the total variation in grain yield. Among the five traits, plant aspect had the highest total effect (0.52) on yield followed by stalk lodging (0.42), days to silking (0.36), and plant height (0.22), and the least was ear aspect (0.18) (Fig. 13.1). The stay-green characteristic contributed to yield indirectly through plant aspect (0.33) and stalk

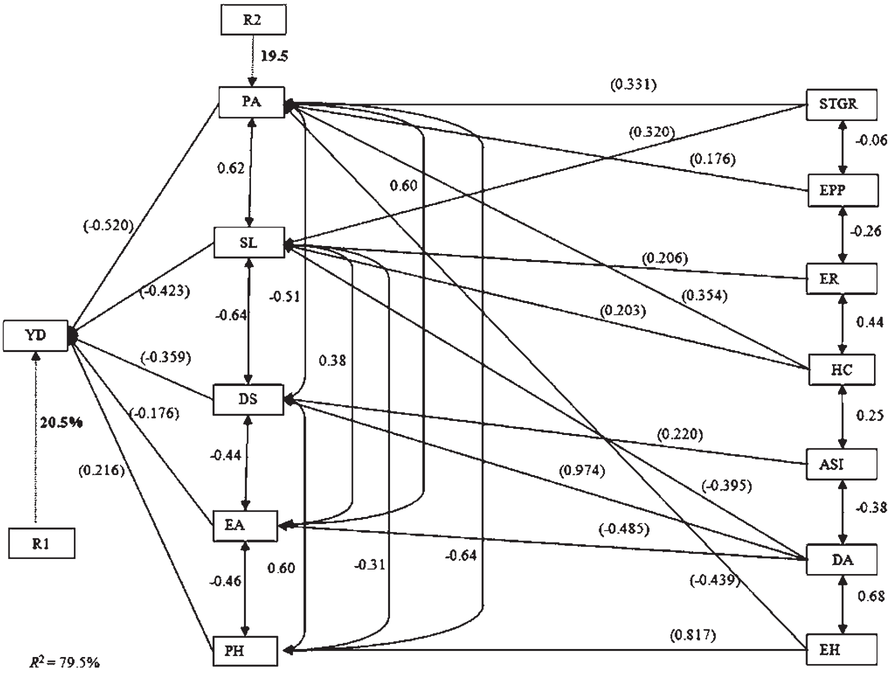

Fig. 13.1 Sequential path analysis showing relationship between grain yield and other agronomic traits of 56 maize cultivars evaluated under low-N conditions at four locations in Nigeria between 2013 and 2014 growing seasons. Values in parenthesis indicate direct effects, and those without parenthesis indicate correlation coefficients. "R" means residual effects. Lines with single-arrow head imply direct effects, and double-arrowed lines indicate indirect effect. *YD* grain yield, *PA* plant aspect, *SL* stalk lodging, *DS* days to silking, *EA* ear aspect, *PH* plant height, *STGR* stay-green characteristic, *EPP* ears per plant, *ER* ear rot, *HC* husk cover, *ASI* anthesis–silking interval, *DA* days to anthesis, and *EH* ear height

lodging (0.32). Ears per plant had an indirect contribution to yield through only plant aspect (0.18). Ear rot indirectly contributed to grain yield through stalk lodging (0.21). Also, husk cover had an indirect contribution to yield through plant aspect (0.35) and stalk lodging (0.20). Anthesis–silking interval contributed to yield indirectly through days to silking (0.22). Days to anthesis had the highest contribution to yield indirectly through days to silking (0.97) followed by ear aspect (0.49) and stalk lodging (0.40), while ear height had an indirect contribution to yield through plant aspect (0.43) and plant height (0.82). Under high-N environments, plant aspect (0.55) and ear aspect (0.45) were the only traits identified to have high direct effects on grain yield (Fig. 13.2). The two traits accounted for 93.6% of the total variation in grain yield. The days to anthesis contributed to yield indirectly through plant aspect (0.28) and ear aspect (0.27). Husk cover indirectly contributed to yield through only plant aspect (0.29). Moreover, stalk lodging indirectly contributed to grain yield through plant aspect (0.29) and ear aspect (0.52). Plant height had an indirect

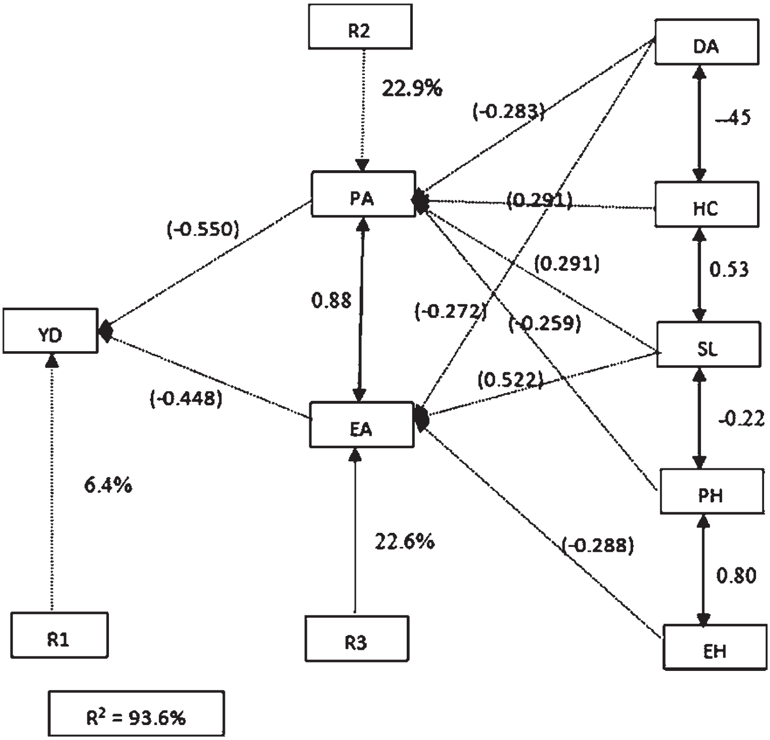

Fig. 13.2 Sequential path analysis showing relationship between grain yield and other agronomic traits of 56 maize cultivars evaluated under high-N conditions at four locations in Nigeria between 2013 and 2014 growing seasons. Values in parenthesis indicate direct effects, and those without parenthesis indicate correlation coefficients. “R” means residual effects. Lines with a single arrow head imply direct effects, and double-arrowed lines indicate indirect effect. *YD* grain yield, *PA* plant aspect, *EA* ear aspect, *DA* days to anthesis, *HC* husk cover, *SL* stalk lodging, *PH* plant height, and *EH* ear height

contribution to yield through plant aspect (0.26), while ear height contributed to yield indirectly through ear aspect (0.29).

Significant gains in grain yield obtained under low N were associated with decrease in ASI and stalk lodging, increase in plant height, and improved husk cover, plant and ear aspects, and stay-green characteristic. However, under high-N environments, increase in grain yield was associated with decrease in stalk lodging and ear rot, increase in plant height, and improved husk cover, plant, and ear aspects.

An impressive production improvement in era 3 relative to earlier eras was observed in the present study. For example, mean grain yield of era 3 genotypes was 242 and 296% higher than the mean of era 1 under low and high N, respectively. The mean genetic gains of 314,292 and 49,353 kg ha^{-1} per era (2.14 and 2.56% per year) in grain yield under low- and high-N environments in the present study are substantially greater than the 165 and 225 kg ha^{-1} per era (0·55 and 0·94% per year) gains reported by Badu-Apraku et al. (2015) for early-maturing cultivars under low- and high-N environments and the 0·41% per year reported by Kamara et al. (2004) for late-maturing maize cultivars developed from 1970 to 1999 in the West African savannas. Similar estimates obtained in the USA (e.g., Castleberry et al. 1984; Russell 1984) and Canada (Tollenaar 1989) were also much lower than those of the present study. Results of the present study and those of an earlier study involving the 56 extra-early cultivars evaluated under *Striga*-infested and *Striga*-free conditions, along with those obtained from studies involving 50 early-maturing cultivars conducted under drought, *Striga*-infested, optimum, and multiple stress environments (Badu-Apraku et al. 2013), together led to three deductions: (i) early and extra-early maize respond favorably to selection under imposed abiotic and biotic stresses of sub-Saharan Africa; (ii) selection for drought and/or *Striga* tolerance/resistance improves tolerance to low N but not as much as the response to direct selection for low-N tolerance; and (iii) selection under stress gives value addition to performance under the non-stress (or optimum) counterpart of the stress conditions.

The breeding approach used in this program may be considered as a type of tandem selection. During the first era, the major focus of the genetic enhancement program was on the selection for drought tolerance and resistance to maize streak virus disease. During the second era, the major breeding emphasis was on recurrent selection for improved *Striga* resistance with increased emphasis on selection for drought tolerance. Beginning from 2007 (the third era), selection for *Striga* resistance continued, but, in addition, the source populations were subjected to improvement for tolerance to drought and low N. Usually, the best materials in one era formed the base populations for improvement in the next era. This strategy resulted in the development of several cultivars with combined resistance and/or tolerance to the three stresses (Badu-Apraku et al. 2016). Improvements in the preceding era definitely made significant positive contributions to the performance of the next era, cumulatively resulting in the outstanding performance of era 3 cultivars compared with the eras 1 and 2 cultivars.

This study reports on the first extensive genetic research on extra-early maize in WCA, covering nearly a quarter of a century. Outstanding materials developed in each era have been submitted for international trials, and a number of them have been released as varieties in the different WCA countries. The genetic gains made in the study are quite high, an evidence that improved varieties can continue to be developed and released for commercial production in the near future. However, the breeders should not expect such high gains to continue, unless conscious efforts are made and adequate precautions are taken to preempt decreased responses. Such preparations could include introgression of new sources of favorable genes for the desired stress tolerance or resistance, study of the best strategy to sustain improved response, development of optimum stress screening sites, identification of secondary traits for improved response under stress, and development of efficacious methodology that would make research execution progress at minimum cost. Scientists at IITA, in collaboration with national scientists in WCA, have initiated investigations in nearly all of these areas, although more work needs to be done for perfection. For example, screening sites for drought, *Striga*, and low N have been identified and are being used in our research, including the study reported here.

A second important objective of this study was to determine trait associations for improved performance under low and high N in WCA. In this case, stepwise regression and sequential path coefficient analyses were used to partition the secondary traits into groups and their level of influence on grain yield (the primary trait) under low-, high-, and across N environments. Sequential path coefficient analysis effectively led to clear knowledge and understanding of the interrelationships among the traits evaluated in the present study. Apart from the STGR (assayed under only low-N environments), the same traits were determined under low and high N. The structures of the path diagrams of the traits with grain yield were strongly influenced by N level. Whereas under low N, the secondary traits were only in two groups, they were in four groups under high N. However, two traits—plant aspect (PA) and ear aspect (EA)—were common to both N levels in the first group of secondary traits having direct effect on grain yield. In earlier studies, IITA scientists (Badu-Apraku et al. 2013b; Badu-Apraku et al. 2011) have reported that the stay-green characteristic, plant and ear aspects, husk cover, and plant and ear heights were the most reliable traits for selecting for improved grain yield in low-N environments. Results of our study justify the use of some of these traits. The decrease in ASI, and improvement in ear aspect, plant aspect, and stay-green characteristic, which were associated with the gains in grain yield under low N, justifies the inclusion of the traits in the IITA base index for selecting for improved grain yield under low-N environments. It is striking, however, that the anthesis–silking interval, the stay-green characteristic, and ears per plant, which have been used in the base index for selecting low-N-tolerant early genotypes (Lafitte and Edmeades 1994; Meseka et al. 2006; Badu-Apraku et al. 2011), were not among the traits associated with increased grain yield in the present study. Under low N, means for these traits had little or no changes from era 1 to era 3, whereas grain yield improved drastically among the eras. The present study, therefore, indicated that improvement in grain yield of extra-early maize germplasm may not result from changes in anthesis–silking interval, the stay-green characteristic, and ears per plant, unlike in some other maturity groups. An important selection strategy for extra-early maize germplasm, therefore, is to keep these traits, along with the traits plant height, ear height, and days to flowering (anthesis and silking) constant so that the extra-early cultivars do not become unnecessarily later maturing and/or taller.

13.11 Conclusions

Low-N-tolerant early and extra-early maize germplasm have been developed and are being subjected to genetic improvement at CIMMYT-Kenya and IITA-Nigeria in collaboration with national programs of some SSA countries. Reduced or non-firing of lower leaves of maize which is an N-deficiency symptom, along with timely flowering, short ASI, normal plant height, and high grain production indicated low-N tolerance. Application of only 30 kg N ha^{-1} to soils completely depleted of native N was quite effective for screening for low-N tolerance in maize.

Breeding for *Striga* resistance and drought tolerance in maize, both of which are normally done under low-N rates, was found to be also effective for developing low-N-tolerant maize in WCA. Low-N-tolerant selections maintain their performance when evaluated under high-N environments, but selections under high N do not necessary perform well under Low-N conditions. Both additive and nonadditive gene action condition the mode of inheritance of low N, although with a preponderance to additive gene action. Recurrent selection has been effectively used to improve several maize populations, including early and extra-early germplasm for low-N tolerance in SSA, and low-N-tolerant populations, varieties, inbred lines, and hybrids are now available in the region. Results of studies involving early and extra-early maize indicated that breeders must determine the best level of N rate and specific traits to use for screening and breeding maize for low-N tolerance. Breeding for tolerance to low N offers the most appropriate and sustainable approach for increased maize yields by small-scale farmers who utilize low agricultural input in SSA.

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Chapter 14
Breeding for Disease Resistance in Maize

14.1 Introduction

Around 15% of the world crop production is lost each year through outbreak of plant diseases (McDonald and Stukenbrock 2016). However, the proportion of crops lost due to plant diseases is higher in emerging and developing nations, especially in the tropics, and this increases food insecurity. Among the plant disease control methods are cultural practices, application of chemicals, the use of biocontrol agents, and the use of resistant germplasm. The use of resistant germplasm appears the most effective and practical means of controlling plant diseases. However, the usefulness of disease-resistant germplasm is dependent mainly on other agronomic characteristics of interest (e.g., yield and quality).

In order for disease infection to occur, it is necessary to have:

- A virulent pathogen, also known as disease-causing agent. Living or biotic agents described as pathogens are parasitic and include fungi, bacteria, viruses, mycoplasmas, nematodes, some insects, mites, and a few flowering plants.
- A host, which the causal organism will parasitize. Individuals on which the causal agent can survive (live and reproduce) are described as susceptible to the causal agent. Such individuals develop the characteristic symptoms of the disease associated with the presence of the causal agent.
- A conducive environment for infection. Atmospheric and soil environments greatly influence disease development by affecting activities of the pathogen and host physiology. The most critical environmental factors influencing disease development are air and soil temperature, free moisture, leaf wetness, soil pH and fertility, wind, and radiation.

Disease outbreaks may occur on a small or large scale. Large-scale, area-wide plant diseases are considered of epidemic nature. Knowledge and understanding of disease epidemiology is crucial for preventing and/or controlling diseases.

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Table 14.1 Effectiveness of host plant resistance relative to other methods in disease control of field, vegetable, and fruit crops

		% disease control by		
Crop	No. of diseases	Host resistance	Chemicals	Other means
Field crops	350	80	10	13
Vegetable crops	180	30	25	45
Fruit crops	120	15	20	60

Conditions that favor plant disease epidemics are:

- Narrow genetic base of crop germplasm
- Introduced pathogens
- Breakdown of genetic resistance
- Inadvertent breeding for susceptibility

14.2 Host Plant Resistance

The development of crop varieties that resist, tolerate, or escape the attack of pathogens is the most effective, simple, and economic means of reducing losses attributable to plant diseases in field crops, including maize (Table 14.1). Resistance to diseases varies among maize varieties, inbred lines, and hybrids. Inherent resistance or susceptibility may determine whether a large-scale epidemic of a given disease will occur or not. Hosts react differently to various pathogens. A *susceptible* host supports profuse disease development characterized by symptoms of the disease, poor growth, reduced physiological development, poor economic yield, and reduced quality of produce. A *tolerant* host supports profuse disease development characterized by symptoms of the disease but with little or no reduction in growth, physiological development, economic yield, and quality of produce. In this case, the host is attacked, but losses are below economic levels. The *resistant* host does not support disease development to any appreciable extent. Reduction in growth, physiological development, economic yield, and quality of produce are virtually negligible. An *immune* host prevents the establishment of the pathogen; therefore, it cannot reproduce on the host, and symptoms of the disease cannot be observed.

14.3 Maize Diseases of Economic Importance in SSA

All parts of the maize plant may be infected by one disease-causing organism or another. The most prominent diseases include the foliar diseases and the stem and ear rots. Foliar diseases of maize include the gray leaf spot (GLS) , northern corn leaf blight, corn rust, maize streak virus, and sorghum downy mildew. The *Aspergillus* and *Fusarium* ear rots constitute major ear rots.

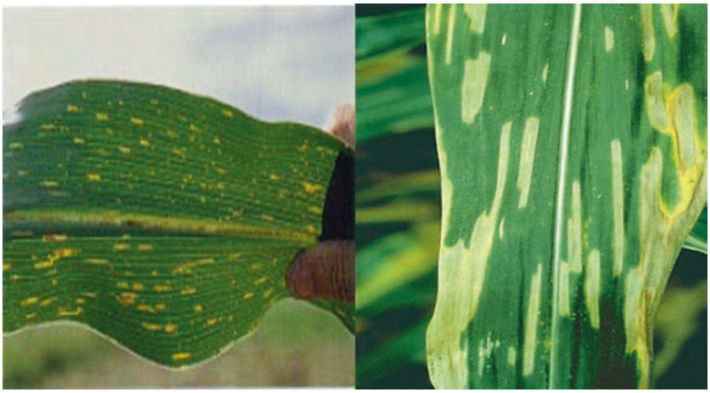


Plate 14.1 Typical symptoms of gray leaf spot (GLS)

Gray leaf spot GLS, incited by *Cercospora zeae-maydis*, is a major problem in SSA, particularly in mid- and high altitudes. In WA, it is a major problem in the mid-altitude savannas of Nigeria and Cameroon. The disease infection is favored by extended periods of leaf wetness and cool, cloudy conditions. The disease is characterized by lesions which run parallel to the leaf veins (Plate 14.1). Host plant resistance is the most effective and economically sustainable control method.

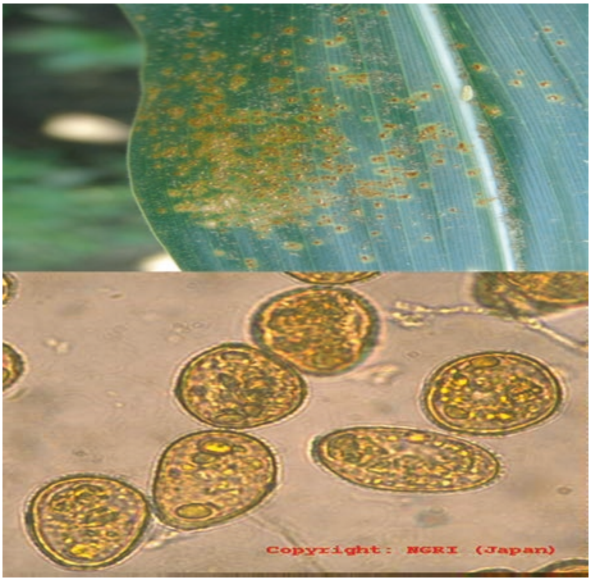
Northern corn leaf blight This disease is incited by *Exserohilum turcicum.* It is a worldwide disease of maize and occurs in the mid- and high altitudes of SSA. The disease development is favored by extended periods of leaf wetness and cool, cloudy conditions. However, we have observed that the disease has, in recent years, spread to the lowland areas of Nigeria including the forest agroecology (Ibadan, Ile-Ife, and Ikenne), the southern Guinea (Mokwa and Abuja), and the northern Guinea (Zaria and Samaru) savannas. The disease is characterized by oval, water-soaked spots which turn to elongated spindle-shaped necrotic lesions (Plate 14.2). The disease may be controlled by the use of crop rotation and resistant varieties.

Southern corn rust It is incited by *Puccinia polysora*. The disease is very prominent in the lowland tropics. It is characterized by light orange circular pustules that are present on both leaf surfaces; the pustules darken at plant maturity (Plate 14.3). The disease may be controlled by the use of crop rotation and resistant varieties. Host plant resistance is, however, the preferred method for control. Most IITA and CIMMYT maize varieties have resistance to *P. polysora*.

Maize streak virus (MSV) disease MSV is transmitted by the leafhopper, *Cicadulina mbila*. The disease is widespread on maize across Africa and is characterized by broken to almost continuous, narrow chlorotic streaks centered on secondary and tertiary leaf veins (Fajemisin and Shoyinka 1976). Streaks are distributed uniformly over the leaf surface (Plate 14.4). The infected leaves are chlorotic with broken yellow streaks along the veins, leaving irregular green lines or islands centered between veinlets. The disease results in severe stunting of infected maize.

Plate 14.2 Symptoms of the northern corn leaf blight incited by *Exserohilum turcicum*

Plate 14.3 Symptoms of the southern corn rust incited by *Puccinia polysora.* The rust spores are shown on the *right*



Most IITA and CIMMYT varieties possess resistance to MSV. Information on the genetics of resistance and the development of resistant varieties that attracted the King Bouldin International Award by IITA is presented in greater detail later in this chapter.

Sorghum downy mildew It is incited by *Peronosclerospora sorghi* (Weston and Uppal) C.G. Shaw and attacks sorghum and maize among other cereals. The disease is commonly found on these crops in Asia and Africa. The strain associated with maize survives in hydromorphic valleys as well as on some grasses during the dry season. The disease is characterized by chlorotic striping of leaves and leaf sheaths (Plate 14.5), along with dwarfing. The disease is systemic, and symptoms intensify

Plate 14.4 The vector of maize streak virus and the leaf hopper *Cicadulina mbila* (*left*) and the symptoms of the disease on a single maize leaf (*middle*) and foliage (*right*)

Plate 14.5 Symptoms of the maize strain of downy mildew incited by *Peronosclerospora sorghi* (Weston and Uppal; C.G. Shaw), with "crazy top" on the *right*

with age, resulting in a symptom referred to as "crazy top," a malformation of the upper portion of the adult plant, including the tassel. Downy mildew may be controlled by seed treatment with the systemic fungicides such as the Apron Plus and resistant varieties developed by IITA. Most varieties released in Nigeria within the last three decades are downy mildew resistant (DMR), and the spread of the disease has been effectively curtailed.

Plate 14.6 Maize ear rots incited by *A. flavus* Link:Fr. and *F. moniliforme* Sheldon

Ear rots Maize ear rots occur in most parts of the world where maize is cultivated. *Aspergillus* species and *Fusarium* species are the primary causal agents of ear rots in maize (Plate 14.6). Incidence of ear rots in the field and/or in storage reduces grain quantity and quality, especially in places where maize is harvested under high rainfall conditions or with high grain moisture content. *A. flavus* Link:Fr. and *F. verticillioides* are the predominant fungi that incite ear rots. Apart from damage caused to the grain, these fungi produce mycotoxins on the grain. The contamination of maize and maize products by mycotoxins is responsible for several human and animal diseases in many parts of the world, particularly in Africa (Ngoko et al. 2003; Bandyopadhyay et al. 2007; Udomkun et al. 2017).

Human populations across SSA are chronically exposed to dangerous mycotoxin levels (Probst et al. 2014; Udomkun et al. 2017). *F. verticillioides* produces fumonisins, a carcinogenic mycotoxin that targets the liver and kidney (Waalwijk et al. 2008). *A. flavus* produces aflatoxins, the most potent carcinogen found in nature, which causes immune system suppression, liver cancer, child stunting, and, in some cases, death (Probst et al. 2012). The presence of these fungi and their associated mycotoxins has been reported in all WA countries where surveys have been conducted. For example, in a study conducted by Probst et al. (2014), more than 300 maize samples from 18 countries in SSA were examined for both aflatoxin-producing fungi infection and content of aflatoxin, fumonisins, and deoxynivalenol (a mycotoxin produced primarily by *F. graminearum*). Over 60% of the maize samples contained aflatoxins, and 47% exceeded the tolerance thresholds. The majority of maize (81%) contained fumonisins with 49% of it harboring dangerous concentrations. In addition, 40% of the maize had deoxynivalenol, although only 4% had concentrations above the safe thresholds (Table 14.2). This study provided evidence that contamination of maize with multiple mycotoxins is common throughout SSA. The researchers provided a strong case to implement interventions aimed to reduce incidences and severities of mycotoxin contamination events across SSA.

Table 14.2 Mycotoxin contamination of maize samples from 18 African nations

Country, region	No. of samples	Aflatoxin (μg/kg)[a]			Fumonisin (μg/g)[a]			Deoxynivalenol (μg/g)[a]		
		Avg.[b]	Min.[c]	Max.[d]	Avg.	Min.	Max.	Avg.	Min.	Max.
Burkina Faso	50	25	0	609	1	0	4	n/a[c]	n/a	n/a
Cameroon	16	15	0	122	1	0	4	0	0	0
DR Congo, East	12	63	0	393	2	0	9	1	0	4
DR Congo, Bas	10	12	0.1	57	1	0	5	0.1	0	0.4
Ethiopia	81	3	0	23	5	0	150	0.4	0	3
Ghana	7	0.1	0.2	0.2	0.4	0	1	0	0	0
Ivory Coast	4	7	2	21	0.2	0	0.5	0.2	0	0.4
Kenya, Coast	9	102	0	525	18	0.5	50	0.2	0	0.4
Kenya, Rift Valley	13	11	0	87	1	0	4	0.3	0	1
Malawi	9	12	5	20	2	1	9	0	0	0
Mali	7	4	0	6	1	0	3	0	0	0
Mozambique	42	0	0	0	2	0	10	0	0	0
Rwanda	16	0	0	0.3	0.3	0	1	0	0	0.5
Senegal	20	47	0.3	395	2	0	9	0.1	0	0.5
Sierra Leone	17	23	2	162	0.1	0	1	0.1	0	0.5
Somalia	6	133	1	1407	5	0	9	0.2	0	1
Tanzania	5	2	0	7	1	0	5	0	0	0
Uganda	17	95	0	435	2	0	19	0.8	0	8
Zambia	28	7	0	108	2	0	21	n/a	n/a	n/a
Zimbabwe	19	9	0	123	105	36	159	1	0.0	12

[a] Mycotoxin concentrations were determined by EUSA. Limits of detections are 1 μg/kg (aflatoxins), 0.5 μg/g (fumonisins), and 0.1 μg/g (DON)

[b] Avg., average concentration

[c] Min., minimum concentration

[d] Max., maximum concentration

[e] n/a, data not available

Ear rots may be controlled through the use of host plant resistance and, in the case of *Aspergillus* ear rot, the use of biological control agents, such as non-toxigenic (i.e., atoxigenic that do not produce aflatoxins) strains of *A. flavus*. Atoxigenic strains competitively displace toxigenic strains of *A. flavus* when applied in the field at the right maize development stage. Other options that mitigate ear rots include early planting, timely harvesting of the grains, proper drying of the grain to a safe storage moisture immediately after harvesting, storing in bags and in optimal structures, and effective insect control, especially the field-to-store pests such as weevils.

Maize lethal necrosis (MLN) Maize lethal necrosis (MLN) is incited by the synergistic effect of *maize chlorotic mottle virus* (MCMV; Tombusviridae: *Machlomovirus*) and any *potyvirus*, including *maize dwarf mosaic virus* (MDMV), *sugarcane mosaic virus* (SCMV), and *wheat streak mosaic virus* (WSMV) (Achon et al. 2017). First reported in Kenya in 2011 (Wangai et al. 2012), MLN has spread to Tanzania, Uganda, Rwanda, Ethiopia, Democratic Republic of Congo (Lukanda et al. 2014), Swaziland, and probably other surrounding countries (Isabirye and Rwomushana 2016), a clear indication that the disease has a great potential to devastate maize production across Africa. Simulation studies by Isabirye and Rwomushana (2016) indicated that Ethiopia, Tanzania, and Democratic Republic of Congo have the potential to lose over 600 km^2 potential maize landmass each due to attack by MLN. Rwanda, Burundi, and Swaziland have the potential to lose 100% and Uganda over 88% of their maize crop by 2020 if MLN is not controlled. MLN risk in Africa is high, especially in East and Central Africa, which are the hot spots for the disease. MLN symptoms include chlorosis, stunted growth, dead heart and necrosis, mottling of leaves, and sterility or poor grain fill. Symptoms start manifesting at about 4 weeks after planting (WAP), popularly referred to as the "knee height" stage or the 7–8 leaves stage. In some environments, symptoms do not appear until booting or tasseling and, very rarely, at the seedling stage (Kagoda et al. 2016). Most of the maize varieties and hybrids grown in Kenya, Uganda, and Tanzania are highly susceptible to MLN, and the disease now poses a potentially significant threat to maize production in WCA also.

14.4 History of Breeding for Disease Resistance in West Africa

In West Africa (WA), the importance of maize as a food crop was more widely recognized in 1950 during the epidemic outbreak of the American rust (caused by *Puccinia polysora* Underw.) that nearly wiped out the crop in the sub-region (van Eijnatten 1965). Governments in the sub-region responded rapidly to the outbreak and saved the situation through mass importation of rust-resistant varieties from Central America and making these available to farmers. Also a program was put in place to conduct sustainable long-term research to control the disease. One of the major measures put in place was the establishment of the West African Maize Research Unit (WAMRU) in Ibadan, Nigeria. Through the WAMRU, a systematic collection of locally available maize germplasm was initiated in 1953 for evaluation and improvement. Based on the results of the evaluation trials, the local varieties were grouped into four distinct classes by Van Eijnatten (1965). The classes included the Western floury types, Eastern floury types, Southern flints, and Northern flints. By 1965 research into maize improvement had been initiated with the four maize classes as the source materials for the genetic enhancement. The breeders quickly recognized the differential response of the different maize classes to the natural

Table 14.3 Percentage of total area in subtropical, mid-altitude, transition zone, and highland maize with the economic losses to diseases[a]

Diseases	(%)
Turcicum leaf blight (*E. turcicum*)	58.6
Common rust (*P. sorghi*)	34.2
Downy mildew (all genera and spp.)	29.4
Maize streak disease	15.5
Corn stunt complex (CSS, MBS, MRFV)	1.8
Ear rots (*Fusarium* spp., *Stenocarpella* spp., *Aspergillus* spp.)	55.9
Stalk rots (*Fusarium* spp., *Stenocarpella* spp., *M. phaseolina*, *C. maydis*, *A. strictum*, *Pythium* spp., and *E. chrysanthemi*)	32.1

[a]CIMMYT Maize Program 1988. Maize production regions in developing countries

Table 14.4 Percentage of total area in tropical lowland maize with economic losses to diseases[a]

Diseases	(%)
Maydis leaf blight (*B. maydis*)	25.5
Polysora rust (*P. polysora*)	33.3
Downy mildew (all genera and spp.)	30.5
Maize streak disease	17.6
Corn stunt complex (CSS, MBS, MRFV)	11.1
Ear rots (*Fusarium* spp., *Stenocarpella* spp., *Aspergillus* spp.)	44.0
Stalk rots (*Fusarium* spp., *Stenocarpella* spp., *M. phaseolina*, *C. maydis*, *A. strictum*)	26.7

[a]CIMMYT Maize Program 1988. Maize production regions in developing countries

agroecologies in Nigeria. Experiences gained by the maize breeders in those early years of maize improvement led to the establishment of several important concepts that have largely guided maize breeding in WA to date. The concepts include:

- Continuous germplasm collection and evaluation of sources of disease-resistant genes for upgrading breeding populations
- Incorporation of multiple disease defenses into breeding populations before extraction of varieties from such populations for release to farmers

Apart from *P. polysora*, several other diseases received research attention at the initial stages of maize improvement in WA. These included the leaf blight incited by *Cochliobolus heterostrophus* (*Helminthosporium maydis* Nisik. and Miy.); leaf and sheath rot (*Corticium solani*); maize gray leaf spot (*Pyricularia grisea*); adult maize stem rot [*Pythium aphanidermatum* (Eds.) Fitz.]; leaf scorch, also referred to as leaf scald; and white blast (*Trichometaspheria turcia*). Presented in Table 14.3 is the summary of the diseases and the extent of damage caused on maize in subtropical, mid-altitude, transition zone, and highland agroecologies, while Table 14.4 is the summary for tropical lowland agroecologies. There is an urgent need to update the information summarized in Tables 14.3 and 14.4, especially when one considers the much intervention that has gone into breeding for disease resistance since the 1980s when the data summarized in the two tables were collected.

14.5 Breeding for Disease Resistance in IITA

Breeding for disease resistance was the first step, and has continued to be part of efforts, to improve maize in WA. Diseases such as *Curvularia* leaf spot, *Physoderma* brown spot, *Physopellazeae* (Mains) Cummins and Ramachar, downy mildew incited by *P. sorghi* (Weston and Uppal), several virus diseases, and the stalk, ear, and storage rots have received focused research attention during the last three decades (Fajemisin 1975, 1978; Fajemisin et al. 1976; Oyekan 1977; Ladipo et al. 1993; Fakorede et al. 2001b).

The efforts, however, were complicated by several factors that made it difficult to achieve the desired impact in a relatively short time. First, the important diseases changed with time. For example, streak virus disease that was relatively unimportant up to about 1970 became the most devastating disease in WA in the 1980s. Downy mildew that was unknown in the early stages of maize breeding in the subregion "came on stage" in the early 1970s, specifically in Nigeria from where it would have spread to the other countries but for the timely intervention with the development of resistant varieties. GLS was for many years affecting maize production only in East Africa but has now become an important disease also in the mid-altitudes of Nigeria and Cameroon where it was not known for many years.

Second, some diseases were specific to particular agroecologies, whereas others were present in all agroecologies. The highland blight (*E. turcicum* Pass.) and the highland rust (*P. sorghi* Schw.) were confined to the mid-altitude savannas of Nigeria and Cameroon. Downy mildew of maize was first reported in Africa in South Africa (Storey and Mclean 1930), followed by Egypt (Melchers 1931) and, thereafter, many other eastern, southern, and central African countries, including Zimbabwe, Zambia, Botswana, Malawi, Kenya, Uganda, Tanzania, Rwanda, Sudan, Somalia, Mozambique, Zaire, and the Democratic Republic of Congo (Adenle and Cardwell 1999). The first report of downy mildew in WA was on sorghum in Northern Nigeria by Harris (1962), but by 1970 maize was also found to be susceptible to the disease in Nigeria, specifically in Samaru, Kaduna State, Nigeria (IITA 1975). By 1975, the disease was observed on maize in Ondo State, Southwest Nigeria, and in Kabba around the same time (IITA 1979; Oyekan et al. 1990). For many years, the disease was largely confined to these parts of the country with a rather slow spread to parts of Edo and Delta States and certain parts of Ondo State. In 1990, however, the disease started spreading rapidly to the southwestern part of Nigeria, through Ilesha and Ile-Ife to the whole of the present Osun and Oyo States. By the early 1990s, it had virtually covered the states south of the Niger River from which the disease has been reported in other countries of WA including Ghana and Côte d'Ivoire (Kenneth 1976), although the disease did not reach epidemic proportions in the two countries.

Third, it was difficult to inoculate maize with some of the disease-causing organisms for effective screening of the germplasm for resistance. Particularly, the downy mildew organism could not be cultured artificially, and maize plants had to be artificially inoculated during the night with infected plants. Similarly, the natural occurrence of *Cicadulina* leafhopper, the insect that transmits streak virus to maize, was erratic and unreliable for breeding for resistance. Furthermore, the cost of facilities for artificial rearing of the insect was too high for the national programs to bear.

Fourth, because of the difficulty of artificially inoculating maize plants for screening for resistance, breeders could not study the genetics of resistance of some of the diseases. It was therefore difficult to develop resistant varieties.

The idea of breeding for resistance to multiple diseases was initiated during the early years of maize breeding in the sub-region. In Nigeria, for example, a synthetic variety, ES2 with resistance to lowland leaf blight (*Helminthosporium maydis*), and NCBRbU, which combined resistance to rust and blight with upright leaf orientation, were released by NARS in the 1960s. Because of the menace of the streak virus disease, the two varieties and another two, TZB and TZPB, developed by IITA in the 1970s could not produce yield up to their genetic potential.

For a long time, the yield potential of the mid-altitude savanna (MAS) could not be exploited because varieties specifically adapted to the agroecology were not available. Varieties developed for lowland agroecologies performed poorly in the MAS. In the mid-1980s, IITA developed the variety TZMSR that combined SR with resistance to highland blight (*E. turcicum*) and highland rust (*P. sorghi*). TZMSR was designated Plateau No. 1 by the Plateau State Agricultural Development Project (PSADP) and released to farmers.

14.6 Screening for Disease Resistance in WA: General Considerations

Two broad approaches are used for screening for disease resistance in the IITA Maize Program, including natural infection in hot spots and artificial inoculation. Hot spots are locations where a disease of interest is endemic and the host plant cannot escape attack by the disease-causing organism. Artificial inoculation is carried out by the researcher or technicians in experimental stations or other locations directly under the control of the researcher. Depending on the number of genotypes, the type of disease, the environmental requirements for infection, the inoculum availability, and the type of study, artificial inoculation could be carried out in a screenhouse, greenhouse, or field. For the two methods, the type of disease (foliar vs soilborne), the nature of infectivity of the disease organism, the stage of plant growth for optimal infection, and the available facilities are carefully considered.

Hot spots facilitate screening of large numbers of genotypes at relatively low costs with a high certainty of no escapes. Artificial inoculation may rely on the spreader (infector) row approach or direct inoculation in individual maize plants. The spreader rows are planted 3 weeks earlier than the genotypes to be screened and become infected by conidia produced on the border plants. The artificial inoculation method is quite effective in ensuring that there are no escapes, but it is time-consuming and much more expensive than the hot-spot approach. Furthermore, both resistant and susceptible varieties are included in trials to serve as checks for the genotypes being screened. Disease screening sites utilized by IITA in Nigeria included Ibadan and Ikenne for maize streak virus (MSV) and ear/stalk rots, Jos for gray leaf spot (GLS), and Akure for downy mildew.

14.7 Case Studies of Breeding Maize for Disease Resistance in SSA

Case Study 1: Breeding for Resistance to Maize Streak Virus

In 1975, a collaborative research project involving IITA, the NARS of WA, and, later, CIMMYT was initiated with emphasis on breeding streak-resistant maize germplasm. Scientists developed reliable screening methods for resistance; identified and reared the most active vector, *Cicadulina triangular*, for virus transmission; identified sources of resistance; studied the genetics of resistance; and screened thousands of lines and populations from CIMMYT, IITA, Agricultural Research Institutes (ARIs) from WA, and other parts of the world for resistance (Efron et al. 1989).

14.7.1 Development of Streak-Resistant Maize Germplasm and Varietal Improvement

Employing the backcross method, elite varieties and breeding populations from various sources were converted to streak resistant (SR) at IITA by breeders from IITA, CIMMYT, and the ARIs. Two sources of resistance were identified in IITA. The first was from an inbred line, IB 32, derived from a maize population, TZ-Y, developed from a cross between Tuxpeño Planta Baja and an unknown yellow germplasm source from East Africa. The second source of resistance was found in La Revolution, a variety from Réunion Island. These sources served as the donor parents in the SR Conversion Project.

Studies on the genetics of resistance to the streak virus revealed monogenic inheritance from some sources such as La Revolution (Bjarnason 1984; Efron et al. 1989) and oligogenic inheritance controlled by two to three genes from other sources such as IB 32 (Kim et al. 1982). This implied that in general, simple selection procedures could be used to breed for resistance to the disease. In some cases,

Plate 14.7 MSV-susceptible variety surrounded by resistant varieties under field conditions at the vegetative (*top*) and flowering (*bottom*) stages

the level of resistance was upgraded from as low as 2% to nearly 100% after a few cycles of selection under streak pressure. Studies at IITA revealed that for all practical purposes, four backcrosses are sufficient for conversion of open-pollinating populations to SR. Consequently, selection was done during backcrossing, and recurrent selection was used to further improve the converted populations. In order to ensure that escapee plants were not selected, a conscious effort was made to avoid selecting symptomless plants during backcrossing. Selected plants had at least a trace of the streak symptom to confirm that they had been truly infected but had the capacity to restrict the reproduction and spread of the virus (Plate 14.7).

Varietal improvement was initiated at IITA in the early 1970s. Using the Nigerian Composite A (NCA) and Nigerian Composite B (NCB) as base populations, two varieties, TZA and TZB, were developed in the mid-1970s. TZB was high yielding and well adapted to the savanna agroecologies, and soon became more widely accepted than TZA by farmers in WA.

Plate 14.8 MSV-susceptible variety planted into spreader rows 3 weeks before planting the genotypes to be screened for resistance under field conditions

14.7.2 Field Screening for MSV Resistance

Around the same period in the mid-1970s, another variety, TZPB, was developed from Planta Baja of the Tuxpeño land race from CIMMYT, Mexico. TZPB had outstanding grain-yield performance in all agroecologies but appeared more adapted to the forest and forest–savanna transition agroecologies than the savanna (Fakorede et al. 1989). The two varieties TZB and TZPB, along with a yellow-grained variety designated Western Yellow developed by the Institute of Agricultural Research and Training (IAR&T), in Ibadan, Nigeria, gained much popularity among farmers in the northern and southern agroecological zones of Nigeria. Although high yielding, these as well as other varieties in the country were susceptible to the maize streak virus. To develop SR varieties, resistant plants from the TZ-Y maize population were crossed to TZPB, and resistant plants and the progeny were separated into yellow and white grain types to form the first two SR varieties, TZSR-W and TZSR-Y. This was followed by the development of several other varieties including TZSR-W-1 and TZSR-Y-1, which were improved versions of TZSR-W and TZSR-Y, respectively. Early-maturing SR populations were also developed including TZESR-W and TZESR-Y. The initial set of SR varieties was developed either by crossing existing elite varieties to SR sources or through the recombination of streak-resistant individual plants at the S_3 or S_4 generation of inbreeding to form synthetic varieties. Intrapopulation improvement methods (recurrent selection) were also used to increase the frequency of SR genes in several populations. This was achieved through the International Progeny Testing Trials (IPTTs). For the IPTTs, about 250 families (half-sibs, full-sibs, or S_1's) were extracted from the population to be improved, and this was evaluated in four to six international locations. The families were challenged by controlled infection of the streak virus (Plate 14.8) and other diseases. Remnant seeds of the most outstanding ten families were recombined to form an experimental variety (EV) for each location. The top ten families across locations were also recombined to form an EV. The EVs were named after each location or across locations, year, and source population, for example, Farako-Ba 85 TZSR-W-1 across 8443-SR. Apart from improving the SR level, the IPTT approach resulted also in the improvement of the agronomic traits and grain yield of the populations. More importantly, IPTTs served as one of the vehicles through which SR germplasm was disseminated to the NARS. IITA scientists produced seed of the EVs for each site, packaged the international trials, and dispatched them to interested NARS for evaluation. The NARS were encouraged to select the most adapted and outstanding varieties in the trials for commercialization. At various times during the execution of the SR Conversion Project at IITA, NARS maize breeders from Benin, Cameroon, Ghana, Nigeria, and Togo were offered visiting collaborating scientist positions for about 1 year to acquire hands-on experience in breeding for SR. *Cicadulina*-rearing facilities were also established in several ARI research stations. Presently, many NARS scientists have been trained to carry out SR conversion at the national level. Artificial infestation of breeding materials with viruliferous *C. triangular* is now a standard practice for maize breeders at IITA and many WA national maize programs.

14.7.3 Effects of the SR Gene Block on Other Traits of Maize

A common observation of plant breeders is that selection for one trait often leads to changes in other (unselected) traits. Such associated changes are referred to as correlated responses. While some correlated responses are desirable, others are not. The desire of maize breeders therefore is that increased grain yield would be associated with the SR gene block with negligible changes, if any, in other traits of the converted populations. Several studies to monitor correlated responses in breeding for SR in maize have been carried out. In one such study, the performance of 14 SR maize populations was compared with that of their non-SR counterparts in yield trials during the late season when streak virus infection was known to be highest (Ladipo and Fakorede 1992). The trials were conducted at IITA, National Seed Service (NSS, Ibadan), and Apata (near Ibadan) in 1988 and the Teaching and Research Farm of Obafemi Awolowo University, Ile-Ife, in 1989. The trial at IITA was artificially infested with *Cicadulina*, but the other sites had natural infestation of the insect. Two treatments, streak and streak-free, were imposed on the entries in each location. Application of Furadan, a highly toxic carbamate pesticide, to the plots resulted in the streak-free treatment. The results summarized in Table 14.5 showed that the SR germplasm produced higher grain yield than the non-SR counterpart and had better standability, better husk cover, and better ear aspect.

However, it did not differ from the non-SR counterpart in maturity but was slightly taller. In another experiment, Fakorede (1995) crossed three SR populations and their non-SR counterparts to each of four testers to determine whether the SR

Table 14.5 Means for grain yield and agronomic traits of 14 SR maize populations and their non-SR counterparts evaluated under streak pressure and streak-free environments (Fakorede et al. 2001b)

Trait	SR	Non-SR	LSD.05	Comments
Grain yield (t/ha)	2.5	1.8	0.16	SR 38% higher
Days to 50% silking	54.8	55.0	NS	No change
Plant height (cm)	178.6	162.2	4.0	SR taller
Ear height (cm)	90.8	82.9	2.7	SR taller
Root lodging (%)	1.9	2.3	NS	No change
Stalk lodging (%)	2.6	3.1	0.5	SR stood better
Husk cover (%)	1.7	2.1	0.3	SR better cover
Ear number per plot	27	22	1.2	SR more productive
Ear aspect rating	3.8	4.6	0.2	SR better
Kernel moisture (%)	27.1	26.4	NS	No change

Table 14.6 Grain yield (t/ha) of three SR maize populations and their non-SR counterparts testcrossed to four testers (Fakorede et al. 2001b)

	Testers				
Entry	4001	9490	9499	8329-15	Mean
EV8731-SR	3.06	3.12	3.04	3.32	3.14
Across 8331	3.24	3.82	2.76	2.78	3.15
Across 8628-SR	2.24	3.16	2.26	4.62	3.07
Across 8328	2.50	3.94	3.46	2.30	3.05
EV 8435-SR	3.90	2.84	2.38	3.58	3.18
Across 8035	2.26	1.76	2.66	2.70	2.35
Mean	2.87	3.11	2.76	3.22	

gene block had induced changes in the combining ability of the maize populations. The plants were protected from streak by the application of Furadan. Means for grain yield showed that on average, the general combining ability (GCA) of the SR and non-SR populations did not change, although a highly significant population × tester interaction was observed (Table 14.6).

Kim and Ajala (1996) also examined the changes in GCA associated with the SR gene block among 10 SR and their 10 non-SR maize populations in diallel crosses evaluated in 1989 and 1990. The sign of the GCA for five of the SR populations remained the same in their diallel cross as in the non-SR populations (Table 14.7). On the other hand, the sign associated with the other five populations changed at the different levels of the SR gene block. This suggested that the introduction of the SR gene may have somewhat affected the additive genetic variance of the latter five populations. Further studies were needed to determine the changes associated with the SR gene block in the converted populations. In 1991 when the project came to an end, most of the available breeding populations and lines from CIMMYT and IITA and many elite varieties from the NARS had been converted to SR. In addition, many NARS scientists had improved capacity to carry out SR conversion at the national level.

Table 14.7 General combining ability (GCA) for the grain yield of 10 SR maize populations and their non-SR counterparts in diallel crosses conducted in Nigeria, 1989 and 1990 (Kim and Ajala 1996)

	GCA, t/ha	
Population	SR	Non-SR
TZB	0.36	0.18
TZPB	0.19	−0.13
TZSR-W	−0.16	0.11
Across 7721	−0.13	−0.11
Poza Rica 7822	−0.08	0.02
Across 7823	0.26	−0.20
Poza Rica 7729	−0.08	−0.01
Across 7832	0.09	0.03
Poza Rica 7843	−0.22	0.25
Population 49	−0.22	−0.13

Also, IITA has been distributing primarily SR maize germplasm to African countries and beyond. Maize varieties released in WA countries during the last three decades are SR. The payoff from these efforts is that MSV is no longer a serious threat to maize production in WA. SR varieties, such as TZSR-W and TZSR-Y, and many derived varieties were released in the late 1970s and early 1980s. Varieties combining downy mildew resistance (DMR) with SR, such as DMR-LSR-W, DMR-LSR-Y, DMR-ESR-W, and DMR-ESR-Y, were developed and released in the 1990s (Fakorede et al. 1993). Maize production in WA has been greatly boosted by the availability of SR germplasm.

Case Study 2: Breeding for Downy Mildew Resistance

Increased production and productivity of maize is threatened in many SSA countries by downy mildew, a fungal disease caused by *Peronosclerospora sorghi*. The pathogen causes one of the most destructive diseases of maize in the world (Frederiksen and Renfro 1977). Infection results in plants with stiff, narrow, yellowed leaves, and inflorescences can be so distorted that cobs are not formed normally but are replaced by a mass of twisted leaves referred to as "crazy top."

Two pathotypes of *P. sorghi* have been reported, one capable of infecting both maize and sorghum and the other specific to maize (Anaso et al. 1987; Olanya and Fajemisin 1993). In Northern Nigeria, downy mildew has been reported on sorghum since 1962 (Harris 1962) and on maize since 1970 (King and Webster 1970). In that region, maize plants become infected primarily from oospores in the soil, and generally disease incidence is low (Bock and Adenle 1991). In Southern Nigeria, downy mildew occurred on maize in 1975 (IITA 1975; Fajemisin 1980). The maize strain of *P. sorghi* in the south does not seem to infect sorghum, even when susceptible varieties are exposed to *P. sorghi* conidia from infected maize (Olanya and Fajemisin 1993). The strain associated exclusively with maize has been reported in several other countries in Africa, including Botswana, Kenya, Malawi, Mozambique, Rwanda, Somalia, Sudan, Tanzania, Uganda, Zambia, Zaire, Cameroon, and Zimbabwe (Adenle and Cardwell 1997, 1999; Ngoko et al. 2008).

P. sorghi produces conidia and oospores. The conidia, which are copiously produced, are thin walled and ephemeral and allow for rapid polycyclic increase and spread of an epidemic within a season. Oospores are thick-walled, long-lived perennating stages for the pathogen and are involved in its long-distance movement through seed and soil. Early workers in Nigeria could not find oospores of the maize strain of *P. sorghi* in either maize or sorghum; therefore, seed transmission was considered unlikely (Anaso et al. 1987; Olanya and Fajemisin 1993). It was hypothesized that *P. sorghi* survived the dry seasons only on maize grown in perennially wet inland valleys (Anaso 1989; Olanya and Fajemisin 1993; Bock 1995; Gupta 1995). However, seed-borne mycelia and oospores of *P. sorghi* found in nubbins of systemically infected maize were believed to indicate at least some potential for disease transmission through seed (Adenle and Cardwell 1997). Adenle and Cardwell (1999) examined several maize seed sources for the maize-infecting strain of *P. sorghi* and to clarify survival of the pathogen between cropping seasons. The studies established that the disease was seed-borne and could be transmitted from seed bought from the open market, the popular seed source for most of the farmers in the downy mildew endemic parts of Southwest Nigeria (Adenle and Cardwell 1997, 1999). The studies further established that nubbin seed disease transmission was quite prevalent, especially when the seed was freshly collected and without fungicide treatment. In both cases, after the seed had been allowed to dry and had been stored for some time, infection levels did not decrease. In some of the experiments, infected seedlings were observed from Apron Plus-treated seed, an indication of internal infection by *P. sorghi*, possibly due to the presence of oospores. The levels of transmission from seed from the local market also confirmed that seed transmission can occur even at low seed moisture content as noted earlier by Safeeulla and Shetty (1977). This is significant because a single diseased plant is enough to generate an epidemic under favorable climatic conditions. It has been shown that infected leaves can produce as much as 12,000 conidia per cm^{-2} leaf area per day (Safeeulla 1976).

According to Chang (1970), infected seed of maize can act as a carrier of disease only if planted immediately after harvest or if moisture content remains >20%. Results of the studies of Adenle and Cardwell showed that moisture content had no effect on downy mildew development from nubbin seeds, as infections were observed even on seeds stored for >9 months and at 8.5% moisture content. Another important point that came out of the studies of Adenle and Cardwell (1999) is that seeds collected from healthy-looking maize plants are not necessarily free of *P. sorghi*, as shown in the silk-inoculation experiments. Seed transmission of the maize strain of *P. sorghi* was a subject of speculation. Histological evidence of both mycelia and oospores in the kernels of systemically infected maize seeds, and mycelia in seeds inoculated via silks, showed the potential for seed transmission. After many years of finding no oospores of the strain associated exclusively with maize, it is now apparent that over-seasoning spores will occur in the seeds of late, systemically infected maize plants.

14.7.4 Screening Maize for Downy Mildew Resistance

Methods of inoculum delivery and timing of test-row planting were assessed for efficacy in promoting development of downy mildew in susceptible maize and for cost of implementation in terms of personnel and labor. Direct inoculation of pregerminated seed of spreader rows resulted in consistent and high incidence of downy mildew-infected plants and required substantially less labor and inoculum than the spray inoculation of spreader rows. The optimum time to plant test rows was around 15 days after inoculation of spreader rows. Breeding lines were screened for resistance using the improved inoculation method. Following a cycle of screening using the new method, resistance levels improved by about 44% over the previous cycle. When seed of the silk-inoculated varieties was planted in the greenhouse, there was a significant effect of time of inoculation relative to pollination and a significant variety by treatment interaction ($P < 0.05$) on percentage infection. Suwan 1, the "resistant" variety, had more seed-borne infection than the susceptible variety in the inoculated treatments, but the non-inoculated controls of Suwan 1 showed no infection. The susceptible variety, TZSR-W, had a greater percentage of infected plants in the inoculated treatments than the control, but the treatment difference in this variety was insignificant.

14.7.5 Improvement of Maize Populations for Resistance to Downy Mildew

Upgrading levels of disease resistance is a prime objective of maize breeding programs. Effectiveness of the S_1 recurrent selection in improving levels of resistance to downy mildew (DM) infection was assessed in Nigeria from 1997 to 2000 in six maize populations. Improvement procedures involved the evaluation of S_1 progenies under artificial infection with DM spores and in disease-free environments and using a selection index to select simultaneously for reduced DM infection with appropriate agronomic characters from more than one environment. Three to four cycles of selection were completed in each of the populations. Products from the different cycles of selection were evaluated, and data were collected on DM infection parameters and agronomic traits. Result demonstrated that three to four cycles of selection were adequate to reduce DM infection levels significantly and increase grain yield. DM infection decreased by between 58 and 100%, while grain yield increased from 10 to 98% for the two to four cycles of selection relative to the C_0. Selection increased grain yield accompanied by acceptable changes in plant height while maintaining maturity in disease-free environments.

14.7.6 Deployment of Downy Mildew-Resistant Maize Varieties in West and Central Africa (WCA)

DM can reach epidemic proportions within a relatively short period, and in the early 1990s, a DM epidemic struck parts of Africa. Before this period, the disease appeared to have been confined to the areas where it was first found in 1975–1976. IITA breeders had been working on the problem for over 20 years, and a small stock of improved DM-resistant maize seed was available. It was estimated that 6000 tons of seed was required to combat the disease, and it became apparent that this was beyond the capacity of either the public or private sector seed multiplication and distribution systems to provide. IITA developed an integrated pest management (IPM) program incorporating the use of resistant varieties combined with practices such as early planting, chemical seed treatment, and good farm sanitation (removal of infected plants). There was a joint effort with the Nigerian Federal Ministry of Agriculture to create awareness about the disease. Sponsored by the Food and Agriculture Organization of the United Nations (FAO), the World Bank, and Novartis, this campaign reached an estimated 50% of those at risk through radio broadcasts and other media. In 1995, various initiatives began to implement the IPM program and to produce sufficient quantities of seed of resistant varieties. IITA, the Nigerian National Seed Service, private seed companies, and the World Bank pooled human and material resources together to increase and distribute DM-resistant varieties of maize to farmers in SSA. An NGO, World Vision, teamed up with IITA to saturate parts of Oyo State, Nigeria, with resistant varieties, working with local farmers themselves to multiply seeds. Spore traps were set up to monitor the spread and intensity of the disease. The pathogen lost the battle, with fewer and fewer spores being produced and the dreaded “crazy top” disappearing from maize fields in Nigeria. Assessments conducted in 1998 showed that >50% of farmers were aware of the disease. Farmers now know how to recognize and control the disease and prevent its spread, using an IPM package of improved DM-resistant varieties and fertilizers. Maize yield and total production have as a result increased in WCA.

Although the epidemic was controlled in Nigeria, DM disease is still present in some other parts of SSA. Seeds of resistant varieties must continue to be made available in such areas, and priority attention should be given to continual adaptation of varieties for DM resistance, training of extension agents on IPM principles for disease control, and, with sufficient donor support, large-scale deployment of seeds of resistant varieties to endemic regions.

Case Study 3: Breeding Maize for Ear Rot and Mycotoxin Resistance

The fungus *Aspergillus flavus* is the primary producer of aflatoxins, a group of highly toxic and carcinogenic mycotoxins that is frequently found in several crops including maize, groundnut, cottonseed, and tree nuts (Amaike and Keller 2011). Aflatoxins undermine human health in several ways: cause liver cancer, are immune system suppressors, and cause stunted growth of children. In addition, reduced weight gain, capillary fragility, reduced fertility, and even death have been attributed to aflatoxin exposure. Typically, the fungus has an olive-green/yellowish appearance when growing on maize kernels. The fungus is ubiquitous in nature, but its population increases during hot, dry weather. Aflatoxin contamination is typically greater in maize that has been produced under stress conditions. Thus, stresses resulting from drought, heat, insect, nematode, and fertilizer are all conducive to production of high aflatoxin concentrations.

Aflatoxin contamination of crops have received substantial attention in WCA during the past two decades (Bandyopadhyay et al. 2016; Bankole et al. 2006). The presence of aflatoxin in maize can result in reduced price for grain or even rejection. However, those maize lots that become rejected from premium markets enter local and informal markets at a low price, and this results in increased aflatoxin exposure of poor people. Infection of maize kernels by toxigenic fungi is still a major challenge facing researchers of WCA despite considerable progress from decades of research. The available infrastructure and grain storage practices in WCA are not able to prevent postharvest development of mycotoxins, and as a result aflatoxins remain a major threat to maize production, productivity, and grain quality in the sub-region. Because most mycotoxin problems start in the field, strategies are urgently needed to prevent infection of growing plants by toxigenic fungi.

Mycotoxin-producing fungi, particularly aflatoxin-producing fungi, are widely distributed in nature and are favored by high temperature and humidity. Temperatures ranging from 80 to 100 °F (about 27–37 °C) and a relative humidity of 85% (18–20% moisture in the grain) are optimum for fungal growth and toxin production. Growth of these fungi does not occur below 12–13% moisture in the grain. In order to minimize the level of mycotoxins in maize, the following practices are recommended:

- Use recommended crop production practices.
- Plant early.
- Irrigate to reduce drought stress.
- Minimize insect damage.
- Harvest early.
- Avoid kernel damage during harvest.
- Dry and store maize properly—13% or less moisture.
- Keep storage facilities clean.

The use of cultural practices such as crop rotation, tillage, planting date, and fertilization may not be sufficient to reduce fungal infection and subsequent mycotoxin accumulation. Development of genetic resistance to the fungus *A. flavus*, but also to *Gibberella zeae*, and *Fusarium* spp. in maize is, therefore, a high priority in WCA. Maize breeders at IITA are in the process of developing maize inbred lines and hybrids with good levels of resistance to the mycotoxin-producing fungi mentioned above or that have less tendency to accumulate the respective toxins that those fungi produce. Sources of resistance to each of these pathogens have been identified and have been incorporated into our breeding program. However, none of the available commercial cultivars have adequate levels of resistance. For example, although the available aflatoxin-resistant cultivars developed by IITA and partners tend to have lower levels of aflatoxin than other cultivars grown under the same conditions, complete resistance has not been achieved. A combination of host plant resistance and management practices such as the use of atoxigenic fungi, good insect control, and timely fertilization may reduce damage to the maize plant, and thus lower aflatoxin levels will occur. Various options have been proposed for minimizing aflatoxin contamination in maize. However, host plant resistance remains the most widely explored strategy as *A. flavus* infects the susceptible maize crop before harvest. The following section discusses the progress made by the IITA Maize Improvement Program in combating the threat of aflatoxin through host plant resistance and the use of atoxigenic fungi.

14.7.7 Host Plant Resistance

The IITA Maize Improvement Program in partnership with scientists from the US Department of Agriculture-Agricultural Research Service (USDA-ARS-SRRC) has developed and released six maize inbred lines with resistance to aflatoxin contamination. The lines are well adapted to the lowlands of WCA. These lines, designated TZAR101 through TZAR106, have also been registered in the USA. The research was co-funded by FAS-USDA-ARS, USAID, and IITA. Through collaboration for almost a decade, USDA-ARS plant pathologist, Robert Brown, and IITA maize breeder, Abebe Menkir, developed the new maize lines through conventional breeding by crossing the best aflatoxin-resistant lines from the USA (GT-MAS:gk, MI82, and Mp420) with tropical elite lines found in WCA (1368, 4001, and KU1414-SR) (Brown et al. 2001). Apart from demonstrating good resistance against aflatoxin accumulation under laboratory and field tests, most of these new maize lines also possess other commercially desirable traits and resistance to diseases such as leaf blight and southern corn rust.

According to Brown et al. (2006), as these inbred lines were derived from parents of both tropical and temperate origin, they are likely to contain new combinations of complimentary alleles contributing resistance to aflatoxin accumulation. These are being exploited by maize breeders as new sources of resistance for developing maize cultivars with higher levels of resistance to *A. flavus* infection and aflatoxin contamination. The inbreds are also serving as invaluable sources of resistance to foliar diseases as well as desirable agronomic traits for broadening the genetic base of adapted US and tropical maize germplasm to accelerate the development of productive new cultivars. The resistant lines with good agronomic traits could be used as parents to accelerate breeding efforts against aflatoxin contamination of national programs in WCA.

Plate 14.9 Maize kernels infected with aflatoxin (*left*) and inoculation of an ear of maize with conidial suspension of the fungus using a syringe (*right*)

14.7.8 Screening Methodologies for Aspergillus *and* Fusarium *Ear Rot*

Two approaches are being used in screening maize genotypes for resistance to *Aspergillus* and *Fusarium* ear rots. These are the field screening and in vitro screening methods. The inoculation method for *Fusarium* ear rot caused by *Fusarium verticillioides* in IITA is described in detail by Afolabi et al. (2007). The inoculum is prepared from cultures of *F. verticillioides* (ATCC MYA 836) for field inoculation. The *F. verticillioides* isolate was obtained from a naturally infected ear in Ibadan, routinely maintained on modified Czapek-Dox complete medium (20), and stored in 15% glycerol at −80 °C. Prior to inoculation, cultures are grown on modified Czapek-Dox complete medium at approximately 25 °C under 12 h of diurnal fluorescent light for 7 days. Conidia are washed from the surface of the agar media with sterile distilled water, and the resulting propagule suspension is strained through two layers of cheesecloth. Sterile distilled water is used to adjust the conidial concentration to 1×10^6 conidia/ml as determined using a hemacytometer and amended with Tween-20 surfactant (polyoxyethylene (20) sorbitan monolaurate; Fisher Biotech, Fairlawn, NJ) at 0.2 ml/liter. The inoculum suspension is used within 2 h of preparation. Ears are inoculated using a syringe (Cornwall Luer-Lok) fitted to a continuous pipetting outfit (Becton, Dickinson and Company, Rutherford, NJ). The conidial suspension (4 ml) is injected down the silk channel of the primary ears of all plants at the blister (R2) growth stage (Plates 14.9, 14.10, and 14.11).

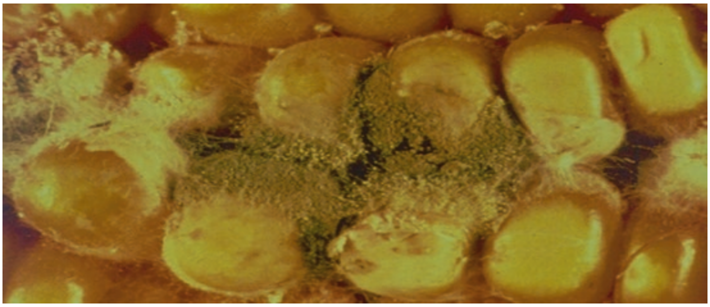


Plate 14.10 The fungus *Aspergillus flavus* sporulating on corn (By courtesy of Bandyopadhyay 2010)

Plate 14.11 Corn kernels infected with *Fusarium moniliforme* (*upper row*) showing "starburst" symptom (By courtesy of Bandyopadhyay 2010)

Ears are covered after inoculation with waxed paper shoot bags for 2 days to maintain high humidity and to protect the inoculum from being drained by rain or dried by excessive heat. For disease assessment, ears are manually harvested at maturity. At each harvest date, ten ears in an experimental unit (plot) are hand-picked, dehusked, and evaluated for severity of ear rot symptoms. Disease severity is assessed by determining the percentage of each ear covered by symptoms using a seven-class rating scale in which 1 = no infection, 2 = 1–3%, 3 = 4–10%, 4 = 11–25%, 5 = 26–50%, 6 = 51–75%, and 7 = 76–100% of the kernels exhibiting visible symptoms of infection, such as rot and pinkish or white mycelial growth. Based on this scale, genotypes with disease severity ≤3 (i.e., with less than 10% visible symptoms on ears) are selected. Ears are sun-dried after disease assessment to approximately 14% grain moisture content. The grains are hand-shelled and bulked by plots, and samples of each plot are separated into symptomless and symptomatic fractions (discolored kernels). The latter fraction contains kernels that are visibly moldy, darkened, streaked, or chalky in appearance. The incidence of discolored kernels was determined by expressing the number of visibly discolored kernels as a proportion of 200 grains from bulked samples of each plot multiplied by 100.

14.7.9 Field Screening for Resistance to **Aspergillus** *Ear Rot and Aflatoxin Accumulation*

Initial strategies employed by the IITA Maize Improvement Program to increase the level of resistance to aflatoxin in maize were to screen maize germplasm at Ikenne and Ibadan under natural aflatoxin-producing fungal pressure (hot spots) for resistance to ear rot using a score based on the proportion of the ears showing ear rot infection on a scale of 1–5 where 1 = little or no rot and 5 = most of the ears rotten. Through this program, most of the materials from the improvement program have moderate levels of resistance to ear rot. However, resistance to *Aspergillus* ear rot is not correlated with resistance to aflatoxin formation. Some maize germplasm may allow low levels of fungal infection but would allow accumulation of high aflatoxin levels (Brown et al. 1999; Ortega-Beltran et al. 2014). Indeed, maize germplasm may have quantitative trait loci (QTL) associated with resistance to both fungal infection and aflatoxin formation or solely to one of those traits (Mayfield et al. 2011; Warburton et al. 2011; White et al. 1995). Current strategies rely on field inoculation of toxigenic *A. flavus* strains broadcasted in a similar manner as biocontrol agents (Meseka, unpublished). Briefly, maize field soils are inoculated with toxigenic strains 2–3 weeks before flowering. Roasted, sterile sorghum grains coated with spores of the toxigenic strains are broadcasted in the field at a rate of 100 kg of coated sorghum per hectare, which is 10× the dose used for biocontrol application. Using this type of inoculation ensures that >80% of the fungi colonizing the target crop (i.e., maize) belongs to the applied strain (Atehnkeng et al. 2016; Bandyopadhyay et al. 2016). Hence, all tested germplasm is exposed to high densities of the toxigenic strain. This strategy has been employed since 2014.

14.7.10 Aflasafe™

It is estimated that about US $1.2 billion is lost annually due to aflatoxin contamination, with African economies suffering some US $450 million yearly losses. Aflatoxins presently constitute nontariff barriers to international trade since agricultural products that have more than the permissible levels of contamination are rejected (Bandyopadhyay 2010).

IITA scientists have developed a cost-effective, safe, and natural biocontrol technology that limits aflatoxin accumulation in maize when used during maize development (Bandyopadhyay et al. 2016). The biocontrol technology works by introducing native (local) strains of the fungus *A. flavus* that do not produce aflatoxins (i.e., atoxigenic) and which will outcompete aflatoxin producers in the treated fields. When applied at the correct growth stage (i.e., 2–3 weeks before crop flowering), the beneficial fungi competitively displace the aflatoxin-producing fungi residing in the treated field. IITA has developed several aflatoxin biocontrol products under the tradename Aflasafe. Currently, Aflasafe products have been registered for use in Nigeria, Kenya, Senegal, and the Gambia. Products for Burkina Faso, Ghana, Burundi, Mozambique, Malawi, Zambia, Tanzania, Uganda, and Rwanda are under different stages of the development process (Bandyopadhyay et al. 2016). In addition, more Aflasafe products are expected to be developed for other nations. Institutions involved in the development of Aflasafe products include IITA, Agricultural Research Service of the US Department of Agriculture, AATF, and NARS partners of nations where activities are being conducted.

The atoxigenic strains of Aflasafe remain with the crop throughout harvest and storage and until crops are consumed; hence, the protection is from field to fork. Aflasafe™ manufacturing plant is operating in Nigeria and supplies Aflasafe™ to maize growers throughout this nation. Products used in other nations were manufactured in this plant as well, although new Aflasafe plants will become available in Kenya and Senegal, in the near future. Throughout SSA, there is a huge demand for quality maize and groundnut. Bandyopadhyay (2010) estimated that over 60% of harvested maize in Nigeria has high levels of aflatoxins and are likely to be rejected by the feed industry. This is typical in many SSA nations (Udomkun et al. 2017). However, through the use of Aflasafe™, the large majority of the treated maize harbors concentrations of less than 20 ppb, which is a safe aflatoxin concentration. This represents aflatoxin reductions in treated fields of up to 99% less aflatoxins in comparison to maize from non-treated fields. Farmers, aggregators, traders, and industries throughout Nigeria now have their first practical aflatoxin mitigation tool. Health and trade sector within this nation receive benefits due to the production of aflatoxin safe crops. In the near future, large-scale use of Aflasafe in Kenya, Senegal, and the Gambia will result in similar benefits. This is also expected to occur in the other nations where Aflasafe will become available in the next few years.

14.7.11 Combination of Maize Resistance and Aflasafe™

One other aspect of the effort to minimize aflatoxin acceptable safe levels involves a combination of aflatoxin-resistant variety with Aflasafe™ treatment at the farmer's level. On-station trials of the combination conducted at IITA (Table 14.8) effectively reduced aflatoxin production on the resistant maize varieties relative to the susceptible variety (personal communication with Dr. Togola, Plant Pathologist, IITA, Ibadan, Nigeria).

Table 14.8 Aflatoxin (ppb) in aflatoxin-resistant (low-aflatoxin) maize synthetics and a susceptible variety with and without Aflasafe™ treatment

	At harvest		After poor storage	
Experimental variety	Control	Aflasafe™	Control	Aflasafe™
RSYN2-Y	19.6	1.7	462	44
RSYN3-W	6.9	1.8	627	38
SYN3-Y	18.4	1.7	387	19
TZB-SR (susc.)	57.5	4.7	1152	163

Case Study 4: Breeding Maize for Maize Lethal Necrosis (MLN) Resistance
MLN outbreak in East Africa clearly shows that infection by MCMV alone can cause severe chlorosis and severe yield reduction in maize. MCMV is transmitted by thrips and beetles, and SCMV is transmitted by aphids. These insects are known to be endemic in most maize production regions. Susceptible crop varieties can sustain yield loss of 30% to 100%. As the virus can be transmitted by seeds harvested from infected plants, importation of commercial seeds to WCA from areas that are affected by MLN can have negative impact on food security of the farming communities that depend on maize as a source of their livelihoods. The MDMV, transmitted by the leafhopper, *Peregrinus maidis*, is more damaging than MCMV (Ming et al. 1997). However, the former disease can be effectively controlled by regular insecticide applications. MDMV resistance in maize is monogenic, but its resistance does not provide resistance to MCMV. When both viruses are present in maize, MLN results and the plants often age prematurely (Nelson and Brewbaker 2011).

Breeding for host plant resistance is the most effective strategy for virus disease control. The development of maize inbred lines, hybrids, and synthetics with resistance to MLN for testing, release, and deployment with active involvement of partners is urgently needed in SSA to preempt MLN from wiping out maize in the continent. Research along this direction has been initiated primarily by CIMMYT in collaboration with IITA and national programs. In some studies, CIMMYT screened over 700 maize inbred lines collected from CIMMYT, IITA, and KALRO and pre-commercial hybrids in Naivasha (Kenya) under artificial inoculation with the two viruses (MCMV and MDMV) and found that most of the materials were susceptible to MLN. A good source of germplasm for MLN resistance is the facility established in East Africa with support from the Bill & Melinda Gates Foundation and the Syngenta Foundation for Sustainable Agriculture to combat MLN. Since its inception in 2013, researchers have evaluated over 60,000 accessions from more than 15 multinational and national seed companies and research programs (Munyiri and Fakorede 2016). Also, all of the several thousands of maize germplasm at IITA are routinely screened for resistance to several diseases, including viruses. The extensive screening of lines from the diverse sources led to the identification of some promising CIMMYT and IITA inbred lines with moderate levels of resistance to the disease. These encouraging results formed the basis for increasing the level of resistance through breeding to develop new MLN-resistant maize hybrids and varieties with high-yield potential and other desirable traits. The strategy for breeding MLN-resistant maize varieties includes the following activities:

- Continuous screening of a large number of elite drought and/or low soil nitrogen-tolerant and/or *Striga*-resistant germplasm under artificial inoculation in partnership with CIMMYT to identify MLN/MCMV-resistant lines and populations.
- Development of hybrids and synthetics from MLN/MCMV-resistant elite inbred lines.
- Extensive evaluation of the hybrids for immediate promotion, release, and commercialization by partners in the national programs.

- Provision of seed of MLN-resistant parental lines, hybrids, and open-pollinated varieties of maize to private seed companies and community-based seed producers for production, distribution, and marketing.
- Continued genetic enhancement of the maize germplasm by using the double haploid facilities at CIMMYT in Mexico to speed up the process of development of new inbred lines with much higher levels of resistance to MLN/MCMV from biparental crosses, backcrosses, and broad-based populations.
- Support the production of foundation and certified seeds of MLN-resistant varieties and hybrids that will be released in each participating country.

14.8 Conclusions

Maize disease resistance in SSA is under genetic control, some monogenic and others oligogenic or polygenic. Many inbred lines, hybrids, synthetic varieties, and populations resistant to the prevailing diseases are now available in all SSA countries and may be exploited to advantage by farmers. Level of resistance varies for each disease and the varieties; therefore, genetic enhancement must continue at the national and international institutes. Fortunately, there has been no report of breakdown of resistance, although it is potentially possible. CIMMYT and IITA must continue to backstop plant breeding research with advanced scientific methods such as molecular and double haploid approaches to genetic enhancement. This will speed up the development, release, and deployment of disease-resistant varieties, thus ensuring food security in SSA. Several important lessons in breeding for disease resistance have been learnt by SSA maize researchers: (i) occurrence of maize-devastating diseases changes with time, (ii) resistance to multiple diseases will result in stability of maize production, and (iii) diseases entering or developing in one section of the region may be curtailed from spreading across the region by quick action on screening the germplasm for resistance and deploying resistant varieties to neighboring areas/countries. This approach was successfully used in WCA to contain downy mildew from spreading beyond the areas of mass infection in Nigeria. That strategy may now be used to prevent MLN from spreading beyond the areas it has presently affected.

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Chapter 15
Breeding Maize for Insect Pest Resistance

15.1 Importance of Insect Pests of Maize

Insect pests severely limit the production and productivity of maize worldwide, with losses reaching millions of dollars annually. Many factors limit maize production; insects and mites are among the most important. Lepidopterous larvae are the most damaging insects of maize worldwide. This group includes stem and ear borers, armyworms, cutworms, and grain moths. Next in importance are the beetles (weevils, grain borers, rootworms, and white grubs), followed by the virus vectors (aphids and leafhoppers). Although it is difficult to estimate the losses caused by insects that attack maize in Africa, the figure is certainly in the millions of dollars annually.

From the evolutionary point of view, insects occupy the most diverse agroecologies on earth. Scientifically, insects are considered as one of the most successful classes of animals; over a million species are known to exist, and many are yet to be researched and classified into taxonomic groups. This success is attributed to the insect's great reproductive potential, small size, dispersal mechanisms, and ability to survive in harsh environments.

Daramola (1993) grouped insect pests of maize into three subheadings with emphasis on the damage they cause and available technologies to contain them. These are the field pests, the field-to-store pests, and the storage pests. Field pests are the insects that cause economic damage to the maize crop at any growth stage in the field; the stem and ear borer complex, armyworms, silkworms, and leafhoppers belong to this group. Stem and ear borers are members of the family Lepidoptera and are the most widely distributed, most destructive, and the best-known insect pests of maize in WCA (Adeyemi et al. 1966; Usua 1966; Adenuga 1977; Daramola 1993; Schulthess and Ajala 1999). The borer complex consists of *Sesamia calamistis* (Hampson), *Eldana saccharina* (Walker), and *Busseola fusca* (Fuller) (Lep: Noctuidae) which are stem borers, and the ear borer *Mussidia nigrivenella* (Ragonot)

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(Lep: Pyralidae). The borers have evolved with native grasses, sedges, some other wild hosts and, in the case of *M. nigrivenella*, various tree species. The borers occur on maize plants during the two seasons of the forest ecology of WCA, starting with *B. fusca* in the early season and later by *S. calamistis* and *E. saccharina*. Consequently, the borer complex causes greater damage in the late than early cropping season and in the forest and forest–savanna transition than the savanna agroecology. Armyworms, *Spodoptera exempta* Wik., are occasional insect pests whose larvae emerge in large numbers and, like an army, invade maize farms at the seedling or early vegetative phase. The larvae feed voraciously on the leaf blades leaving only the midribs thereby giving the plants a broom-like appearance. Because of the nature of attack, extensive damage is done within 1 or 2 days of infestation. Maize silkworms, *Diacrisia maculosa* Cr, and *D. penicillata* feed on the silk and most often into the husk thus preventing or reducing effective pollination and fertilization. The leafhoppers, *Cicadulina* spp., are the vectors for the streak virus of cereals and some grasses; otherwise, they are not known to cause any damage to maize on their own. Field-to-store pests are insects that infest maize in the field and continue their life cycle postharvest even into the store. The maize weevil, *Sitophilus* sp., is the most common field-to-store pest of maize. Others are the square neck beetle, *Cathartus quadricollis* Guer., *Heliothis armigera* Hbn., and, occasionally, *B. fusca*.

Storage pests are insects that attack maize grain in storage, including the maize and rice weevils, *Sitophilus zeamais* Moench, *S. oryzae* L., and, more recently, *Prostephanus truncatus* Horn. These pests and many others bore holes into and feed on the grain, beginning from the embryo. Within a short time, the grains are turned to powder that has no economic value.

For the purpose of this book, insect pests of maize are discussed in some greater detail in the following order:

- Stem borers
- Leaf and sap feeders
- Storage pests

15.1.1 Stem Borers

Lepidopterous stem borers are among the most important insect pests of maize in Africa. Four borer species cause significant yield loss:

- The maize stalk borer, *Busseola fusca* Fuller (Lepidoptera: Noctuidae)
- The pink stalk borer, *Sesamia calamistis* Hampson (Lepidoptera: Noctuidae)
- The African sugarcane borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae)
- The spotted stalk borer, *Chilo partellus* Swinhoe (Lepidoptera: Pyralidae)

The first three originated from Africa and are present in most countries of sub-Saharan Africa, while *C. partellus* is of Asian origin and only recently introduced to East Africa. It is not known in WCA.

Severity and nature of stem borer damage depend upon the borer species, the plant growth stage, the number of larvae feeding on the plant, and the plant's reaction to borer feeding. Almost all plant parts— leaves, stems, tassels, and ears— are attacked. Crop losses may result from death of the growing point (dead hearts), early leaf senescence, reduced translocation, lodging, and direct damage to the ears. The incidence of stalk and ear rots is increased by larval feeding, and the ears of lodged plants are often rotten. Yield losses caused by maize borers in Africa have been estimated to range from 10% to100%.

Maize stalk borers *Busseola fusca B. fusca* is often considered the most important pest of maize in sub-Saharan Africa. *B. fusca* is distributed from approximately 12 °N to 30 °S, but it does not occur in Madagascar or the Comoros. *B. fusca* was recognized as a major pest of cereals when originally described in 1901. In West Africa, the maize stalk borer is abundant in the drier savanna zone, especially where sorghum is grown. Sorghum is the native host of *B. fusca* in West Africa, and the insect is also abundant in the mid-altitude regions across the continent.

The adult moths generally emerge in the evening and mate. Females lay their eggs between the leaf sheaths of the host plant; egg batches contain from 30 to 100 eggs. On average, a female lays 400 eggs, and the eggs hatch in 6–7 days. Infestations start at young plant stages. Larvae crawl over the plants, congregate in the funnel, and feed on the rolled leaves. As the leaves grow away from the funnel, a characteristic pattern of holes or "window panes" can be seen. Continuous feeding by the larvae might result in the destruction of the growing point, typically referred to as "dead hearts." After killing a plant, larvae usually migrate to new plants and enter by boring into the stem near the base. Tunneling of the stem and ears then occurs. Larval development will take 26–33 days. When fully grown, larvae are 3–4 cm long and a pinkish-white color with small bluish-black spots along the sides of their bodies.

During the dry season, larvae (usually the third generation) enter diapause—a period of arrested development which usually occurs during adverse environmental conditions—and take up to 6 months to complete their development. With the initiation of the rains, the larvae pupate within the stems and adult moths emerge. Adults emerge 10–12 days after pupation.

Pink stalk borer *Sesamia calamistis*. Tams and Bowden (1952) described fifteen species of *Sesamia,* of which *S. calamistis* and *S. botanephaga* are the two most important ones in Africa. According to Bordat et al. (1977), the former species is present in most countries of sub-Saharan Africa, Madagascar, and the Comoros, while the latter is present in West Africa, Sudan, Uganda, and Kenya.

Adults of the pink stalk borer emerge in the late evening and behave similarly to *B. fusca*. The moths are pale-brownish with darker margins on the forewings and white hind wings. Eggs are laid between the leaf sheaths of the host plants. On average, each female lays around 300 eggs in a period of 5 days. Egg laying occurs from the time plants are 2 weeks old until flowering. The most serious damage, however, occurs at early plant stages.

Most larvae penetrate the stem shortly after the egg hatches. Larval feeding might result in dead hearts, and the tunneling and girdling activity of the larvae often results in stalk breakage. During the grain-filling period, the majority of the larvae are found in the ears. Development of the larvae takes 4–6 weeks; mature larvae are pink with a brown head, buff, and pink dorsal markings and about 3 cm long. Most larvae pupate within the stem or cobs.

Sesamia in contrast to *Busseola* breeds throughout the year and has no resting stage. However, it is less abundant during the dry season when it is limited to mature grasses (such as *Pennisetum purpureum*, *Setaria* spp., and *Rottboellia exaltata*) as a food source. The adult *Sesamia* spp. which emerge at the beginning of the cropping season are smaller and less fecund than those emerging later in the year. The combined effects of smaller numbers of less fecund adults result in lower incidence of *Sesamia* spp. in first season maize crops. As the rains progress, new growth of the native grasses and first season maize provide a suitable host for insect growth. In WCA, the population of this borer increases until it peaks around August–September. This occurs when second season maize crops are being grown, and as a result, *Sesamia* spp. can be a very serious problem; consequently, many farmers do not plant second season maize.

African sugarcane borer *Eldana saccharina*. This stem borer, presumably of West African origin, was first described in Sierra Leone and has progressively spread toward East Africa. It probably occurs in all suitable maize-growing areas of sub-Saharan Africa from approximately latitude 15 °N to 30 °S. The African sugarcane borer has been known as a pest of graminaceous crops in West Africa for more than a century. It has also been a very important pest in East Africa for many years, although its incidence in East Africa has increased since the 1970s.

In WCA, the importance of *Eldana* appears to be increasing in the savanna zones. *Eldana* is often the most abundant borer species at the end of the maize-growing season. Adults have pale brown forewings, with two small spots in the center, and whitish hind wings. Females begin laying eggs around flowering time of the maize plants. Eggs are yellow and oval and are laid on the plants or on debris on the soil. Up to 300 eggs are laid per female. Eggs hatch in 5 or 6 days, and larvae penetrate the stems or cobs. Larvae are grey or black and more active in habit than other stem borers. Larval development takes 21–35 days. Pupation occurs inside the stem, and the pupa is covered by a cocoon made of silk and plant debris. Adults emerge in 7–14 days, mate, and start the cycle all over.

A good external sign of *Eldana* attack is the adult exit-hole cut by the larvae prior to pupation, which often has a large amount of frass hanging from it. Although infestations by this stem borer occur relatively late in the development of the maize plants, damage as a result of their feeding can be severe with yield losses of up to 20%.

Spotted stalk borer *Chilo partellus*. The genus *Chilo* includes many species of borers which attack grasses and cereals and has worldwide distribution. In Africa, two species are of major importance, *C. partellus* and *C. orichalcociliellus*. *C. partellus*, an introduced species, was first recorded in Uganda in 1953 and is a very serious pest of maize and sorghum in East Africa. Its behavior and life cycle are similar to those of *Busseola*, but it does not undergo diapause. Infestations start when plants are young. Adults are brown-yellowish, with beige-colored front wings. The hind wings are pale straw in color in the male and white in the female. Females of *C. partellus* often lay their eggs on the lower surface of the leaves close to the midvein. Up to 300 eggs are laid per female in overlapping rows of 50–100. After 7 days, the eggs hatch and larvae crawl to the top of the plant where they feed on the leaves. Later, they move to the base of the stem and penetrate above an internode. Fully grown larvae are 2.5 cm long and buff in color with four longitudinal broken bands. After feeding inside the stem, larvae pupate; the complete life cycle has a duration of 6–7 weeks.

15.1.2 Leaf and Sap Feeders

Aphids Aphids are often present in large and dense colonies on leaves and tassels. If many aphids are present, leaves will be distorted and will show signs of chlorosis. A heavily damaged tassel might become sterile. This could be a problem for seed production. Vigorous plants are tolerant of aphid attack, and natural enemies usually provide sufficient control. If heavy infestations occur, Pirimor, an insecticide specific for aphids, or a systemic insecticide such as Dimethoate may be used.

Leafhoppers (*Cicadulina* spp.) (Homoptera: Cicadellidae) *Cicadulina* spp. are important as vectors of maize streak virus (MSV) and maize mottle/chlorotic stunt virus. *C. mbila* and *C. storeyi* are known to be the most important vectors of both viruses. Adult leafhoppers are small (2–3 mm long) and have transparent wings with a longitudinal stripe. Their body is yellowish with dark markings on the dorsum. Adults are commonly found resting on the upper surface of young maize leaves. The best control method is the use of streak-resistant varieties. Development of streak-resistant varieties has been discussed in Chap. 9.

Spittle bugs (*Poophilus* sp., *Locris* spp.) (Homoptera). Spittle bugs feed on leaves and within leaf whorls resulting in chlorotic spots and blotches on the leaves. Nymphs remain inside a foamy spittle mass (thus the name), while adults are active. Spittle bugs feed on various native grasses and can achieve high densities in late planted crops. In most cases, infested plants recover from damage, and natural enemies are active in controlling these pests so that no intervention is needed.

15.1.3 Storage Pests

Harvested maize grain, unless consumed soon after harvest, is vulnerable to attack by certain groups of insects, including weevils and grain borers.

Weevils *Sitophilus zeamais* and *S. oryzae* (Coleoptera: Curculionidae) *Sitophilus* weevils are the most important pests of stored maize. They occur in all warm and tropical parts of the world and cause heavy losses every year. Adults are long-lived (up to a year), and females lay eggs throughout most of their adult life. Each female can lay as much as 150 eggs. Eggs are laid individually in small holes made into the kernel by the female. Eggs hatch in 6 days, and the larvae feed inside the grain for approximately 25 days. Pupation occurs inside the grain, and the adult chews its way out of the kernel leaving a characteristic emergence hole. Total development periods ranges from 35–110 days depending on humidity, temperature conditions, and host. Adult weevils are reddish-brown to black with four reddish-orange circular markings on the wings. Separation of the two species requires examination of the genitalia.

Infestation normally starts in the field. A tight, long husk cover and harvesting as soon as possible after physiological maturity will reduce infestation. Storage should be free of weevils. Storage of maize on the cob with intact husks reduces weevil infestation. Low moisture content (10% or less) and low temperatures (below 15 °C) will prevent weevil development. Prior to storage, maize can be treated with Actellic 25 EC (20% solution) by spraying the insecticide with a spray gun. There is wide genetic diversity in maize in relation to susceptibility to weevil attack, and it is possible to develop varieties with some degree of resistance to weevils.

Larger grain borer (LGB) *Prostephanus truncatus* (Coleoptera: Bostiychidae) The LGB is a serious pest of maize and was recently introduced to Africa. It was first found in Tanzania from where it spread to other East African countries. More recently, it was accidentally introduced to Togo from where it moved into Benin and Ghana. According to experts, *P. truncates* has the potential to spread to all major maize-producing regions of Africa. Adults feed on maize grains on the cob both before and after harvest. Larvae also feed on grain. Damage is severe, and losses of maize stored in cribs are as high as 34% after 3–6 months storage. Grain dust is produced by the adults as they feed. Adults also feed on wooden structures and dry cassava. The strategy for the control of the LGB varies according to location/situation and has not yet been fully established. Hygiene of the storage place/containers is essential. Although the current recommendation is to shell the maize and treat with an admixture of pyrethroid insecticides, this is not practical under many situations due to unavailability of insecticides or cash to purchase them and farmers' reluctance to shell the grain due to labor constraints or in order to reduce weevil damage. The following insecticides are recommended (g/100 kg maize):

Permethrin	0.5% dust	–	55 g
Deltamethrin	0.2% dust	–	50 g
Fenvalerate	1.0% dust	–	50 g

Since the LGB is an introduced pest, there is potential for biological control. A predatory beetle, *Teretriosoma* sp., has been identified as a natural enemy of LGB, and work is underway in Africa for its possible release.

15.2 Principles of Insect Pest Control in Maize Production

Very few insects are pests; the great majority is beneficial to humans. For those insects that are pests, control measures must be devised to minimize the economic impact of their damage. Effective control requires knowledge on damage, biology, distribution, and life cycles of insects. Control methods include cultural, chemical, biological, and host plant resistance. Cultural control includes agronomic practices such as crop rotation, planting, and harvesting dates, crop refuse destruction, etc. Chemical control includes the use of insecticides as well as other chemicals (i.e., attractants, repellents). Biological control is the action of natural enemies (parasites, predators, and microbial agents) including naturally occurring agents and agents which are introduced and managed by humans for pest control (also referred to as "classical biological control"). Host plant resistance to insects is the genetic property that enables a plant to avoid, minimize, tolerate, or recover from injury caused by insects. The most effective and economical way of controlling pests is by combining agronomic practices with two or more control methods. The term integrated pest management is used to describe this concept, i.e., the management of pests by integrating control methods in an environmentally friendly manner.

When considering control of insect pests of maize in Africa, it is important to keep in mind that maize is an introduced crop which evolved in the Americas. The most damaging insect pests of maize in Africa, however, originated in the continent and evolved with the native grasses (i.e., stem borers and *Cicadulina* leafhoppers) and only "recently" adapted to feed on maize. Any attempt to control these pests must take into consideration the close association between their ecology and that of the native grasses. It is also essential to remember that farmers in Africa are already doing many things to reduce pest damage (though inadvertently) and that a great majority of them cannot purchase insecticides.

15.3 Breeding Maize for Borer Resistance

Whereas field-to-store and storage pests may be controlled effectively by insecticides, host plant resistance is the most effective means of controlling the field pests, especially the borers. Unfortunately, resistant or tolerant varieties were not available in WCA during the early (1961–1984) era of maize improvement in the sub-region. Breeding for insect resistance with emphasis on borers has been intensified since the mid-1980s by the Plant Health Management Division (PHMD) of IITA. Artificial borer rearing facility was established at IITA, Ibadan, thus making it possible to infest large numbers of lines and populations for screening purposes. The use of artificial diets became a big challenge because the ingredients were very expensive. However, they could now be reared on a more affordable pinto bean-based diet. Apart from the ingredients, other rearing materials could be obtained from MegaView Science (www.megaview.com.tw).

IITA's first approach to solving the borer problem is host plant resistance, and that was initiated in the early 1980s (Schulthess and Ajala 1999). IITA scientists studied and concluded that the inheritance of resistance was polygenic with varying levels of additive and nonadditive gene action involved. Several populations with varying levels of resistance have been developed and are now available. All the populations have streak resistance as well. Other approaches being studied at IITA include system analysis, biological control, habitat management, and integrated pest management.

Plant resistance to insect pests has advantages over other direct control strategies. For example, Teetes (2009) indicated that plant resistance to insects is compatible with insecticide use, and it is not density dependent, whereas biological control is. Plant resistance is specific, only affecting the target pest, and the effects are often cumulative over time. Usually the effectiveness of resistant cultivars is long-lasting. The role of plant resistance to insects in IPM has been well defined, at least in theory. However, the specific role a resistant cultivar plays in a particular IPM situation is crucial to successful deployment of the resistant cultivar. The impact of the resistant cultivar on standard cultural, biological, and insecticidal control methods should be well defined. Likewise, the impact of each of these control tactics on the resistant cultivar also must be defined.

15.4 Basic Terminology in Insect Resistance Studies

Several definitions have been used to convey the relative level of resistance in a plant. However, the problem of quantifying resistance continues to be a problem influencing farmer acceptance of insect-resistant cultivars. According to Teetes (2009), a better way to define resistance levels in agronomically improved resistant cultivars is through quantified comparisons of insect pest damage or plant yield loss of susceptible cultivars. Once insect pest abundance and damage to yield loss relationships have been established, economic threshold levels can be determined and combined with factors such as crop value and insect pest control costs to develop dynamic thresholds for use by producers. Dynamic thresholds provide a description of resistance and can reduce crop loss risk because limitations are known, and remedial action can be taken when necessary. By using this system to define relative differences in insect pest resistance between cultivars, it may be possible to simply indicate that a resistant cultivar has a higher economic threshold level than a traditional susceptible cultivar.

Insect-Resistant Plant Definitions of an insect-resistant plant are many and varied. In the broadest sense, plant resistance is defined as "the consequence of heritable plant qualities that result in a plant being relatively less damaged than a plant without the qualities." In practical agricultural terms, an insect-resistant crop cultivar is one that yields more than a susceptible cultivar when both are equally challenged with insect pest invasion. Resistance of plants is relative and is based on comparison with plants lacking the resistance characters, i.e., susceptible plants.

Insect Pest–Plant Host Relationship Insect-resistant crop varieties suppress insect pest abundance or elevate the damage tolerance level of the plants. In other words, insect-resistant plants alter the relationship an insect pest has with its host plant. How the relationship between the insect and plant is affected depends on the kind of resistance, including antibiosis, antixenosis (non-preference), or tolerance. ***Antibiosis*** resistance affects the biology of the insect so much that pest abundance and subsequent damage is reduced compared to that which would have occurred if the insect was on a susceptible crop variety. Antibiosis resistance often results in increased mortality or reduced longevity and reproduction of the insect. ***Antixenosis*** resistance affects the behavior of an insect pest and usually is expressed as non-preference of the insect for a resistant plant compared with a susceptible plant. ***Tolerance*** is resistance in which a plant is able to withstand or recover from damage caused by insect pest abundance equal to that damaging a plant without resistance characters (susceptible). Tolerance is a plant response to an insect pest. Thus, tolerance/resistance differs from antibiosis and antixenosis resistance in how it affects the insect–plant relationship. Antibiosis and antixenosis resistance cause an insect response when the insect attempts to use the resistant plant for food, oviposition, or shelter.

15.5 Artificial Infestation and Maize Screening Technique

Breeding maize for resistance to the European corn borer (ECB), *Ostrinia nubilalis* (Hübner), had been an important component of maize improvement in the Corn Belt of the USA for many years. The experience gained by the US maize researchers, specifically breeders and entomologists, over the years has been well documented in technical journals and other forms of publication. In addition, many graduate students from African countries have been trained in maize research in the universities located in the Corn Belt and elsewhere in the USA. Availability of this wealth of experience and the establishment of IITA in WCA, along with the presence of CIMMYT in several SSA countries, have served as the springboard that greatly facilitated the breeding efforts to improve maize for borer resistance in Africa.

Effective breeding for borer resistance started at IITA with the establishment of an insect rearing facility. This is a very expensive aspect of the research, especially the provision of the diet and conducive environment for the growth and reproduction of the insects. Egg masses are used for artificial infestation of the test plants; therefore, the conditions must be such that the insects would lay eggs maximally. For artificial infestation, egg masses are placed in leaf whorl of the maize plants about 2–3 weeks after emergence. The spreader row approach may also be used. In artificial infestation of the spreader row and/or test varieties or lines, individual plants must be infested with the egg masses. This makes the availability of mass rearing facility very important to the success of a breeding program for borer resistance. Natural infestation leads to a lot of escapes and is, therefore, not reliable. However, in the late 1990s, CIMMYT and IITA collaborated with the NARS of selected countries in WCA and ESA on a donor-funded project tagged Africa Maize Stress (AMS) Project in which "hot spots" were established for screening maize for resistance to specific abiotic and biotic stresses, one of which was the stem borer complex. A location was identified in SW Nigeria where screening under natural infestation is almost as reliable as under artificial infestation. That notwithstanding, genotypes selected under this situation were often subjected to further screening under artificial infestation to ensure that escapes were not selected as resistant.

In a recent study conducted in Kenya to screen 30 maize hybrids for borer resistance, Tefera et al. (2011) obtained first instar larvae (neonates) of *C. partellus* from the Kenya Agricultural Research Institute (KARI), Katumani, stem borer mass rearing laboratory, while *B. fusca* neonates were obtained from the International Center for Insect Physiology and Ecology (ICIPE), Nairobi, Kenya. Trials planted at Kiboko were infested with *C. partellus*, and trials at Embu infested with *B. fusca*. Three weeks after seedling emergence, each row was divided into two unequal portions where each of the five plants in the front part was infested with five neonates. The back part consisting of 14 maize plants were protected using beta-cyfluthrin 0.5 g/kg granules, which is a systemic insecticide, and a synthetic pyrethroid marketed as Bulldock® 0.05 GR. Trials planted at Mtwapa and Kakamega were left for natural infestation by the stem borers, *C. partellus* and *B. fusca*, respectively. Foliar damage for stem borer was assessed by scoring each infested plant on a 1–9 scale, where 1 = no visible damage and 9 = completely damaged. Plants with a leaf damage score of 0–3 were rated highly resistant, 3.1–5.0 moderately resistant, 5.1–6.0 susceptible, and 6.1–9.0 as highly susceptible (CIMMYT 1989). The number of stem borer exit holes per plant was counted at harvest, and the cumulative tunnel length was measured after splitting the stems of each of the infested plants. Results showed significant differences among the 30 hybrids in leaf damage, number of exit holes, tunnel length, and grain yield in Kiboko. The maize hybrids CKPH08014, CKPH08025, and CKPH08026 showed the least leaf damage, exit holes, and tunnel length, similar to the resistant check. Although ten hybrids yielded over 8 *t*/*ha*, two hybrids, CKPH09001 and CKPH08033, gave the highest yield of 8.99 and 8.86 *t*/*ha*, respectively, in Kiboko, the location artificially infested with *C. partellus*.

15.6 Progress from Breeding for Borer-Resistant Maize

In WCA, IITA has used several breeding methods to improve the maize germplasm for resistance to the borer complex, including backcrossing, pedigree selection, and hybridization followed by population improvement (recurrent selection), depending on the source population, and its mode of inheritance of resistance. Progress made at the early stages of the program has been reported for both *Sesamia* and *Eldana* (Kling and Bosque-Perez 1994; Schulthess and Ajala 1999). An example of the progress from recurrent selection is presented in Fig. 15.1. In the study, stem tunneling reduced by about 24% from C0 to C7 and cob damage rating (1 = resistant to

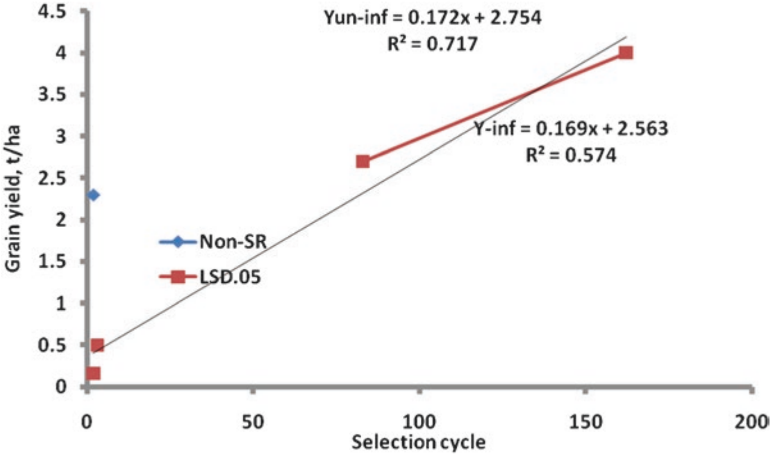

Fig. 15.1 Grain-yield response of TZBR Eldana-1 to seven cycles of recurrent selection for borer resistance evaluated at Ibadan, Nigeria, 1999 (Adapted from Table 1 of Ajala et al. 2001)

9 = susceptible scale) by 21%, and yield increased by about 0.17 t ha^{-1} $cycle^{-1}$ under infested and non-infested conditions. The earlier workers established the infestation and screening technique as well as worked out the scoring scales for the different traits used to quantify resistance or susceptibility, including counting of infested plants, expressing the counts as percentages, scoring 1–5 or 1–9, and the use of quantitative traits. Studies on optimum sample size were also conducted.

Taking a cue from the earlier workers, IITA maize breeders have continued to (i) develop open-pollinated populations with resistance to both borer species, (ii) improve the levels of resistance in the available populations, and (iii) identify resistant lines for the development of inbred lines to be used in the production of borer-resistant hybrids or synthetic varieties. All these were made possible through the use of controlled and uniform infestation with mass-reared insects. Since then, greater progress has been made in the development of populations with better levels of resistance to both borer species, elucidation of mechanisms, and genetic factors controlling resistance and the deployment of the developed population in the farming systems of the region (Ajala et al. 2001, 2009).

15.7 The Insect-Resistant Maize for Africa (IRMA) Project

The Insect-Resistant Maize for Africa (IRMA) Project has been supporting resource-poor farmers to increase their maize crop yield and reduce the loss from storage pests. Currently in its third phase, the project's formal title is: "Developing Maize Resistant to Stem Borer and Storage Insect Pests for Eastern and Southern Africa – IRMA III Conventional (2009–2013)." The present phase is funded by the Syngenta

Foundation for Sustainable Agriculture and is focusing on developing and deploying conventional maize that is resistant to field and storage insect pests. The objectives of the project are to:

(i) Develop insect-resistant maize varieties for the major Kenyan production systems and insect pests.
(ii) Establish procedures to provide insect-resistant maize to resource-poor farmers in Kenya.
(iii) Assess the impact of insect-resistant maize varieties in Kenyan agricultural systems.
(iv) Transfer technologies to Kenya to develop, evaluate, disseminate, and monitor insect-resistant maize varieties.
(v) Plan, monitor, and document project processes and achievements for dissemination to other developing countries.

The project concentrates on ESA countries where insect pests have the greatest impact on maize production, food and income security, and livelihoods. It is placing a relatively greater emphasis on postharvest pests (70%) over stem borers (30%) and is focusing on the major maize-producing countries with significant areas in affected zones. Of particular interest are Ethiopia, Kenya, Malawi, Mozambique, Tanzania, Uganda, Zambia, and Zimbabwe. These countries have a total population of more than 190 million people, which is projected to rise to 230 million by 2015. Although this project does not directly involve the WCA sub-region, the spillover effect and the experiences gained from it will be of immense benefit to the WCA countries.

15.8 Whither, Genetically Modified Maize?

Genetically modified maize (corn) has been genetically modified (GM) to have agronomically desirable traits. Traits that have been engineered into maize include resistance to *herbicides* and resistance to *insect* pests, the latter being achieved by incorporation of a *gene* that codes for the *Bacillus thuringiensis* (Bt) toxin. *Hybrids* with both herbicide and pest resistance have also been produced. In 2009, transgenic maize was grown commercially in 11 countries, including the *USA* (where 85% of the maize crop was genetically modified), Brazil (36% GM), Argentina (83% GM), *South Africa* (57% GM), Canada (84% GM), the Philippines (19% GM), and Spain (20% GM). Most WCA countries are not yet planting GM maize.

Bt corn is a variant of maize, genetically altered to express the bacterial *Bt* toxin, which is poisonous to insect pests. To start with in maize, the emphasis was on the European corn borer, although corn earworm and rootworm have now been included.

The toxin was obtained by inserting a *gene* from the *microorganism B. thuringiensis* into the corn *genome*. This gene *codes for* a *toxin* that causes the formation of pores in the digestive tract of lepidopteran larvae. These pores allow naturally occurring enteric bacteria, such as *Escherichia coli* and *Enterobacter*, to enter the hemocoel, where they multiply and cause *sepsis* (Broderick et al. 2006). This is contrary to the common misconception that Bt toxin kills the larvae by starvation. There has been some serious concern about the yet-to-be-known consequences of planting GM maize, including its effect on nontarget insects and some other invertebrates, the potential danger of Bt resistance in pests, the possibility of Bt maize cross-pollinating with the nearby non-Bt maize, and several issues concerning human safety. There have been no direct solutions to the issues because the Bt maize is still at the infantile stage. If eventually proven to be safe from all perspectives, Bt maize may be one of the best solutions to borer damage in corn production. Until then, host plant resistance, especially in an IPM strategy, offers the best solution to this problem for the resource-poor farmers of SSA.

15.8.1 Recent Pest Problem in Africa

The fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae) is a new alien invasive pest of maize that is spreading through Africa at a tremendous rate (Stokstad 2017). The pest came from the Americas, and outbreaks were recorded for the first time in early 2016 in West and Central Africa (Geoergen et al. 2016). Damage symptoms could be evident on all plant parts, and both vegetative and reproductive growth phases of maize are susceptible to attack. Fall armyworm larvae consume large amounts of leaf tissue resulting in a ragged appearance to the leaves; small holes and "window pane" feeding in the leaves emerging from whorls loaded with larval frass are common (Plate 15.1). Larvae will also move to the tassels and bore in the ears during the reproductive phase, sometimes leading to total crop loss.

Larger larvae are usually found deep in the whorl, and this behavior gives them a level of protection from insecticides, especially contact action insecticides. This shortcoming and emergence of pesticide resistance in armyworms (Adamczyk et al. 1999) led to preference for transgenic Bt maize in the Western Hemisphere. Unfortunately, this is not happening yet in tropical Africa as research effort in this direction is still in its infancy. Nevertheless, application of suitable insecticides, e.g., chlorantraniliprole and lambda-cyhalothrin formulated as Ampligo® 150ZC, at 2 WAP (weeks after planting) and fortnightly thereafter has provided satisfactory level of protection in research fields in Ibadan, Abuja, Mokwa, Zaria, Bagauda and Ile-Ife, Nigeria. Other useful control strategies include application of plant extracts such as neem oil and virus-based biopesticides. Introduction of larval parasitoids, the use of endophytic entomopathogenic fungi, and planting insect-repellant legumes alongside the maize have also been helpful.

Plate 15.1 A maize field infested by the fall armyworm and a close up on a severely affected stand showing the ragged appearance (*top*). The larvae also infect tassels during the reproductive growth phase (*bottom*)

15.9 Conclusion

Maize breeders in SSA observed that natural borer infestation leads to a lot of escapes and is, therefore, not reliable. Taking a cue from the experience of borer resistance work in US Corn Belt, SSA maize breeders, and entomologists developed effective infestation techniques for borer resistance screening. Egg masses of the insect obtained from the borer rearing facility are placed in leaf whorl of the maize plants about 2–3 weeks after emergence. Scoring for borer damage symptoms showed that the method was very effective. Genetic studies revealed that both additive and nonadditive gene actions and heritability estimates are important to varying degrees for the different components of resistance. Backcrossing, pedigree selection, and hybridization have been used to improve maize populations for borer resistance in SSA. In a recurrent selection project conducted at IITA, stem tunneling reduced by about 24% from C_0 to C_7 and cob damage rating by 21%, and yield increased by about 0.17 $t\ ha^{-1}$ cycle^{-1} under infested and non-infested conditions. Borer-resistant populations such as TZBR Eld 4-W and TZBR Eld 4-Y from IITA-Nigeria and hybrids such as CKPH09001 and CKPH08033 from Kenya are now available to farmers in SSA.

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Chapter 16
Genetic Enhancement for Multiple Stress Tolerance

16.1 Introduction

Drought, *Striga*, and low soil nitrogen are presently the three most important constraints to maize production and productivity in the savanna agroecologies of West and Central Africa (WCA). Therefore, maize cultivars targeted to the *Striga*-prone areas of WCA must also be adapted to *Striga*-, drought-, and low-N-prone environments. Consequently, the ultimate goal of maize breeding for biotic and abiotic stress tolerance in IITA is improved grain yield under three specific stress factors, that is, low soil nitrogen, drought, and *S. hermonthica* infestation. During the past decade, the IITA Maize Improvement Program has adopted the S_1 recurrent selection method and improved artificial field infestation with *S. hermonthica* and screening under drought stress as strategies to develop two early- and two extra-early maturing source populations and several cultivars and inbred lines in the two maturity groups. These populations have combined tolerance to drought with moderate levels of resistance to *S. hermonthica* and MSV. Inbreeding, hybridization, and recurrent selection have all been employed in this genetic enhancement endeavor. The two early source populations, TZE-W Pop DT STR (white grained) and TZE-Y Pop DT STR (yellow grained), and two extra-early maturing populations, TZEE-W Pop STR (white) and TZEE-Y Pop STR (yellow), were formed from local and improved drought-tolerant germplasm identified through several years of extensive testing in WCA. By 2007, TZE-W Pop DT STR, TZE-Y Pop DT STR, TZEE-W Pop STR, and TZEE-Y Pop STR had each undergone four cycles of S_1 recurrent selection for improvement in *Striga* resistance. However, the levels of drought tolerance in the two early populations were not as high as desirable, while there was still room for improvement of the *Striga* resistance levels of the extra-early maturing populations. A program was therefore initiated in 2007 to increase the frequency of drought-tolerant alleles in the early populations using S_1 family recurrent selection while continuing the recurrent selection for improved *Striga* resistance in the

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extra-early populations. Population improvement and inbred–hybrid methods have been adopted with relevant and reliable artificial field infestation and screening methods to enhance resistance to the stresses in the breeding materials. Among the products of the program are two *Striga*- and drought-tolerant early-maturing (90–95 days to harvest stage) populations, designated TZE-W Pop DT C_5 STR C_5 (white) and TZE-Y Pop DT C_5 STR C_5 (yellow), and two extra-early (80–85 days) *Striga*-resistant populations, one with white endosperm designated as TZEE-W Pop DT C_1 STR C_5 and the other designated TZEE-Y Pop DT C_1 STR C_5 with yellow endosperm. A particularly striking outcome of these efforts is that several drought- and *Striga*-tolerant early-maturing inbred lines developed in our program have been used as sources of tolerance genes for introgression into the early populations for the enhancement of multiple stress tolerance/resistance. Presented in the rest of this chapter are the summaries and outcomes of these efforts. We first of all make a presentation of the methods common to the different aspects of the enhancement of multistress tolerance/resistance breeding in our program (Sect. 16.2). Thereafter, methods and outcomes specific to each aspect are considered (Sects. 16.3 to 16.9).

16.2 Genetic Enhancement of Source Populations Using Recurrent Selection with Reliable Artificial Field Infestation and Screening Methods to Increase Resistance to Relevant Stresses in the Breeding Materials

The products of the IITA Maize Improvement Program include several source populations, inbred lines, high-yielding OPVs, and hybrids of varying grain types, colors, and maturities with good levels of resistance/tolerance to one or more of the endemic stresses. Improvement of the early populations under controlled drought stress using backcrossing and S_1 recurrent selection has produced new generations of productive varieties that combine enhanced levels of drought tolerance with good levels of resistance to *Striga* and tolerance to low N. The populations and several of the derived varieties have shown superior performance under both *Striga*-infested and non-infested conditions and have proved to be invaluable sources of *Striga*-resistant synthetics and inbred lines. Several *Striga*-resistant and/or drought-tolerant varieties and inbred lines from the two early source populations, TZE-W Pop DT C_5 STR C_5 and TZE-Y Pop DT C_5 STR C_5, have been made available to the national maize programs and farmers of WCA (Badu-Apraku et al. 2006; Badu-Apraku and Lum 2007). Two new *Striga*-resistant and drought-tolerant populations, DTE STR-Y Syn Pop C_0 and DTE STR-W Syn Pop C_0, were developed in 2008 from testcrosses of selected drought- and *Striga*-resistant yellow inbred lines with TZE-Y Pop DT STR and selected drought- and *Striga*-resistant white inbred lines with TZE-W Pop DT STR. In addition to the four early populations, two broad-based extra-early maturing *Striga*-resistant populations [one white (TZEE-W Pop DT C_1 STR) and the other yellow (TZEE-Y Pop DT C_1STR)], several varieties and inbred lines have been developed from the most promising local and improved extra-early germplasm identified through several years of extensive testing in WCA. Further improvement of the early populations under controlled drought stress using recurrent selection has resulted in new generations of productive varieties with enhanced levels of drought tolerance and good levels of resistance to *Striga* and tolerance to low N. Presently, the source populations and the stages of the recurrent selection programs are as follows: early populations, TZE-W Pop DT C_5 STR C_5, DTE –W Syn Pop DT C_3 STR (white), TZE-Y Pop DT C_5 STR C_5, and DTE –Y Syn Pop DT C_3 STR (yellow); two extra-early source populations also with combined tolerance/resistance to *Striga* and drought, TZEE-W Pop DT C_3 STR C_5 (white) and TZEE-Y Pop DT C_3 STR C_5 (yellow). The QPM versions of each of these normal endosperm source populations (TZE-W Pop DT STR QPM C_0, TZE-Y Pop DT STR QPM C_0, TZEE-W Pop STR QPM C_0, and TZEE-Y Pop STR QPM C_0) have also been developed and some selected varieties released and widely adopted by farmers in Ghana and Nigeria.

The populations are presently being improved for combined resistance/tolerance to *Striga hermonthica*, drought and low soil nitrogen (low N) using the S_1 family selection method, artificial *Striga* infestation at Mokwa and Abuja, and tolerance to low N at Ile-Ife and Mokwa, Nigeria, in plots continuously depleted of N by cropping maize for several years without the application of fertilizer.

16.3 Introgression of Drought Tolerance Genes from Selected Extra-Early Inbreds into Extra-Early White and Yellow *Striga*-Resistant Populations

Following the identification of extra-early inbred lines and hybrids which are not only tolerant to low N and drought escaping (characteristics of extra-earliness) but also possess genes for tolerance to drought during flowering and grain-filling periods (Badu-Apraku and Oyekunle 2012), a program was initiated in 2011 to introgress genes for drought tolerance at the flowering and grain-filling periods from selected extra-early inbreds into extra-early white and yellow *Striga*-resistant populations, TZEE-W Pop STR C_5 and TZEE-Y Pop STR C_5. Nineteen extra-early white and 20 yellow inbreds selected for high tolerance to drought were crossed to the extra-early *Striga*-resistant white (TZEE-W Pop STR C_5) and yellow (TZEE-Y pop STR C_5) populations in an effort to introgress drought tolerance genes into the populations. Two hundred testcrosses involving each population and selected drought-tolerant inbreds were evaluated at Ikenne under induced drought stress during the 2011/2012 dry season. The top 25% testcrosses of each population were identified and recombined to reconstitute the populations, TZEE-W Pop DT C_0 STR C_5 and TZEE-Y Pop DT C_0 STR C_5. In addition, the top ten best testcrosses of each population were recombined to form experimental varieties designated 2012 TZEE-W DT STR C_5 and 2012 TZEE-Y DT STR C_5. The two experimental varieties were made available for the DT regional trials in 2013. Two hundred and 252 S_1 families of TZEE-W Pop DT C_0 STR C_5 and TZEE-W Pop DT C_0 STR C_5, generated during the minor season of 2012, plus four checks were evaluated under drought stress at Ikenne during the 2012/2013 dry season. Based on the evaluation at Ikenne, the best 130 white (TZEE-W Pop DT C_0 STR C_5) and 70 S_1 yellow populations were further evaluated under heat stress at Kadawa in 2013. The top 25% testcrosses of each population were identified and recombined to reconstitute the populations, TZEE-W Pop DT C_1 STR C_5 and TZEE-Y Pop DT C_1 STR C_5. In addition, the top ten best S_1 families of each population were recombined to form experimental varieties designated 2013 TZEE-W DT STR C_5 and 2013 TZEE-Y DT STR C_5. The program for the introgression of drought tolerance genes into the extra-early white and yellow populations is progressing very well with each population presently at the cycle 2 stage of the recurrent selection program.

16.4 Introgression of Novel *Striga* Resistance Genes into *Striga*-Resistant Extra-Early White and Yellow Populations and Development of Superior *Striga*-Resistant Varieties and Inbreds

A study of the effects of recurrent selection on the genetic variances, heritabilities, and genetic correlations in the extra-early white *Striga*-resistant population following four cycles of S_1 family selection under *Striga* infestation in Nigeria has revealed low-to-moderately high heritability estimates for *Striga* emergence count and damage levels under *Striga* infestation as well as the low predicted gain cycle^{-1} for grain yield and all other traits, except number of emerged *Striga* plants. This suggested that for faster progress from selection for *Striga* resistance and hence improved grain yield, there was a need to introgress novel resistance genes into the available extra-early germplasm. Therefore, novel *Striga* resistance sources from four IITA intermediate maturing white inbred lines derived from crosses between normal white endosperm maize and *Zea diploperennis*, TZSTRI 104, TZSTRI 105, TZSTRI 107, and TZSTRI 108, were crossed to TZEE-W Pop STR C_4, while TZSTRI 106, a yellow-grained inbred also derived from crosses between normal yellow endosperm maize and *Zea diploperennis,* was crossed to the extra-early yellow population TZEE-Y Pop STR C_4 in 2008 to improve the level of resistance to *S. hermonthica*. This was followed by two backcrosses to the respective populations during the growing season of 2009 to recover earliness. The BC_1S_1 families were evaluated under *Striga* infestation at Abuja and Mokwa in 2010, and the best families were introgressed into the respective population. Also, the BC_1S_1 involving each population was planted in the 2010 major season nursery for advancement to the BC_1S_2 stage. The BC_1S_2 families of each population were planted in September 2010 and advanced to the BC_1S_3 and subsequently advanced to the BC_1S_6 stage during the dry season of 2012. The BC_1S_6 inbreds were evaluated under *Striga* infestation during the growing season of 2012 and were screened for drought tolerance under drought stress at Ikenne during the 2012/2013 dry season and heat stress at Kadawa during the dry season of 2013. Five experimental varieties derived from the backcrosses between the populations and the BC_1S_1 families were evaluated in preliminary trials during the 2011/2012 and 2012/2013 dry seasons. Results of the analysis showed that cultivar, TZEE-W STR 104 $BC_{2,}$ was the highest yielding under drought environments and outyielded the best DT extra-early variety (2008 Syn EE -W DT STR) by 51%. Based on the outstanding performance of TZEE-W STR 104 BC_2 in multilocation trials in Nigeria, it has been released in Nigeria and is presently being commercialized.

16.5 Development of *Striga*-Resistant QPM Inbred Lines and Hybrids with Enhanced Adaptation to Drought Stress

A total of 22 early white, 15 early yellow, and 2 extra-early white normal endosperm elite *Striga*-resistant inbred lines were crossed to QPM donor sources (Pool 15 SR for the white and Pool 18 SR for the yellow) in 2003 in an effort to convert them to QPM. The F_1 crosses were backcrossed to the recurrent parents during the major season of 2005 to obtain BC_1. The BC_1 ears were screened under the light box, and the kernels with desirable endosperm modification were selected and advanced to the BC_2 stage during the dry season of 2005. The BC_2 kernels with the desirable endosperm modification were selected for planting and selfing during the dry season of 2006. One hundred BC_2S_0 kernels of the early and extra-early QPM inbred lines in the conversion program with the desirable endosperm modification were selected and advanced to the BC_2S_1 and BC_2S_2 stages during the dry season of 2006 and rainy season of 2007, respectively. The selected BC_2S_2 of the early and extra-early inbreds with appropriate endosperm modification were planted in Ibadan in June 2008, and the inbreds with agronomically desirable characteristics were advanced to the BC_2S_3 stage. The BC_2S_3 inbreds were screened under the light box, and those with appropriate endosperm modification were selected. The BC_2S_3 lines were planted at Ikenne at the end of November 2008 for screening for enhanced adaptation to drought stress. The S_3 lines with enhanced adaptation to drought-prone environment were recombined to form QPM synthetics. Five hundred BC_1S_3 early-maturing lines in the QPM inbred line conversion program were planted at Ikenne during the 2008–2009 dry season for screening for drought tolerance. Based on the results, 270 drought-tolerant lines were selected and evaluated under *Striga* infestation at Mokwa during the 2009 growing season. In addition, 80 $BC1S_2$ extra-early QPM inbreds in the conversion program were evaluated under artificial *Striga* infestation at Abuja in 2009. During the Striga evaluations at Mokwa and Abuja, the BC_1S_3 of the early QPM inbreds and the BC_1S_2 lines of the extra-early QPM were advanced to the BC_1S_4 and BC_1S_3 stages, respectively. Based on the results of the

Striga evaluations, the best lines of each maturity group were selected and recombined in a diallel fashion to form synthetic cultivars for each maturity group and grain color. Furthermore, the selected S_3 lines of the extra-early and S_4 lines of the early QPM lines were advanced to the S_4 and S_5, respectively. Based on the results of the *Striga* evaluations, the best 30 lines of the early QPM inbreds and best 23 lines of the extra-early QPM were selected and advanced to the S_6 and S_5, respectively, during the 2010 growing season. Ninety-three of the early QPM lines at S_6 stage comprising of 71 white-grained and 22 yellow-grained colors were given TZEQ designations and analyzed for lysine and tryptophan contents in the laboratory in August 2010. Based on the analysis, the best 14 yellow endosperm QPM lines were planted, and 91 single-cross hybrids were generated using a diallel mating scheme. The 168 diallel crosses were evaluated under induced drought stress and well-watered conditions at Ikenne during the 2010–2011 dry season. Also, the best 30 white endosperm early-maturing QPM inbreds were selected, and single-cross hybrids were made using North Carolina Design II (factorial) mating scheme to determine the performance of their crosses under drought stress and well-watered conditions, examine the combining abilities and inheritance patterns of the inbred lines, and identify the best testers for use in our breeding program. Preliminary results showed that the highest-yielding single-cross QPM white hybrid outyielded the normal endosperm check (TZEI 3 × TZEI 26) by 42%, while the best single-cross yellow hybrid outyielded the best yellow endosperm single-cross hybrid by 18%.

16.6 Genetic Analysis of Grain Yield and Other Traits of Early-Maturing Yellow and White Quality Protein Maize Inbreds Under Multiple Stress Conditions

Promotion of quality protein maize (QPM) hybrids with elevated levels of lysine and tryptophan and combined resistance to multiple stresses would help achieve food security and reduce malnutrition in the sub-region. One hundred and fifty hybrids generated by crossing 30 early-maturing white endosperm QPM maize inbreds in six sets using the North Carolina Design II plus six checks were evaluated under drought, low-N, and *Striga*-infested conditions at five locations in Nigeria between 2011 and 2012. The objectives were to determine the (i) mode of gene action for grain yield in the QPM inbreds and (ii) heterotic groups of the inbreds and identify the best testers. General combining ability (GCA) and specific combining ability (SCA) mean squares were significant ($P < 0.01$) for grain yield and most other traits across research environments, indicating that additive and nonadditive gene actions were important in the inheritance of grain yield and other traits in the inbreds. The GCA effects were greater than SCA effects for days to anthesis (67.0%), silking (64.9%), stalk lodging (62.6%), and stay-green characteristic (62.0%), indicating that additive gene action largely controlled the inheritance of these traits. Preponderance of GCA-female over GCA-male for grain yield, plant and ear aspects, suggested that maternal effects played a greater role in the inheritance of these traits. However, larger GCA-male than GCA-female for *Striga* damage at 8 and 10 weeks after planting indicated that paternal effects modified *Striga* damage. Narrow-sense heritability for grain yield and other traits ranged from 54.7% for number of emerged *Striga* plants to 93.3% for days to anthesis. The inbred lines were classified into three heterotic groups based on the GCA effects of multiple traits (HGCAMT). Inbreds TZEQI 14, TZEQI 17, and TZEQI 56 were identified as the best male testers and TZEQI 12, TZEQI 26, and TZEQI 55 as best female testers. The GGE biplot analysis identified TZEQI 28 × TZEQI 60, TZEQI 35 × TZEQI 59, and TZEQI 55 × TZEQI 35 as the ideal hybrids across environments and should be commercialized to contribute to sustainable maize production, improved nutrition, and food security in SSA. In another study, 91 diallel crosses derived from 14 early-maturing yellow endosperm QPM maize inbreds were evaluated under *Striga*-infested environments at Mokwa and Abuja in Nigeria between 2011 and 2012. The objectives were to (i) examine the combining ability for grain yield of early QPM yellow inbreds, (ii) determine the heterotic groups of the inbreds, (iii) identify the best testers for use in our breeding program, and (iv) determine the performance and stability of the inbreds in hybrid combinations under *Striga*-infested environments. Additive and nonadditive gene actions were important in the control of the inheritance of grain yield and other traits in the inbreds. General combining ability (GCA) effects were greater than specific combining ability (SCA) effects across *Striga*-infested environments suggesting that additive gene action was more important than the nonadditive in the set of inbred lines. The inbred lines were classified into three heterotic groups based on the GCA effects of multiple traits (HGCAMT) of inbred lines and three groups based on heterotic groups' specific and general combining ability (HSGCA) . There was close correspondence between classification based on HSGCA and the HGCAMT methods, indicating the effectiveness of the two methods in classifying inbred lines. TZEQI 78, TZEQI 89, TZEQI 87, and TZEQI 82 were identified as the best inbred testers. Inbreds TZEQI 87 and TZEQI 91 had the highest GCA effects and TZEQI 89 the lowest. TZEQI 78 × TZEQI 92, TZEQI 79 × TZEQI 92, and TZEQI 78 × TZEQI 91 were identified as the highest-yielding and stable hybrids across *Striga*-infested environments and should be promoted for adoption and commercialization in SSA.

16.7 Genetic Enhancement of Extra-Early Maize Inbreds Under Low N and Drought for Hybrid Production

During the last two decades, IITA in collaboration with the National Agricultural Research Systems (NARS) of WCA has developed a wide range of high-yielding, drought-tolerant, or escaping early and extra-early populations (white and yellow endosperm), inbred lines, and cultivars in an effort to combat the threat posed by recurrent drought and low N in the savannas of WCA. The extra-early populations from which the inbred lines and cultivars were derived were formed from crosses between local (landraces) with exotic and introduced germplasm identified through extensive multilocation trials in WCA (Badu-Apraku and Fakorede 2001; Badu-Apraku et al. 2007). We observed that some of the extra-early inbred lines in the IITA Maize Program would not only escape drought stress but also seemed to possess drought tolerance genes. The inbreds should therefore be able to withstand the mid-season drought that occurs during the flowering and grain-filling periods in the savannas of WCA as have been found in the early-, intermediate-, and late-maturing cultivars. Several studies were conducted from 2007 to 2010 in Nigeria to evaluate the per se performance of early and extra-early inbreds for tolerance to low N and/or drought stress at the flowering and grain-filling periods (Badu-Apraku et al. 2011). The potential of the inbreds for hybrid production and as source germplasm for the improvement of breeding populations were also evaluated. In two experiments, 90 extra-early maturing inbred lines developed in the IITA Maize Program were evaluated under managed drought stress and in well-watered environments during the dry seasons of 2007/2008 and 2008/2009 at Ikenne (60°53′N, 30°42′E, 60 m altitude, 1200 mm annual rainfall) and in low-N (30 kg ha^{-1}) and high-N (90 kg ha^{-1}) studies at Mokwa (9°18′N, 5° 4′E, 457 m altitude, 1100 mm annual rainfall), during the planting seasons of 2008 and 2009. The data were subjected to the genotype × trait (GT) biplot analysis to identify low-N- and drought-tolerant extra-early inbreds with favorable alleles for introgression into maize breeding populations and for the production of extra-early hybrids with tolerance to drought at the flowering and grain-filling periods. Results revealed significant genotypic mean squares for grain yield and most other traits of the inbreds under drought and/or low-N conditions. The inbreds TZEEI 6, TZEEI 4, TZEEI 36, and TZEEI38 were identified as ideal inbreds under drought. Under low N, TZEEI 19, TZEEI 96, and TZEEI 45 were outstanding in performance with TZEEI 19 as the ideal inbred. TZEEI 19, TZEEI 29, TZEEI 56, TZEEI 38, and TZEEI 79 were tolerant to both stresses. Eighteen of the 36 hybrids produced above-average grain yields across environments with four hybrids identified as very stable. TZEEI 29 × TZEEI 21 was the closest to the ideal hybrid because it combined large mean performance with high-yield stability. Hybrid yield under drought had large positive correlation with grain yield under well-watered environments. Selection for inbred traits such as days to silking and anthesis–silking interval under drought predicted fairly accurately hybrid yield under well-watered environments.

Statistically significant genotypic mean squares for grain yield and most other traits of the inbreds were observed under drought conditions, indicating that genetic variability existed among the lines. Under drought, TZEEI 6 was closest to the ideal inbred and was therefore the best under drought. TZEEI 4, TZEEI 36, and TZEEI 38 were also identified as ideal inbreds under drought (Fig. 16.1). TZEEI 19, TZEEI 29, TZEEI 56, TZEEI 38, and TZEEI 79 were tolerant to both drought and low N. Eighteen hybrids produced above-average grain yields across environments. Four hybrids were very stable, while the best two open-pollinated checks were the least stable (Fig. 16.1). TZEEI 29 × TZEEI 21 was the closest to the ideal genotype. This study provided further evidence that extra-early inbred lines were not only drought escaping but also possessed drought- as well as low-N-tolerant genes.

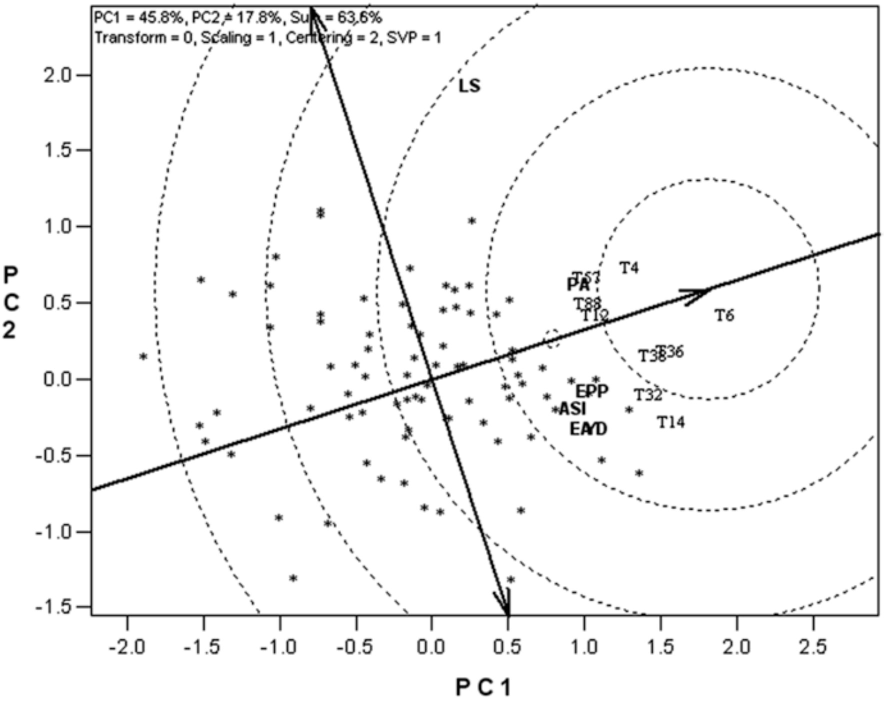

Fig. 16.1 A vector view of genotype-by-trait biplot showing the ranking of the 90 extra-early inbreds on the basis of their mean performance across 6 selected drought tolerance traits. "T" (TZEEI) followed by a number represents inbred lines that were closest to the ideal genotype under drought stress, while* represents exact positions of other inbreds that were less responsive under drought stress

16.8 Genetic Analysis of Grain Yield and Other Traits of Early-Maturing Yellow and White Quality Protein Maize Inbreds Under Multiple Stress Conditions

The development and adoption of early and extra-early maize with tolerance to multiple stresses are vital for increased productivity if maize-based farming systems are to be sustained and expanded. Hence, maize varieties targeted to the drought-prone areas of SSA must be tolerant to low N or *Striga* infestation. Thus, breeding for tolerance to drought, *Striga*, and low nitrogen has been the focal point of the maize improvement program of IITA during the past two decades. A wide range of high-yielding extra-early inbreds and hybrids with tolerance to low N and resistance to *Striga* and also possessing genes for tolerance to drought at the flowering and grain-filling periods are presently available in SSA to combat these threats (Badu-Apraku and Oyekunle 2012; Badu-Apraku et al. 2013b). Parker and Riches (1993) reported that resistance genes may not exist in cultivated maize to combat the biotic stresses limiting maize production. This has led to the search for novel genes for tolerance to low N, drought, and *Striga hermonthica* in the wild relatives of maize, *Zea diploperennis* (Lane et al. 1997). Due to the high-yield potential of maize hybrids, they are widely used throughout the world for increased maize production.

In breeding programs, it is very important to know the combining abilities of inbred lines that are used as parents in hybrid combinations. Increase in maize production can be enhanced by gathering relevant and basic information on the heterotic patterns and combining ability of inbreds. To revolutionize maize production in the sub-region, a number of countries have adopted hybrid maize production, and several high-yielding hybrids in the early-, extra-early, intermediate- and late-maturing groups are presently available for commercial seed production (Badu-Apraku et al. 2013b). Information on the combining abilities and heterotic patterns of inbred lines is important in identifying productive hybrids for commercial production (Badu-Apraku and Oyekunle 2012). Accurate assessment of inbred lines in hybrid combinations is critical to the success of a commercial hybrid program. Also, classification of inbreds into heterotic groups is essential in order to maximize their potential usefulness for the development of productive hybrids and synthetics as well as refining and identifying new heterotic groups.

Combining ability studies provide information on the genetics of the inheritance of traits and enable breeders to select suitable parents for further improvement or use in commercial hybrid breeding programs (Ali et al. 2012). Amegbor et al. (2017) studied the general combining ability (GCA) and specific combining ability (SCA) effects of grain yield and other traits and the performance of extra-early hybrids under contrasting environments. Sixty-three extra-early white maize inbred lines containing genes from *Zea diploperennis* were crossed to four elite testers to obtain 252 single-cross hybrids. The hybrids were evaluated together with four checks at four locations for 2 years under drought, *Striga*-infested, low-N, and optimal environments in Nigeria. The GCA and SCA effects were significant with preponderance of GCA over SCA effects for all measured traits indicating that additive genetic effects were predominant in the lines under all the contrasting environments.

The GCA effect of an inbred is important for the improvement and target trait in a population and for the development of synthetic varieties and hybrids (Akinwale et al. 2014). The significant and positive GCA effects observed for grain yield of the inbreds TZdEEI 51, TZdEEI 23, TZdEEI 45, TZdEEI 47, TZdEEI 50, TZdEEI 55, and TZdEEI 91 under drought and TZdEEI 34 and TZdEEI 90 under low N implied that these inbreds possess favorable alleles for grain yield and would contribute high yield to their progenies under drought and/or low N as suggested by Badu-Apraku et al. (2015a). Similarly, under *Striga* infestation, TZdEEI 34, TZdEEI 50, TZdEEI 59, and TZdEEI 71 and fourteen other inbred lines recorded significant and positive GCA effects for grain yield under optimal conditions indicating that the inbreds would contribute high yield to their progenies. On the other hand, the significant and negative GCA effects observed for the stay-green characteristic of inbreds TZdEEI 21, TZdEEI 59, and TZdEEI 74 under low-N and TZdEEI 22, TZdEEI 23, TZdEEI 33, TZdEEI 43, and TZdEEI 72 under drought environments indicated that these inbreds will slow down the rate of leaf senescence of their progenies. The significant negative GCA effects detected under *Striga* infestation for *Striga* damage of inbreds TZdEEI 16, TZdEEI 34, TZdEEI 50, and TZdEEI 71 and TZdEEI 34, TZdEEI 50, and TZdEEI 71 at 8 and 10 WAP, respectively, implied that the inbreds possess genes for *Striga* tolerance which could easily be introgressed into tropical white maize populations for the improvement of the tolerance to *Striga* and for the development of *Striga*-tolerant hybrids and synthetic varieties. Furthermore, TZdEEI 55 showed significant negative GCA effects for the number of emerged *Striga* plants at 8 and 10 WAP indicating that it possesses genes for resistance to *Striga*. Furthermore, the significant negative GCA effect displayed by inbred (tester) TZEEI 29 for *Striga* damage at 8 WAP and number of emerged *Striga* plants at 8 and 10 WAP indicated that this inbred possessed both tolerance and resistance genes, and it could be an invaluable source of favorable alleles for improving tropical.

The HSGCA was more efficient than the SCA method in the classification of the inbreds into heterotic groups. The hybrids TZdEEI 74, TZEEI 13 and TZdEEI 74, and TZEEI 29 were high yielding and most stable across research environments. It was recommended that these hybrids should be further evaluated in on-farm trials to confirm the consistency of performance for commercialization in SSA.

Makumbi et al. (2011) evaluated 15 tropical maize inbred lines to determine the combining ability for grain yield (GY); assess the genetic diversity of the set of inbred lines using RFLP, SSR, and AFLP markers; estimate heterosis and assess the relationship between F_1 hybrid performance, genetic diversity, and heterosis; and assess genotype × environment interaction of inbred lines in hybrid combinations. The F_1 diallel crosses and parental inbreds were evaluated under drought stress, low-N stress, and well-watered conditions at six locations in three countries in East Africa. Results revealed that general combining ability (GCA) effects were highly significant for GY across stresses and well-watered environments. Inbred lines CML258, CML339, CML341, and CML343 had the best GCA effects for GY across environments. Additive genetic effects were more important for GY under drought stress and well-watered environments but not under low N, suggesting that different gene action controlled GY. Clustering was based on genetic distance (GD) computed using combined marker data grouped lines according to pedigree. Positive correlation was obtained between mid-parent heterosis (MPH) and specific combining ability (SCA), GD, and GY. It was concluded that hybrid breeding programs targeting stress environments would benefit from the accumulation of favorable alleles for drought tolerance in both parental lines.

16.9 Progress from Recurrent Selection for Tolerance to Multiple Stresses in Source Populations

16.9.1 Components of Variances in an Early-Maturing Yellow Maize Population Evaluated Under Drought Stress and Low-Soil-Nitrogen Environments

TZE-Y Pop DTC_4 STR C_4, an early-maturing yellow maize population, had gone through four cycles of recurrent selection for *Striga* resistance followed by another four cycles for drought tolerance. It was not known whether sufficient genetic variability still existed in the population for response to further selection. A study was therefore conducted to estimate genetic variability and correlations and predicted responses to selection for grain yield and other traits in TZE-Y Pop DTC_4 STR C_4 maize population when evaluated under drought and low soil nitrogen (low N). Two hundred and fifty full-sib progenies were developed from the population using North Carolina Design I (NCD I). The progenies were evaluated in three environments (Ikenne, Kadawa, and Ile-Ife) under drought stress and two environments (Ile-Ife and Mokwa) under low N (30 kg ha^{-1}) from 2011 to 2013. Under drought, estimates of additive genetic variance were positive and moderate to large for all traits except anthesis–silking interval, stalk lodging, and moisture at harvest. The additive genetic variance was much larger than the dominance variance for all traits except ears per plant, days to anthesis, days to silk, anthesis–silking interval, stalk lodging, and moisture at harvest. Narrow-sense heritability (h^2) estimate was 20% for grain yield and 0–36% for 13 other traits. Direct response to selection for grain yield (5.53% cycle^{-1}) was greater than the indirect response through selection for ears per plant (1.68% cycle^{-1}), ear aspect (4.93% cycle^{-1}), and plant aspect (4.61% cycle^{-1}). Under low N, estimates of additive genetic variance were moderate to large for all traits except husk cover. The additive genetic variance was much larger than the dominance variance for all traits except ears per plant, plant height, ear height, plant aspect, and grain moisture at harvest. However, additive genetic variance and dominance variance for husk cover were zero. Narrow-sense heritability (h^2) estimate was 31% for grain yield and 0–78% for 13 other traits. Direct response to selection for grain yield (8.72% cycle^{-1}) was greater than the indirect response through selection for ears per plant (3.06% cycle^{-1}), ear aspect (5.96% cycle^{-1}), and plant aspect (2.50% cycle^{-1}). Ears per plant, ear aspect, and plant aspect were identified as important secondary traits for indirect selection for improved grain yield under both drought and low-N stresses. It was clear from this study that adequate residual genetic variability exists in TZE-Y Pop DTC_4 STR C_4 to justify further selection for improved grain yield under drought and low-N stresses.

16.9.2 Genetic Variances and Covariances in an Early-Maturing White Maize Population After Four Cycles of Recurrent Selection Under Drought and Striga Environments

The magnitude and type of genetic variability are of prime importance to breeders in determining whether or not to improve a breeding population and the method to use. A study was conducted to examine the residual genetic variability, correlations, type of gene action, and the predicted responses to selection for grain yield and yield components of TZE-W Pop DTC_4 $STRC_5$ an early-maturing white maize population when evaluated under drought and *Striga* environments. Two hundred and fifty full-sib progenies within half-sib groups were developed from the population using North Carolina Design I (NCD I). The progenies were evaluated in three environments Ikenne (under drought stress and optimal growing condition) and Abuja and Mokwa (under *Striga* infestation and optimal growing conditions) between 2012 and 2014. Under drought, estimates of additive genetic variance were positive and moderate to large for all traits except anthesis–silking interval, stalk lodging and grain moisture at harvest. Additive genetic variance was much larger than dominance variance for all traits except ears per plant (EPP), days to anthesis, days to silking, anthesis–silking interval, stalk lodging, and grain moisture at harvest. Under *Striga* environments, there was wide range of genetic variation for emerged *Striga* plants, *Striga* damage. Several progenies were, therefore identified that combined reduced *Striga* emergence and *Striga* damage implying that it should be possible to extract from the population experimental varieties that combine both low *Striga* emergence and *Striga* damage. Grain yield had a large positive additive genetic correlation with EPP, a large negative genetic correlation with *Striga* damage, and moderately large negative genetic correlations with flowering traits and emerged *Striga* plants at 10 WAP. In conclusion, the population can be further subjected to S_1 recurrent selection for the two stresses.

16.9.3 Genetic Gains in Grain Yield and Other Traits of Early-Maturing Maize Developed During Three Breeding Eras Under Multiple Stress Environments in West Africa

Majority of the rural population of WCA grows maize because it fits into the different farming systems and has great potential for increasing yield under improved management practices compared with other cereal crops. The response of maize to fertilizer and the availability of high-yielding, disease-, and pest-resistant varieties have stimulated production in the savannas of WCA since the 1980s. The new maize varieties adopted by farmers during the past three decades have had significant impact including livelihoods of farming communities (Alene et al. 2009). The production of early (90–95 days to maturity) and extra-early (80–85 days to maturity) maize varieties that can be consumed either as green maize or grain has helped in addressing seasonal and transitory food insecurities. At the same time, increased maize production has helped to overcome chronic food insecurity, increasing the availability of food for the most vulnerable groups including women, children, and the poor. The increased production and promotion of maize by all categories of farmers is proving an important step in achieving food security in WCA. Early-maturing cultivars are crucial to the fight against hunger in the savannas of WCA because they are more responsive to fertilizer application, mature more quickly, and can be harvested much earlier in the season than the traditional sorghum and millet crops. Such varieties are used for filling the hunger gap in July in this zone when all food reserves are depleted after the long dry period and the new crop of the normal growing season is not ready for harvest. There is also a high demand for early maize in the forest zone for peri-urban maize consumers because they allow farmers to market the early crop at a premium price in addition to being compatible for intercropping with cassava (*Manihot esculentum* Crantz), cowpea [*Vigna unguiculata* (L) Walp.] and soybean [*Glycine max* L. (IITA 1992)]. Another important advantage of the early maize is that it provides farmers in the various agroecological zones with flexibility in the dates of planting. Early maize can be planted when the rains are delayed or used for early plantings when the rainfall distribution is normal. The development of early-maturing maize varieties with tolerance to drought, nutrient use efficiency, and resistance to the major foliar diseases and resistance to *Striga hermonthica* has been the major focus of the maize improvement program at IITA. A drought-tolerant population (Pool 16 DT SR) developed through eight cycles of recurrent selection (Badu-Apraku et al. 1997) and subsequently converted for resistance to the maize streak virus disease (Badu-Apraku et al. 2012) was used as a source population for developing the first generation of drought-tolerant early-maturing maize cultivars with resistance to the maize streak virus disease between 1988 and 1993 (Table 5.12). Two new broad-based populations of white and yellow kernel colors were formed by intermating promising local and adapted germplasm followed by introgression of drought tolerance and *Striga* resistance genes from selected inbred lines. The populations were subjected to recurrent selection under artificial *Striga* infestation without intentionally selecting for drought tolerance to develop the second generation of *Striga*-resistant and drought-tolerant early white and yellow maize cultivars (Badu-Apraku et al. 2007, 2008, 2009). Additional cycles of recurrent selection were conducted during the period 2007–2010 to further increase the frequencies of favorable alleles for tolerance to drought and resistance to *Striga* in the two populations. Through this program the third generation of early-maturing drought and *Striga*-resistant cultivars were developed. Furthermore, two populations, DTE STR-Y Syn Pop C_0 and DTE STR-W Syn Pop C_0, were developed in 2008 from selected testcrosses involving drought and *Striga*-resistant yellow and white inbred lines, respectively. The improved cycles of selection of these two populations were other important sources of the third generation of *Striga*-resistant and drought-tolerant early-maturating white and yellow cultivars.

Evaluation of the genetic improvement of yield and the associated changes in agronomic traits in the three generations of the early maize cultivars may help identify traits of potential value for accelerating genetic gains in future breeding. Some studies had been conducted to measure breeding progress by comparing the performance of cultivars developed and released over a long period of time in the same environment (Tefera et al. 2009; Specht et al. 1999; Voldeng et al. 1997; Kamara et al. 2004). For example, Kamara et al. (2004) showed a genetic gain of 0.41% per year for late-maturing maize cultivars released from 1970 to 1999 in the Nigerian savannas. The increase was associated with increase in total biomass and kernel weight and reduction in plant height and days to flowering. Similarly, Russell (1984) reported genetic gain of 0.68% per year for US Corn Belt cultivars from the 1930s to the 1980s, while Tollenaar (1989) reported higher genetic gain in yield of 1.7% per year for commercially important maize hybrids in Central Ontario from the late 1950s to the late 1980s.

Research and development of early-maturing maize at IITA had been in place for at least three decades in WCA. Evaluation of the genetic improvement of yield and the associated changes in agronomic traits in the three generations of the early maize cultivars may help identify traits of potential value for accelerating genetic gains in future breeding. However, no direct comparisons of grain-yield potential and other agronomic traits had been made for early-maturing drought-tolerant, *Striga*-resistant, and/or low-nitrogen-tolerant maize cultivars developed in WCA during the three breeding eras to justify the huge investments in maize breeding in WCA. A number of separate studies were therefore conducted during the period 2009–2010 to document the progress that had been made in breeding for drought- and low-nitrogen-tolerant and/or *Striga*-resistant early-maturing maize during the three breeding eras. These are discussed next.

16.9.4 Gains in Grain Yield Under Low Nitrogen After Three Decades of Breeding for Drought Tolerance and Striga Resistance in Early Maize

Three breeding periods or eras may be identified in the IITA Maize Program based on the germplasm and methodologies used, that is, 1988–2000, 2001–2006, and 2007–2011. A total of 50 early-maturing cultivars, combining *Striga* resistance with drought tolerance, were developed, including 15, 16, and 19 cultivars for the three periods, respectively. Although the cultivars were not selected intentionally for low-N tolerance, it was hypothesized that tolerance to low N had been significantly improved while selecting for drought tolerance and *Striga* resistance. This hypothesis was tested by evaluating the 50 cultivars in 2010 and 2011 in Nigeria at Mokwa and Ile-Ife under both low- (30 kg ha^{-1}) and high-N (90 kg ha^{-1}) levels. Under low-N conditions, grain yield improved from 2.28 ± 0.056 t/ha during the first period to 2.61 ± 0.054 t/ha during the third period, an increase of 0.165 t/ha per period with r^2 of 0.99. Under high N, yield increased from 3.2 ± 0.176 t/ha to 3.65 ± 0.068 t/ha, an increase of 0.225 t/ha and r^2 of 0.93. Relative gain per period was 0.03 t/ha for the two N rates with r^2 values of 0.99 and 0.94, respectively. Grain-yield performance of the 50 cultivars under low-N conditions adequately predicted their performance under high N.

Based on the results of this study, it was concluded that selection for *Striga* resistance and drought tolerance in early-maturing maize populations enhanced low-N tolerance in the maize cultivars derived from the populations. The improvement was higher in later than earlier breeding periods. It may be concluded that substantial progress has been made in breeding for high-yielding, *Striga*-resistant/*Striga*-tolerant, drought-tolerant, and low-N-tolerant cultivars during the past three decades. It was proposed that the outstanding cultivars, TZE-W DT C_2 STR, TZE-W DT C_1 STR, 2009 TZE-W Pop DT STR, EV DT-W 2008 STR, 2009 DTE-W STR Syn, 2009 DTE-Y STR Syn, and DTE-W STR Syn C_1, in the study should be extensively tested in WCA and vigorously promoted for commercialization to contribute to food security in the sub-region.

16.9.5 Gains in Grain Yield of Early Maize Cultivars Developed During Three Breeding Eras Under Multiple Environments

During the last three decades, the IITA Maize Improvement Program has devoted considerable effort and resources to develop early-maturing maize varieties with tolerance to drought, low soil N, and resistance to *Striga hermonthica*. The research efforts have covered three breeding eras: 1988–2000 (Era1), 2001–2006 (Era 2), and 2007–2010 (Era 3). The strategies used for the development of the cultivars in each era have been described in detail by Badu-Apraku et al. (2001). The breeding eras have covered a total period of 22 years with funding from international donor agencies, including USAID, UNDP, and Bill & Melinda Gates Foundation along with IITA, while collaborating countries of WCA contributed research facilities in kind and as human resources. No direct comparisons of grain-yield potential and other agronomic traits have been made across multiple stresses for the early-maturing drought-tolerant and *Striga*-resistant maize cultivars developed during the three breeding eras. Since drought, *Striga* infestation, and low N do not occur singly but occur together under field conditions, a holistic evaluation of the gains from the efforts over the three eras was conducted to determine the direction to pursue in future breeding efforts in the sub-region. The study was conducted at 16 locations in WCA for 2 years to determine genetic improvement in grain yield under drought, *Striga*-infested, low-soil-nitrogen, and optimal growing environments. Grain yield had annual genetic gain of 1.52% and 1.24% under multiple stresses and optimum growing environments, respectively. The average annual rate of increase in grain yield was 30 kg ha^{-1} $year^{-1}$ across stresses and 37 kg ha^{-1} $year^{-1}$ across optimal growing environments. The annual genetic gains in grain yield were 0.56% for the period 1 cultivars, 1.52% for the period 2 cultivars, and 1.62% for the period 3 cultivars. Among the agronomic traits under stress, only ears per plant (0.32% $year^{-1}$), ear aspect (−0.51% $year^{-1}$), plant aspect (−0.24% $year^{-1}$), and days to anthesis (0.11% $year^{-1}$) changed significantly ($P < 0.05$ or <0.01) during the three eras. The increase in grain yield from the first- to the third-generation cultivars across stress environments was associated with significant improvements in plant and ear aspects, increased ears per plant, and the stay-green characteristic. Under optimal growing environments, the increase in grain yield from the first- to the third-generation cultivars was 1.24% per annum. The gain was associated with significant improvements in plant and ear heights, plant and ear aspects, husk cover, and increased ears per plant. The results indicated that substantial progress has been made in breeding for cultivars with combined tolerance/resistance to the three stresses during the past 22 years. The varieties EV DT-W 2008 STR, 2009 DTE-Y STR Syn, and TZE-W DT C_2 STR, all from the latest era, were identified as the highest-yielding and most stable cultivars across stress environments and should be promoted for adoption to contribute to food security in this sub-region.

16.9.6 Genetic Gains in Grain Yield of Extra-Early Maize Cultivars During Three Breeding Eras Under Multiple Environments

Under field conditions, drought, *Striga*, and soil nutrient deficiency occur simultaneously, and the combined effects can be devastating (Cechin and Press 1993; Kim and Adetimirin 1997). For example, Badu-Apraku et al. (2004) reported a grain yield loss of 53% under drought and 42% under *Striga* infestation. Consequently, breeding for extra-early (80–85 days to maturity) cultivars that are drought-tolerant-nitrogen use efficient with enhanced tolerance to drought and resistance to *Striga* is crucial to improved productivity and stable maize production in WCA. Therefore, it is desirable to incorporate drought tolerance into cultivars that have resistance to *Striga* in the Sudan and northern Guinea savannas where intermittent drought is prevalent, as the two stresses occur together. Presently, farmers in *Striga* endemic agroecologies of WCA are demanding extra-early and early (90–95 days to maturity) cultivars with combined resistance or tolerance to *Striga* and drought and are unwilling to adopt maize cultivars that do not possess both adaptation to drought-prone environments and *Striga* resistance (Badu-Apraku et al. 2013a, b, 2015a, b). Improvement for drought tolerance has most often resulted in specific adaptation and improved performance under low-N conditions, indicating that tolerance to either stress involves common adaptive mechanism (Bänziger et al. 1999; Badu-Apraku et al. 2011, 2015a, b). It is therefore becoming increasingly important to adopt a holistic approach to identify genotypes with tolerance to a range of stresses expected in the target environment in WCA instead of compartmentalizing different stresses (Badu-Apraku et al. 2010a, b).

The International Institute of Tropical Agriculture Maize Improvement Program (IITA-MIP), in collaboration with several public institutions in the region, has therefore paid increasing attention to develop new products endowed with high-yield potential and stability across a broad range of moisture availability and growing conditions. The extra-early varieties developed by IITA during the past three decades may be broadly divided into three breeding eras (1995–2000, 2001–2006, and 2007–2012). An era refers to the breeding period, a methodology during which a cultivar was developed and/or improved based on specific breeding goals. Extra-early maturing maize cultivars are drought escaping because they mature and complete critical physiological processes of their life cycles before severe moisture deficit occurs or before the onset of terminal drought. During the first breeding era 1, the emphasis of the IITA Maize Program was on breeding for resistance to maize streak virus (MSV) and improved high-yield potential. The era 2 cultivars were bred for improved resistance to *Striga* under artificial *Striga* infestation using 30 kg N ha^{-1} (low N). Therefore, the source populations from which the era 2 cultivars were extracted were improved concomitantly for combined resistance to *Striga* and tolerance to low soil nitrogen. The era 3 cultivars were bred for tolerance to drought tolerance which is under genetic control in addition to the drought and not only through escape mechanism. Backcrossing, inbreeding, hybridization, the S_1 and recurrent selection methods, and screening under drought, low soil nitrogen, and artificial infestation with both *S. hermonthica* and maize streak virus have been used as strategies to develop several extra-early maturing source populations, cultivars, and inbred lines with tolerance to low N, drought escape, and/or tolerance to drought at the flowering and grain-filling periods as well as moderate levels of resistance to *S. hermonthica* and the maize streak virus. The availability of these extra-early maize cultivars has resulted in the expansion of maize production into new frontiers replacing the traditional cereal crops such as sorghum (*Sorghum bicolor*) and pearl millet (*Pennisetum glaucum*) in the savannas of WCA (IITA 1992).

Information on the genetic gains achieved over time in extra-early cultivars released and registered in WCA is crucial (i) for determining whether or not the investments in research in the sub-region are justified and (ii) to better understand as to how the selection methods influenced the relationship between grain yield and other agronomic traits under normal and stressed (drought, low N, and *Striga)* growing environments (Kamara et al. 2012; Badu-Apraku et al. 2013b, 2015a, b). Several studies have been carried out routinely in temperate maize to compare genetic gains of cultivars of different eras in the temperate zones in an effort to understand how genetic improvement has influenced important traits such as for grain yield in maize under optimal growing conditions (Cechin and Press 1993; Kim and Adetimirin 1997; Badu-Apraku et al. 2015a, b, 2014; Castleberry et al. 1984; Tollenaar et al. 1997; Sangoi et al. 2002; O'Neill et al. 2004; Duvick 2005; Campos et al. 2006; Wang et al. 2011). Similarly, several comparisons of hybrids developed in different eras and under contrasting N levels have been reported

(Castleberry et al. 1984; Tollenaar et al. 1997; Sangoi et al. 2002; O'Neill et al. 2004). However, information is completely lacking on the genetic gains in grain yield and other agronomic traits of the extra-early cultivars developed by IITA and other collaborators since 1995 under multiple stresses. The identification of traits of potential value and modifications in breeding methodologies and strategies would be crucial for increased progress in future breeding of the extra-early maize cultivars (Badu-Apraku et al. 2015b). Information on the genetic gains in extra-early cultivars is crucial for determining whether or not the investments in research in the sub-region are justified and to gain a better understanding of how selection has influenced important traits such as grain yield in maize (Kamara et al. 2012; Badu-Apraku et al. 2013b, 2015a). The limited information on genetic gains from selection makes it difficult to ascertain completely the genetic gains that have been made for grain yield in relationship to N fertility, drought tolerance, and *Striga* resistance in the numerous cultivars that have been released in WCA during the past two decades.

The extra-early varieties developed by IITA during the past three decades may be categorized into three breeding eras (1995–2000, 2001–2006, and 2007–2012). However, despite the tremendous advances in the improvement of the extra-early maize, information is completely lacking on the genetic gains in grain yield and other agronomic traits of the extra-early cultivars developed during the three breeding eras. The identification of traits of potential value and modifications in breeding methodologies and strategies are crucial for increased progress in future breeding of the extra-early maize cultivars (Badu-Apraku et al., 2015a, b).

The objectives of this study were to (i) determine the gains in grain yield under drought, low N, and *Striga* multiple stressed and non-stressed environments, (ii) identify traits associated with yield improvement during the three breeding eras under multiple stress and non-stress environments, and (iii) identify high-yielding and stable cultivars under multiple stress and non-stress environments for commercialization in the sub-region.

A major objective of the present study was to determine the gains in grain yield and other agronomic traits of 56 extra-early maturing cultivars under multiple stress and non-stress environments during the three breeding eras. The genetic gain of 2.72% year^{-1} with the average rate of increase in grain yield of 44 kg ha^{-1} year^{-1} obtained for the extra-early cultivars under multiple stresses and the annual genetic gain of 2.28% under non-stress environments are higher than the gains reported for the early-maturing cultivars by Badu-Apraku et al. (2015b) under similar multiple stress and non-stress environments. The authors reported the average rate of increase in grain yield under optimal growing conditions to be 40 kg ha^{-1} year^{-1} with a genetic gain of 1.3% year^{-1} and a gain of 30 kg ha^{-1} year^{-1}, an annual genetic gain of 1.2% across 16 stress environments. In another study involving the same 56 extra-early cultivars, Badu-Apraku et al. (2016) reported genetic gains in grain yield of 2.56% under *Striga* infestation and 1.3% annual genetic gain under *Striga*-free conditions. Results of the evaluation of the extra-early cultivars under low N and high N revealed annual genetic gains in grain yield of 2.14% and 2.56%, respectively, while under drought stress and optimal conditions, the cultivars showed genetic gains of 1.99% and 1.94% per year, respectively (Badu-Apraku et al. 2016, unpublished data, Improvement in grain-yield and low-nitrogen tolerance in extra-early maturing maize cultivars of three breeding eras evaluated under low- and high-nitrogen environments). The genetic gains obtained in the present study under the individual stresses are also greater than those reported in earlier studies for early-maturing cultivars. For example, Badu-Apraku et al. (2013b) reported an average genetic gain in grain yield of 1.7% per era when 50 early-maturing cultivars were evaluated under *Striga* infestation per se. Furthermore, Badu-Apraku et al. (2013a) reported 1.1% annual genetic gain for the early-maturing cultivars under drought stress, while the average rate of increase in grain yield under optimum growing conditions was 40 kg ha^{-1} year^{-1} with a genetic gain of 1.3% year^{-1}. In a study involving the evaluation of the 50 early-maturing cultivars under low- and high-N environments, Badu-Apraku et al. (2015a) reported genetic gains of 165 and 225 kg ha^{-1} (0.55 and 0.94% per year) in grain yield, respectively. Relative gain per period (i.e., gain in grain yield in a period per unit yield in the previous period) was 30 kg ha^{-1}. The genetic gains under low- and high-N environments were exactly the same. The differences in the genetic gains reported in the present study and those of the early-maturing cultivars could be due to the differences in the environments under which the cultivars were evaluated; the stress level imposed during the evaluations; the type of material evaluated, that is, extra-early vs early-maturing cultivars; the methods of development of the cultivars; the breeding periods; and the number of cultivars involved in the evaluations (Badu-Apraku et al. 2015a).

In the present study, extra-early maturing open-pollinated cultivars were evaluated under the three major stress factors limiting maize production and productivity in the savannas of WCA as well as natural, non-stress environments. Results of the study showed an average increase in yield of 44 kg ha^{-1} year^{-1} (2.7%) and 67 kg ha^{-1} year^{-1} (2.3%) under multiple stress and non-stress environments. Gains in yield of extra-early maize cultivars from era 1 to era 3 under multiple stressed environments were associated with increased days to anthesis, reduced stalk lodging, and improved husk cover. The cultivars 2004 TZEE-W POP STR C_4 and TZEE-W POP × LD S_6 (SETA1) of era 2 and TZEE-W STR 105 BC_1 and 2009 TZEE-OR1 STR of era 3 were high yielding and most stable under multiple stressed environments, while cultivars TZEE-W Pop STR C3 of era 2 and TZEE-W STR 108 BC_1, 2008 Syn EE-Y DT STR, TZEE-Y Pop STR C_5, and TZEE-W DT C_0 STR C_5 of era 3 were the most outstanding under non-stress environment. It was concluded that the cultivars should be further tested and commercialized in SSA. While significant gains in grain yield were made during breeding eras for multiple stress-tolerant extra-early maize cultivars, there were no gains in yield under non-stress environments. The mean grain yield under multiple stresses in the present study was 42% lower than mean grain yield under non-stress environments. This is relatively greater than the mean grain-yield reduction of 34–37% obtained across stress environments by Badu-Apraku et al. (2004, 2015a, b) for early-maturing cultivars. The differences in the level of yield reduction in the different studies could be attributed to differences in the levels of resistance/tolerance to the three stresses of the extra-early maize cultivars used in the present study (Akaogu et al. 2012; Badu-Apraku et al. 2015a, b).

The high genetic gains in grain yield under both multiple stress and non-stress environments in the present study is not surprising because during the development of the second- and third-era extra-early cultivars, a major strategy of the IITA Maize Program was to select maize inbred lines with enhanced adaptation to drought-prone environments from diverse sources. The promising inbred lines were also screened for *Striga* resistance under artificial infestation. The inbreds with better adaptation to both drought-prone environments and genes for drought tolerance at the flowering and grain-filling periods and *Striga* resistance genes from *Zea diploperennis* were used as sources of genes for further introgression into the two extra-early maturing breeding populations which were undergoing S_1 family recurrent selection in our program. Further improvement of the extra-early populations under controlled drought and *Striga hermonthica* parasitism using the S_1 recurrent selection method has resulted in the generation of new productive cultivars that combine enhanced levels of adaptation to drought-prone and low-N environments and improved levels of resistance to *Striga*.

In the present study, the significant gain in grain yield under multiple stress environments was associated with increased days to anthesis, decreased stalk lodging, and improved husk cover. The lack of significant gains in grain yield under non-stress environments could be due to the fact that emphasis in the breeding program was more on improvement of traits under multiple stresses than under optimal growing conditions. However, the increased days to anthesis, plant and ear heights, stalk lodging, and EPP as well as the decreased ASI, improved ear aspect, and reduced ear rot obtained under the non-stress environments suggested that the selection index improved yield under multiple stresses but resulted in delayed flowering, increased plant, and ear heights as well as increased stalk lodging of the cultivars under optimal growing conditions (Cechin and Press 1993; Kim and Adetimirin 1997; Badu-Apraku et al. 2015a, b). Badu-Apraku et al. (2014) found that gains in grain yield of early-maturing maize cultivars of the three breeding eras under multiple stresses were associated with significant improvement in plant and ear aspects, increased EPP, and stay-green characteristic, while under optimal growing environments, the gain was associated with significant improvement in plant and ear heights, plant and ear aspects, husk cover, and increased EPP. The findings of these authors are not consistent with our results under multiple stress but are in partial agreement with our findings under non-stress environments in the present study. The differences in the maturity groups might have accounted for these results.

In the present study, the multiple stress environments consisted of drought, *Striga*, and low-N conditions and provided an opportunity to select the outstanding cultivars for further testing across the different environmental conditions. The AMMI biplot was an invaluable tool for the identification of superior cultivars across the multiple environmental conditions (Figure not shown). The cultivar, TZEE-W Pop STR C5, was identified as high yielding and stable both under multiple stress and non-stress environments suggesting that it has a broad adaptation to the growing environments in WCA. The results of this study are of special interest because drought, low N, and *Striga* occur simultaneously under field conditions in

WCA, and when this happens, the combined effect can be devastating (Cechin and Press 1993; Kim and Adetimirin 1997; Badu-Apraku et al. 2015a, b). The superior performance of the cultivars under varying environmental conditions is of utmost importance as maize varieties targeted to the drought-prone areas of WCA must also be tolerant to low N, resistant/tolerant to *Striga*, and have competitive yield under non-stress conditions. These results suggest that the outstanding cultivar should be extensively tested in on-farm trials in WCA and vigorously promoted for adoption and commercialization to contribute to food security in the sub-region.

16.9.7 Identification of Multiple Stress-Tolerant Early and Extra-Early Inbred Lines for Hybrid Production and Introgression into Breeding Populations

Studies were conducted from 2007 to 2009 at three locations in Nigeria under induced drought stress and low-nitrogen conditions. The objective was to identify superior inbred lines for use as parents for hybrid production and for introgression into maize breeding populations. The inbreds TZEI 11, TZEI 2, TZEI 8, and TZEI 22 were identified as tolerant to both drought stress and low N by both the GT biplot and the multi-trait selection tool of the GGE biplot. The implication of these results is that the mechanisms for drought and low-N tolerance in some inbred lines used in this study are probably similar. This finding is consistent with those of Bänziger et al. (1999) who reported that tolerance to either stress may involve similar adaptive mechanisms. It is striking, however, that under drought stress, TZEI 17, TZEI 3, TZEI 23, and TZEI 13 were the closest to the ideal inbred, while different inbreds, TZEI 7, TZEI 2, and TZEI 11, were the closest to the ideal genotype under low-N conditions. This suggested that while in some inbreds, either stress may involve similar adaptive mechanisms in others, different adaptive mechanisms may be involved. The identification of TZEI 11, TZEI 2, TZEI 8, and TZEI 22 as tolerant to both low N and drought stress is not surprising since the inbred lines which are also *Striga* resistant were developed from drought-tolerant and *Striga*-resistant populations. This is further supported by the fact that the lines were selected for *Striga* resistance under artificial *Striga* infestation at low-N levels (30–60 kg N ha^{-1}). According to Badu-Apraku et al. (2009), S_1 progenies improved for grain yield and *Striga* resistance in two extra-early tropical maize populations under artificial *Striga* infestation at low-N levels (30−60 kg ha^{-1}) led to concomitant improvements in grain yield and some other traits in the advanced cycles of selection. The identification of TZEI 17, TZEI 3, TZEI 23, and TZEI 13 as the closest to the ideal inbreds under drought stress while TZEI 7, TZEI 2, and TZEI 11 as the closest to the ideal genotype under low-N conditions seems consistent with the results of Badu-Apraku et al. (2010a, unpublished). The authors studied the combining abilities and heterotic patterns of nine tropical early-maturing white maize inbreds under drought stress, when *Striga*-infested and in optimal growing conditions. They reported that TZEI 17 was the closest to the ideal tester and may be considered as the best under drought stress, TZEI 23 and TZEI 9 under artificial *Striga* infestation, and TZEI 13 across growing conditions. The results of their study also showed that the hybrid TZEI 23 × TZEI 13 had superior performance under all research conditions, suggesting that it has a broad adaptation, and that TZEI 17 and TZEI 13 are outstanding parents for the development of productive hybrids. A similar study involving white early-maturing inbred lines revealed TZEI 3 as the closest to the ideal tester, while TZEI 7 had the highest GCA effects across the test environments, drought stress, *Striga* infestation, and optimal growing conditions (Badu-Apraku et al. 2010b, unpublished). The high-GCA effects of TZEI 7 in the three research environments of the above study and the superior performance in our present study imply that the per se performance of this inbred should be good indicators of the performance of the resulting hybrids (Gethi and Smith 2004), and this should be exploited for the development of drought-tolerant and *Striga*-resistant hybrids.

16.10 Conclusions

In conclusion, the inbred lines TZEI 11, TZEI 2, TZEI 8, and TZEI 22 have combined tolerance to drought stress and low N and are available in our program for use as germplasm sources for introgression of genes for tolerance to the two stresses into tropical maize populations as well as for the development of drought- and/or low-N-tolerant hybrids. In addition, several inbred lines with tolerance to either low N or drought stress have been identified for breeding programs in SSA. For the first time, extra-early inbreds and hybrids that are low-N-tolerant, are drought-tolerant, or have combined tolerance to both stresses are now available in SSA. These inbreds are not only drought escaping (a characteristic of extra-earliness) but carry drought tolerance genes that enable them to withstand sporadic occurrence of drought at any growth stage, but especially at flowering and grain-filling periods. The availability of the low-N- and drought-tolerant extra-early inbreds and hybrids should go a long way in reducing the instability of maize yields in SSA especially in the savannas as well as during the second season in the forest agroecologies. One striking aspect of the outcome of our research efforts is the consistent observation under all stresses that breeding for stress tolerance has the value addition of improved performance under non-stress environments. This is highly desirable because varieties tolerant to the specific stresses may be cultivated by farmers where the stress is not necessarily prevalent. The annual genetic gains obtained for the early and extra-early cultivars under multiple stress and non-stress environments indicated that considerable progress has been made in breeding for multiple stress-tolerant extra-early and early maize cultivars in the sub-region.

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Part IV
Improving Breeding Efficiency

Chapter 17
Genotype x Environment Interaction and Repeatability of Traits

17.1 Introduction

Failure of genotypes to perform consistently in variable environments is termed genotype x environment interaction (G x E or GEI). GEI is advantageous when the breeder is developing varieties for specific ecological niches—narrow adaptation—but it is a disadvantage when developing varieties for broad adaptation. In this case, the genetic worth of the individual genotypes cannot be predicted accurately from their phenotypic performance. Breeders have used several statistical approaches to handle GEI in crops, including:

- Obtaining optimum combinations of number of locations, years, and replications for yield trials to maximize heritability and progress from selection
- Identifying the representative or "ideal" evaluation sites in which the performance of the test genotypes correlates highly with their performance in the range of environments for which they are being developed
- Stratification of the evaluation environments and/or the genotypes being evaluated
- Using regression analysis to characterize the environmental response of individual genotypes

The advent of the personal computer, along with the development of many user-friendly software packages, has greatly facilitated research in this area, and several sophisticated statistical programs are now available for handling GEI data with relative ease.

In crop species, economic traits such as grain yield are inherited quantitatively and are, therefore, greatly subject to environmental variation. Breeders carry out genotype evaluation in multiple environments in what is termed *multi-environment trials* (METs). Data from METs are subjected to the ANOVA (Table 17.1), and

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Table 17.1 Analysis of variance of multi-environment trials

S.V.	df	MS	E(MS)
Year (Y)	$y - 1 = 1$	1.1603	
Loc (L)	$l - 1 = 1$	0.0163	
$Y \times L$	$(y - 1)(l - 1) = 1$	2.2963	
Rep in YL	$(r - 1)yl = 8$	3.8008	
Genotype (G)	$g - 1 = 99$	$M_1 = 450.4857$	$\sigma^2 + 3\sigma^2_{gyl} + 6\sigma^2_{gl} + 6\sigma^2_{gy} + 12\sigma^2_{g}$
$G \times Y$	$(g - 1)(y - 1) = 99$	$M_2 = 8.1335$	$\sigma^2 + 3\sigma^2_{gyl} + 6\sigma^2_{gy}$
$G \times L$	$(g - 1)(l - 1) = 99$	$M_3 = 8.1836$	$\sigma^2 + 3\sigma^2_{gyl} + 6\sigma^2_{gl}$
$G \times Y \times L$	$(g - 1)(y - 1)(l - 1) = 99$	$M_4 = 3.8291$	$\sigma^2 + 3\sigma^2_{gyl}$
Error	$yl(g - 1)(r - 1) = 792$	$M_5 = 6.6349$	σ^2
Total	1199		

significant GEI is further analyzed to decompose the components. The ANOVA model for METs is

$$Y_{ijlk} = \mu + Y_j + L_l + YL_{jl} + R_k\left(YL_{jl}\right) + G_i + GY_{ij} + GL_{il} + GYL_{ijl} + \varepsilon_{ijlk}$$

In this model:

Y_{ijlk} = the observation on the *i*th genotype in the *j*th year, the *l*th location, and the *k*th replication, μ = the overall mean of the trait in the experiment, Y_j = the effect of the *j*th year, L_l = the effect of the *j*th location, YL_{jl} = the effect of the interaction of the *j*th year with the *l*th location, $Rk_{(jl)}$ = the effect of the *k*th replication within the *l*th location in the *j*th year, G_i = the effect of the *i*th genotype, GY_{ij} = the effect of the interaction of the *i*th genotype with the *j*th year, GL_{il} = the effect of the interaction of the *i*th genotype with the *l*th location, GYL_{ijl} = the effect of the *i*th genotype with the *i*th year and the *l*th location, and ε_{ijlk} = the random error or residual.

17.2 Multilocational Testing and Genotype by Environment Interactions in West and Central Africa

The performances of breeding materials or crop varieties differ from one environment to another. While the effect of environment may, in general, be additive in some instances, in others it may not be. Additive environmental effect means that the relative ranking of varieties is maintained. In effect, all or most varieties improve or decrease in their performance by a similar factor from one environment to another. However, varieties may differ considerably in the magnitude of performance they show from a good to a better environment. When the latter is present for a set of genotypes or varieties, genotype–environment interaction is implied. Multilocational trials or multi-environment trials (METs), involving the evaluation of a set of genotypes or varieties in several or many environments that are dissimilar, are required to determine the magnitude of genotype–environment interactions and, by implication, stability of performance of the genotypes or varieties. Multilocational testing can provide information on genotypes with high average performance and in effect stability over a range of different environments. It is also possible, using the results from multilocational trials, to identify genotypes that are best adapted to particular environments. Families that show superiority in such environments are recombined in successive cycles of improvement. Analysis of variance of data obtained from multilocational trials for a set of genotypes can also yield estimates of heritability of important traits considered.

Several methods are available for the analysis and interpretation of multilocational trial (MET) data (Yates and Cochran 1938; Williams 1952; Finlay and Wilkinson 1963; Eberhart and Russell 1966; Gollob 1968; Mandel 1969, 1971; Zobel et al. 1988; Gauch 1988; Gauch and Zobel 1997; Cornelius et al. 1993; Crossa and Cornelius 1997; Yan et al. 2000, 2007). Of these statistical tools, the two most powerful for the analysis of MET data are the additive main effects and multiplicative interaction (AMMI) model proposed by Zobel et al. (1988), Gauch (1988), and Gauch and Zobel (1997) and GGE biplot methodology proposed by Yan et al. (2000). Several reviews have compared and contrasted AMMI and GGE biplot with respect to their suitability for GEI analysis (Gauch 2006; Yan and Tinker 2006; Yan et al. 2007; Gauch et al. 2008; Yang et al. 2009). A major disadvantage of the AMMI model is that it is insensitive to the most important part of the crossover GE. Furthermore, since there is no clear biological separation between the two terms G and GE, the AMMI model does not offer any advantage to the breeder for genotypic and site evaluation when analyzing MET data (Yan et al. 2007). On the other hand, the GGE biplot is a powerful statistical model that takes care of some of the disadvantages of AMMI. The method is an effective statistical tool for identifying the most outstanding cultivar in a given environment and the most suitable environment for each cultivar, the comparison of any pair of cultivars in individual environments, the best cultivars for each environment and mega-environment differentiation, the average yield and stability of the genotypes, and the discriminating ability and representativeness of the environments (Yan et al. 2007; Yan and Kang 2003; Yan and Tinker 2006). The decision as to whether location groups could be considered as mega-environments is based on the consistency of location groupings and of the winning genotypes in the individual location groups across years (Yan et al. 2000, 2007, 2010). There has been a limited use of the GGE biplot method for analysis of METs on maize yield data in WCA by Badu-Apraku et al. (2008a, 2009, 2010). However, there is, presently, an increasing use of the GGE biplot for MET data analysis by researchers of the sub-region (Badu-Apraku et al. 2011a, b, c).

17.3 Repeatability of Traits and Locations in the West African Biotic and Abiotic Stress Screening Sites of IITA

Repeatability is computed as the proportion of the genetic variance over the total phenotypic variance (Fehr 1987). It represents the upper limit for broad-sense heritabilities. Repeatability and broad-sense heritability mean the same thing if the ratio of genotypic to phenotypic variance is considered. However, the term heritability can be misleading, as it can mean that the trait is inherited from one generation to another. However, sometimes the expression is used for one generation with no genetically constant selection units (hybrids, crosses) which are evaluated in different environments with varying repetitions per environment. Under such circumstances, the word repeatability is more appropriate. In this case, reference is made to how repeatable a trait is when assessed in two environments compared to four environments. The repeatability of a trait increases as more replications are used across environments or in the same environment across years.

Repeatability in a series of randomized complete block designs may be represented as follows:

$$x_{gr} = \mu + g_g l_l + y_y + gl_{gl} + gy_{gy} + ly_{ly} + r_{lyr} + e_{glyr},$$

where l is the number of locations, y is the number of years, and r is the number of replications.

Heritability, which is the ratio of practical importance, may be much less than the repeatability, but it cannot be greater. The repeatability differs very much according to the nature of the character and also according to the genetic properties of the population and the environmental conditions under which the individuals are kept. Falconer (1981) indicated that two assumptions are implicit in the idea of repeatability. The first is that the variances of the different measurements are equal and have their components in the same proportions. The second is that the different measurements reflect what is genetically the same character. Unless these assumptions are valid, repeatability becomes a vague concept.

The regional drought-tolerant early maturing variety trials of the Drought-Tolerant Maize for Africa (DTMA) Project serve as the vehicle for testing, identifying, and exchanging drought-tolerant extra-early (80–85 days) and early (90–95 days) varieties and hybrids of maize with broad adaptation to a particular agroecological zone among the four partner countries, Mali, Nigeria, Ghana, and Benin in West Africa (WA). Promising varieties identified based on trial results are used in farmer participatory on-farm trials and demonstrations which serve as important vehicles to showcase the effectiveness of new technology to farmers and thus are instrumental in the identification, release, and commercialization of drought-tolerant maize varieties and hybrids in the participating countries. The trials also give the NARS partners the opportunity to identify promising cultivars for the introgression of favorable alleles into the breeding populations of national maize programs to diversify and broaden the genetic base.

Results of multilocational trials in WA have established the existence of GEIs (Fakorede and Adeyemo 1986; Badu-Apraku et al. 1995, 2003, 2007, 2008a). This implies the need for extensive testing of cultivars in multiple environments over years before taking decisions on cultivar recommendations. However, due to the scarce resources of the national maize research programs of WA, there is a need to conduct cultivar evaluation in a limited number of environments. As pointed out by Yan et al. (2007), it is important to reexamine target environments for their uniqueness as some environments may never provide unique information, because they are always similar to some other environments in separating and ranking genotypes. This facilitates the identification of core testing sites where evaluation of cultivars can be done without losing valuable information about genotypes. Furthermore, stratification of maize evaluation environments can help increase heritability of measured traits, accelerate the rate of gain from selection, strengthen the potential competitiveness for seed production, and maximize grain yields for farmers (Gauch and Zobel 1997). It is therefore very important to develop a better understanding of the target agroecosystems used for the evaluation of drought-tolerant cultivars in WA and to determine if it could be subdivided into different mega-environments to facilitate a more meaningful cultivar evaluation and recommendation. It is anticipated that locations selected for METs should constitute a sample of environments that adequately represents the range of environmental conditions of the target geographical region. Furthermore, a protocol on seeds was ratified by the heads of states of ECOWAS member countries in 2009, and the West African Catalogue of Plant Species and Varieties (COAFEV) is presently available in the sub-region (FAO 2008). The seed catalogue contains the list of varieties whose seeds can be produced and commercialized within the territories of the 17 member countries of ECOWAS and consists of the varieties registered in the national catalogues of the member states. The catalogue offers a unique opportunity for the deployment of good-quality seeds of improved maize varieties and hybrids across the borders of the ECOWAS countries for production and marketing. As a result of these new developments and the implications of global warming, desertification, and recurrent drought in the sub-region, there is a need for reexamination of the current mega-environments in WA and the identification of core testing sites in each of the mega-environments used for the evaluation of the three different regional trials in WA. Several studies have been conducted to examine the effects of genotype and GEI in early and extra-early cultivar evaluation with particular emphasis on identifying core testing sites in the mega-environments of the lowlands of WCA for the early- and extra-early maturity groups. In one study, Badu-Apraku et al. (2011c) analyzed grain-yield data of the Regional Uniform Variety Trials-early (RUVT-early) containing 18 early cultivars evaluated for 3 years in 15 sites representing the dry savanna, moist savanna, and forest–savanna transition zones of WCA (Table 17.2). One of the objectives of the study was to classify the sites of the experiment into mega-environments based on the method proposed by Yan et al. (2007). According to this classification, test locations may be grouped into three types: (1) locations with low genotype discrimination that should not be selected as test locations; (2) locations with high genotype discrimination, representative of the

Table 17.2 Description of the test locations used for the Regional Uniform Variety Trials (RUVTs) of early-maturing varieties conducted in West Africa, 2006–2008

Country	Location	Code	Agroecological zone[a]	Latitude	Longitude	Altitude (m ASL)	Rainfall during growing season (mm)
Benin	Angaredebou	ANG	SS	11°32′N	3°05′W	297	1000
	Bagou	BF	SGS	11°28′N	2°23′W	303	1125
	Ina	INA	SGS	9°58′N	2°44′W	358	900
Ghana	Ejura	EJ	FT	7°38′N	1°37′E	90	1460
	Manga	MAN	SS	11°01′N	0°16′W	270	265
	Nyankpala	NYP	NGS	9°25′N	0°58′E	340	611
	Yendi	YD	SGS	9°26′N	0°10′W	157	1300
Mali	Katibougou	KT	SS	12°50′N	8°09′W	285	700
	Kita	KX	SS	13°05′N	09°25′W	393	1000
Nigeria	Bagauda	BG	NGS	12°01′N	8°19′E	520	681
	Ikenne	IKN	FT	6°53′N	3°42′E	60	1200
	Mokwa	MOK	SGS	9°18′N	5°4′E	457	1100
	Zaria	ZA	NGS	12°00′N	8°22′E	640	1120
Togo	Ativeme	ATV	FT	6°25′N	1°06′E	100	1360
	Sotouboua	SO	SGS	0°59′N	8°34′E	374	1200

[a] *SGS* southern Guinea savanna, *NGS* northern Guinea savanna, *FT* forest–savanna transitional zone, *SS* Sudan savanna

mega-environment as well as close to the ideal mega-environment, which should, therefore, be chosen for superior genotype selection, when few test locations can be managed due to budget constraints; and (3) locations with high genotype discrimination that do not represent the mega-environment, which could be used for unstable genotype evaluation.

The discriminating power of an environment refers to the ability of the environment to identify an ideal genotype, while the representativeness refers to the ability of a test location to typify the mega-environment**.** Using the discriminating power versus representativeness view of GGE biplot analysis of the results of the test locations, the test environments in this study, four mega-environments, were identified as follows:

Group 1 – Katibougou, Sotouboua, Ejura, and Bagou
Group 2 – Manga (MAN), Nyankpala (NYP), Bagauda (BG), Yendi (YD), Angaredebou (ANG), Mokwa (MK), Katibougou (KX), and Zaria (ZA)
Group 3 – Ativeme and Ikenne (IKN)
Group 4 – Ina

There was high correlation between the test locations Ejura, Sotouboua, Bagou, and Katibougou (Fig. 17.1) in their ranking of the genotypes, an indication that a promising early-maturing cultivar selected in any one of these locations will also be suitable for production in the other locations within the same mega-environments in the same or different countries. Similarly, MAN, NYP, BG, YD, ANG, MOK, KX, and ZA showed high correlation in their ranking of the genotypes in the second group indicating that a promising cultivar identified in one location will be most likely adapted to the other locations in this group. Selection of a cultivar out of these two groups of locations will most likely result in cultivars adapted to IKN and other locations within the same mega-environment. Ina stands alone in mega-environment 4 in its ranking of the genotypes and was unique in the ranking of the genotypes. Kita was identified as the ideal location, while Zaria was close to the ideal location.

The four mega-environments identified in the study were different from the maize agroecological zones identified by earlier researchers (Fajemisin et al. 1985; Menkir et al. 2003; Setimela et al. 2007). This result was not surprising since the study by Menkir (2003) was based on climatic data obtained from the geographic information system (GIS) for a large number of locations in SSA while those by Fajemisin et al. (1985) involved intermediate-to-late maturing cultivars. Besides, the earlier studies employed methods different from those used by Badu-Apraku et al. (2010, 2011a). Moreover, fewer locations were sampled with no representative location from the mid-altitude agroecology. These reasons might have accounted for the differences in the results of the studies. Validation of the discriminating power of the mega-environments was done using repeatability as the indicator. The repeatability values computed for grain yield and nine other traits, using the data of Badu-Apraku et al. (2011, unpublished data), are summarized in Table 17.3. The output was subjected to factor analysis for the purpose of grouping the 15 locations into factors, which were considered as mega-environments. Repeatability for individual traits varied widely among locations. For example, repeatability for grain

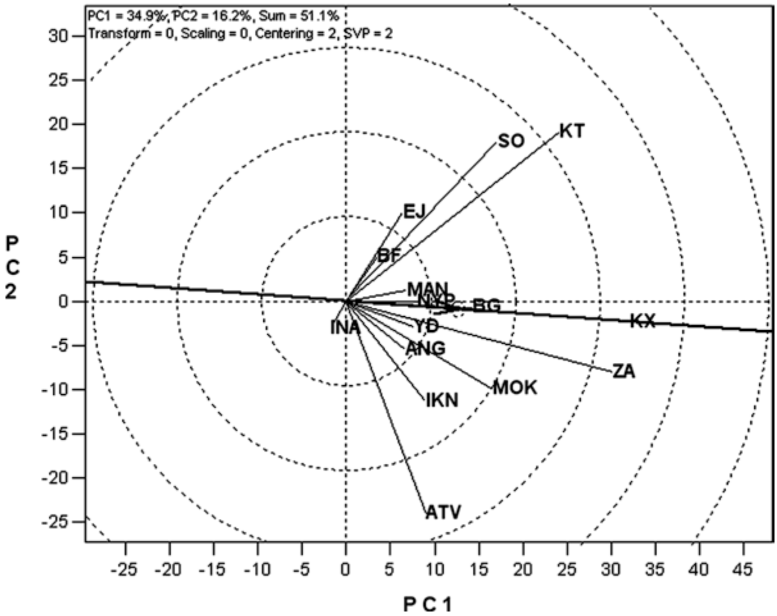


Fig. 17.1 The "discriminating power and representativeness" view of GGE biplot based on genotype x environment yield data of 18 early-maturing maize cultivars evaluated in 15 locations across WA between 2006 and 2008. The data were not transformed ("Transform=0"), were not standardized ("Scaling=0"), and were environment-centered ("Centering=2"). The biplot was based on genotype-focused singular value partitioning ("SVP = 2") and is therefore appropriate for visualizing the relationships among environments. Principal component (PC) 1 and PC 2 explained 51.1% of yield variation

yield ranged from −0.91 at Ina to 0.64 at IKN. Across sites, most of the traits had low repeatability values, mostly below 0.4 with only days to anthesis and silk having values above 0.4 (Table 17.3). Similarly, across traits, repeatability values were low for most sites with only Ikenne and Bagauda having values of about 0.4, while other sites had values much lower. As noted in earlier reports on RUVTs (Fakorede et al. 2007), grain yield had a negative relationship with coefficient of variation (CV) also in this study, but grain yield and CV did not influence repeatability.

Five factors (mega-environments) were identified, and together they accounted for 87% of the variation among the locations for repeatability (Table 17.4). Although the proportions of the variation attributable to the factors were not too far apart (about 15–22%), the number of locations per factor varied from two to five. The five mega-environments identified for evaluating early-maturing maize germplasm in this study are:

1. Kati, Angaradebou, Mokwa, Ejura, and Nyankpala with factor loadings of 0.62–0.82. This group accounted for about 22% of the variability among sites for the repeatability values.

Table 17.3 Repeatability of grain yield and agronomic traits of selected 18 early-maturing open-pollinated maize cultivars used in the RUVT evaluated for 3 years in 15 sites representing the dry savanna, moist savanna, and forest–savanna transition zones of five West African countries

	Repeatability										Grain yield		
Site	Yield	Anthesis	Silk	ASI[a]	PHT	EHT	PASP	EASP	EPP	HUSK	Mean	*t* ha^{-1}	CV %
Benin													
Anga	0.40	0.58	0.40	−1.37	0.01	0.23	0.21	0.55	−0.07	−0.36	0.058	2.8	21.0
Bagou	−0.06	0.55	0.40	0.50	0.37	0.48	0.00	−0.15	0.27	−1.76	0.060	1.8	30.7
Ina	−0.91	0.50	0.72	−0.43	0.23	0.38	−0.46	−0.53	0.24	−0.11	−0.037	2.9	17.0
Ghana													
Ejura	0.20	0.21	0.31	−0.28	0.36	0.25	−0.08	0.37	−0.53	0.63	0.144	3.7	19.0
Manga	−0.08	0.24	0.68	0.22	0.28	0.59	0.00	−0.23	−0.23	0.49	0.196	1.6	25.2
Nyank	0.44	0.68	0.63	0.09	0.75	0.08	0.17	0.41	−1.42	0.77	0.260	4.2	15.9
Yen	−0.73	0.46	0.23	0.36	0.25	0.07	0.06	0.28	0.38	−0.14	0.122	1.9	57.5
Mali													
Kati	0.69	0.62	0.58	−0.21	0.06	0.31	0.6	0.68	−0.03	0.34	0.364	3.0	21.0
Kita	0.57	0.45	0.61	0.35	0.48	0.61	−0.28	−0.34	−0.27	0.54	0.272	2.5	26.8
Nigeria													
Bagauda	0.51	0.64	0.62	0.06	0.27	0.57	−0.07	0.32	0.64	0.60	0.416	3.9	21.6
Ikenne	0.62	0.59	0.55	0.33	−0.18	0.42	0.13	0.52	0.64	0.50	0.412	2.7	18.8
Mokwa	0.54	0.40	0.44	0.25	0.30	0.26	−0.24	0.81	−0.09	0.19	0.286	3.6	17.2
Zaria	−0.45	0.21	0.39	−0.48	0.58	0.35	−0.58	0.81	−0.16	−0.55	0.012	5.2	18.1
Togo													
Ativeme	0.30	−0.16	0.56	0.64	0.28	0.36	0.45	0.46	0.00	0.67	0.356	2.2	32.4
Sotou	0.41	0.28	0.04	0.29	0.45	0.75	0.55	−0.27	0.18	−0.75	0.193	4.1	19.7
Means	0.16	0.42	0.48	0.02	0.30	0.38	0.03	0.25	−0.03	0.07			

[a] *ASI* anthesis-to-silking interval, *PHT* plant height, *EHT* ear height, *PASP* plant aspect, *EASP* ear aspect, *EPP* number of ears per plant, *HUSK* husk cover rating, *CV* coefficient of variation

Table 17.4 Factor loadings of repeatability estimates for 15 sites representing the dry savanna, moist savanna, and forest–savanna transition zones of five West African countries as determined for grain yield and agronomic traits of 18 early-maturing open-pollinated maize cultivars included in the RUVT evaluated in West Africa between 2006 and 2008

	Factor loadings				
Location	1	2	3	4	5
	0.794	−0.107	0.315	0.354	−0.002
Ativeme	−0.088	0.235	**−0.62**	−0.51	−0.205
Bagauda	0.187	0.344	−0.065	**0.885**	0.139
Bagou	−0.031	−0.045	**0.84**	−0.097	0.366
Ejura	**0.7**	0.515	0.422	−0.089	−0.051
Ikenne	0.086	−0.141	−0.191	**0.846**	−0.145
Ina	−0.054	0.507	0.219	0.351	**0.692**
Kati	**0.817**[a]	−0.074	0.018	0.194	−0.333
Kita	0.079	**0.937**	0.044	0.091	−0.16
Manga	−0.024	**0.939**	−0.095	−0.028	0.178
Mokwa	**0.747**	0.078	−0.194	0.052	0.115
Nyankpala	**0.618**	0.544	−0.243	−0.382	0.117
Sotou	−0.12	0.058	**0.941**	−0.233	−0.102
Yen	−0.215	−0.148	0.082	−0.071	**0.912**
Zaria	0.619	0.04	0.162	−0.025	**0.704**
Eigen value	4.06	3.06	2.52	1.93	1.47
Percentage variance explained	21.5	18.9	16.5	15.2	14.9
Cumulative variance (%)	21.5	40.4	56.9	72.1	87

Extraction method: principal component analysis. Rotation method: varimax with Kaiser normalization. Rotation converged in seven iterations

[a] Values in bold figures on the diagonal indicate locations loaded highly (loading >0.6) on a factor (or mega-environment) and are, therefore, considered as components of the mega-environment. Where a site had values >0.6 on two factors (e.g., Zaria), the larger value was considered

2. Manga and Kita with about equal factor loadings of approximately 0.94 each, accounting for about 19% of the variability among sites.
3. Sotouboua, Bagou, and Ativeme with loadings of 0.94, 0.84, and −0.62, respectively. This group accounted for about 16% of the variability among sites. Ativeme had a negative relationship with this group.
4. Bagauda and Ikenne with loadings of about 0.88 and 0.85, respectively, explaining about 15% of the variation among sites.
5. Yendi, Zaria, and Ina with loadings of 0.69–0.91, also accounted for 15% of the variation among sites.

The mega-environments identified in this study were not identical with those from earlier studies, but it was probably the most reliable because it took into consideration several traits of the maize plant. Although both GGE biplot analysis employed by Badu-Apraku et al. (2011c) and factor analysis used the principal component analysis approach, factor analysis has the added advantage that the factor loadings may be subjected to rotation to maximize the correlation among locations loaded on the same factor while minimizing the relationship between factors. Essentially, the mega-environments delineated by the factor analysis are orthogonal to each other (Fakorede 1979).

The five factors identified in this latter study represent five mega-environments. It is anticipated that cultivars with superior performance in any of the locations with positive loadings on a particular factor will perform well in other locations loaded on the factor. Cultivars that perform well in locations with positive loadings on the factor are expected to perform poorly in the location with negative loadings.

The information on the repeatability of traits of the 18 early-maturing cultivars presented in Table 17.5 are useful for identification of locations with high repeatability when averaged across traits, traits with high repeatability when averaged across locations, and location x trait interaction for repeatability. Based on this interpretation, only days to anthesis and silk were moderately repeatable across locations in the study; repeatability values for all other traits were low. Similarly, apart from Ikenne, Bagauda, Ikenne, Kita, Mokwa, and Katibouguo with repeatability estimates of 0.5 or more for grain yield, the aggregate phenotypes of the maize cultivars in the study were poorly repeatable in terms of grain yield at the different testing sites. However, repeatability for some other traits was high in some locations and low or even zero in some others. It is particularly striking that some of the locations with high grain yield and relatively low CV such as Zaria had low repeatability for yield and the aggregate phenotype.

Badu-Apraku et al. (2011b) identified Zaria, Ilorin, Ikenne, Ejura, Kita, Babile, Ina, and Angaredebou in WA as the core testing sites of the three mega-environments for testing the Regional Uniform Variety Trials-Extra-early. In another study, involving the testing sites for the Regional Early Trials, Badu-Apraku et al. (2011a) classified the test environments into four mega-environments. Four test locations were highly correlated in their ranking of the genotypes in group 1, suggesting that a promising early-maturing cultivar selected in one of these locations in one country will also be suitable for production in the other locations within the same mega-environments in different countries (Badu-Apraku et al. 2011a). Similarly, eight test locations were highly correlated in their ranking of the genotypes in group 2. The implication of this is that a promising cultivar identified in one of these locations will likely be adapted to the other locations. The identification of the core testing sites is expected to facilitate the selection of high-yielding and stable cultivars in the four different regional trials of WA [Regional Uniform Variety Trial (RUVT)-early, RUVT-extra-early, drought-tolerant (DT) regional early, and the DT regional extra-early variety trials] and seed production and marketing across the countries of WA.

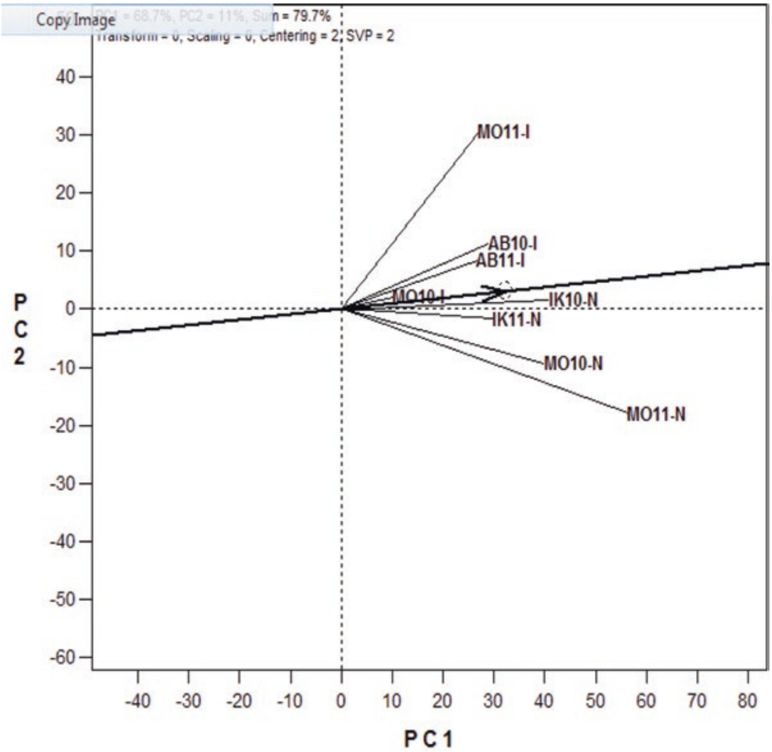
The selection of suitable breeding and testing sites is crucial to the success of a maize breeding program. A test location must be discriminating so that genetic differences among genotypes can be easily detected. It is important therefore that the test locations are representative of the target environments so that selected genotypes have the desired adaptation and are representative of the target environment as well as repeatable so that genotypes selected from year to year will have superior performance. According to Yan et al. (2007), only test locations with high discriminating

Table 17.5 Repeatability of traits of 18 early-maturing cultivars evaluated at 15 locations in West Africa between 2006 and 2008

Location	Year	Grain yield, kg ha^{-1}	Days to 50% anthesis	Days to 50% silk	Anthesis–silking interval	Plant height, cm	Ear height, cm	Plant aspect	Ear aspect	Ears per plant	Husk cover
Angaradebou	2007 and 2008	0.4	0	0.58	0.4	0.01	0.23	0.21	0.55	0	0
Ativeme	2008	0.3	0	0.56	0.64	0.28	0.36	0.45	0.46	0	0.67
Bagou	2007 and 2008	0	0.55	0.4	0.5	0.37	0.48	0	0	0.27	0
Bagauda	2007 and 2008	0.51	0.64	0.62	0.06	0.27	0.57	0	0.32	0.64	0.6
Ejura	2006 and 2007	0.2	0.21	0.31	0	0.36	0.25	0	0.37	0	0.63
Ina	2007 and 2008	0	0.5	0.72	0	0.23	0.38	0	0.0	0.24	0
Ikenne	2006 and 2007	0.62	0.59	0.55	0.33	0	0.42	0.13	0.52	0.64	0.5
Katibouguo	2008	0.69	0.62	0.58	0	0.06	0.31	0.6	0.68	0	0.34
Kita	2008	0.57	0.45	0.61	0.35	0.48	0.61	0	0	0	0.54
Manga	2006 and 2008	0	0.24	0.68	0.22	0.28	0.59	0	0	0	0.49
Mokwa	2006 and 2008	0.54	0.4	0.44	0.25	0.3	0.26	0	0.81	0	0.19
Nyankpala	2006 and 2008	0.44	0.68	0.63	0.09	0.75	0.08	0.17	0.41	0	0.77
Sotouboua	2008	0.41	0.28	0.04	0.29	0.45	0.75	0.55	0	0.18	0
Yendi	2006	0	0.46	0.23	0.36	0.25	0.07	0.06	0.28	0.38	0
Zaria	2006 and 2008	0	0.21	0.39	0	0.58	0.35	0	0.81	0	0
Across locations	**2006–2008**	**0.77**	**0.9**	**0.92**	**0.33**	**0.86**	**0.87**	**0.53**	**0.79**	**0.39**	**0.79**

ability are useful, and only those that are also representative can be used in selecting superior genotypes. The repeatability of genotype ranking across years within test locations is also an essential aspect in test location evaluation. The GEI of the testing sites of the RUVT-early and extra-early varieties in WCA has been studied, and the test locations were characterized and stratified into mega-environments and core testing sites to facilitate efficient and less costly testing of varieties (Badu-Apraku et al. 2011a, b). On the contrary, the testing locations of the regional drought-tolerant trials confined to the drought-prone locations in the four partner countries of the Drought Tolerant Maize for Africa (DTMA) Project, Nigeria, Ghana, Benin, and Mali (Table 17.3), have not been extensively studied. Therefore, there was a need for information on the representativeness, discriminating ability, and repeatability of the testing sites of the DT Regional Variety Trials in WA to facilitate the understanding of the responses of drought-tolerant maize genotypes in target drought environments. This was important in designing an efficient and economic selection strategy for the IITA Maize Breeding Program. Badu-Apraku et al. (2013) evaluated 12 early-maturing maize cultivars for 3 years at 16 locations in WA to determine the representativeness, the discriminating ability, and the repeatability of the test locations used for the evaluation of the DT Regional Early Variety Trials and to identify core testing sites to facilitate testing, seed production, and commercialization of drought-tolerant cultivars in WA. The GGE biplot analysis showed that Zaria (Nigeria), Nyankpala (Ghana), and Ejura (Ghana) possessed the highest discriminating ability. Two mega-environments were identified. Bagou, Nyankpala, Bagauda, Ikenne, and Mokwa represented the first mega-environment (ME1); Ejura, Ina, and Sotuba constituted the second (ME2). The ME1 would be more useful for evaluating early maize genotypes for tolerance to drought than ME2 because locations in ME1 were more strongly correlated to Ikenne (managed drought stress site). Among the testing sites, Bagou and Mokwa were found to be closely related to Ikenne in their ranking of the cultivars for drought tolerance; Zaria was the exact opposite, indicating that this was the least suitable location for evaluating genotypes for drought tolerance. Nyankpala and Ikenne were identified as the core testing site for ME1 and Ejura for ME2. TZE Comp 3 C_2F_2 was identified as the highest-yielding cultivar for ME1 and Syn DTE STR-Y for ME2, indicating that they could be used as check cultivars. Ikenne, Nyankpala, and Ejura had moderately high repeatability. They were closer to the average environment axis of each mega-environment suggesting that they will be useful for culling unstable genotypes during multilocational testing. Other sites were less representative and not repeatable and will not be useful for evaluating early maize cultivars for drought tolerance.

Using the GGE biplot, Akaogu et al. (2012) studied the interrelationship among the test environments for evaluating extra-early hybrids in Nigeria by the IITA Maize Program. In the biplot view presented in Fig. 17.2, the straight line from the origin to the coordinates where an environment falls is denoted as the research environment vector, while the straight line with a single arrow which passes the origin and the average environment represents the average environment axis (AEA). The length of the vector describes its discriminating power, while the angle between an environment and AEA measures its representativeness. According to Yan et al.



Code	Site
AB10-I	Abuja *Striga*-infested 2010
AB11-I	Abuja *Striga*-infested 2011
MO10-I	Mokwa *Striga*-infested 2010
MO11-I	Mokwa *Striga*-infested 2011
MO10-N	Mokwa *Striga*-free 2010
MO11-N	Mokwa *Striga*-free 2011
IK10-N	Ikenne *Striga*-free 2010
IK11-N	Ikenne *Striga*-free 2011

Fig. 17.2 The discriminating power and representativeness view of GGE biplot based on genotype x environment yield of 21 extra-early hybrids evaluated at three locations between 2010 and 2011

(2010), the shorter environmental vectors indicate that the specific environments were not strongly correlated with environments with longer vectors and that they were probably not strongly correlated with one another either. Thus, MO11-N and MO11-I had relatively long vectors and were considered as more powerful in discriminating among the hybrids, while IK11-N and IK10-N environments had small angles with AEA and were considered as the most representative of the test environments. The high repeatability of IKDT is not surprising since the induced drought stress treatment was effectively managed so that the irrigation system provided the same amount of water to all plots. Furthermore, the Ikenne site has deep uniform soils with high water-holding capacity. The high repeatability of IKDT has confirmed the effectiveness of the screening methodology adopted by IITA's Maize Improvement Program for selecting drought-tolerant genotypes. In contrast IKDT had high representativeness, discriminating ability, and repeatability, suggesting that it is the ideal test location. Based on the discriminativeness and representativeness of the research environments used in the present study, it was concluded that Mokwa has the ability to discriminate well among the extra-early maturing hybrids.

According to Yan et al. (2007), representativeness of a test site is a key factor for determining how it should be used in cultivar evaluation, assuming adequate discriminating ability. On the other hand, the usefulness of repeatability in MET data analysis lies in the fact that it is an essential step for assessing the representativeness of the test locations. Not until repeatability analysis based on multiyear and multilocational data is performed, a test location cannot be declared as of high, low, null, or negative representation of a mega-environment (Yan et al. 2011). For a test location to be described as highly representative, it must be repeatable across years in ranking genotypes. Based on repeatability analysis, a test location may be classified into one of four categories (Yan et al. 2011). The type I environments are highly representative test locations, which are also highly repeatable by definition. This type of test locations is considered ideal for use as core test locations. Genotypic differences observed at such locations are both repeatable across years and representative of the mega-environment. It is crucial for a breeding program to have a core test location of this type, particularly for early generation selection when it is not feasible because of availability of limited amount of seed to conduct multilocational tests. In our studies, none of the test locations could be classified as a core test location because of their relatively low repeatability and representativeness. Type II environments are low or moderately representative test locations, which may be highly repeatable or less repeatable. Type III environments are test locations that have zero representativeness but are highly repeatable. Such locations may be used to cull unstable genotypes, and, when employed, it is important that the selection intensity is low, to prevent useful genotypes from being mistakenly discarded. Type IV consists of test locations with negative representativeness. Such locations must not be used as test locations for the mega-environment of interest as the selection would be counterproductive. In the present study, Mokwa, Samaru, and Ejura were classified into type II for each of ME1, ME2, and ME3, respectively, owing to their relatively moderate repeatability and proximity to the average environment axis. These locations are expected to be especially useful in the multilocational test stage for selecting against unstable genotypes. Other locations used in this study are less representative and not repeatable, suggesting that the locations are not very useful for evaluating early-maturing maize genotypes for drought tolerance. Furthermore, the identification of Ejura and Ikenne as the most closely related test locations suggests that the ranking of the genotypes at Ikenne under induced moisture stress was quite similar to the ranking at Ejura, under natural drought. In addition, the result also implied that the mega-environment Ejura (ME3) could be considered the best location for testing early maize genotypes for drought tolerance under naturally occurring drought. According to Yan et al. (2011), the repeatability for a given location may vary with the set of genotypes involved. If highly unadapted germplasm or landraces or cultivars released long ago which may perform poorly every year as well as everywhere are included, the genotype main effect may be artificially inflated, leading to a higher estimation of repeatability. On the other hand, if the variation in mean performance among tested genotypes is very small, a low repeatability will result. In the present study, the sum of squares of the genotypic main effects for all measured traits accounted for only a small proportion of the total sum of squares thus suggesting that there was little variation in mean performance among the genotypes and thus accounting for the low repeatability obtained.

In conclusion, the results of the present study showed that the test locations used for the evaluation of the early-maturing maize genotypes for drought tolerance in the DTMA regional drought trials are not very representative and discriminating. Also, no core testing sites could be identified among the locations used in this study. Therefore, there is a need to sample more testing sites in WA using the modern cultivars with high variation in mean performance developed during the last decade to identify sites such as Ejura which possess high representativeness, discriminating ability, and repeatability. Such sites would be more appropriate for use in evaluating and selecting superior drought-tolerant genotypes as well as for serving as core testing sites within the identified mega-environments for cultivar evaluation, release, and commercialization across WA.

The development and commercialization of early and extra-early maize varieties and hybrids that are very responsive to added inputs have extended the boundaries of suitability of maize to the drier areas of the northern Guinea savanna and Sudan savanna of WCA. Despite the immense potential of maize in the savannas of WCA, production is greatly constrained by *Striga hermonthica* parasitism, recurrent drought, and low soil fertility, especially low levels of soil nitrogen (N). These constraints are more pronounced in the drier savannas that are characterized by reduced annual rainfall. To promote rapid adoption and commercialization of maize in the moist and dry savannas of WCA, there is a need for extra-early and early cultivars with combined resistance or tolerance to *Striga* infestation, drought, and low soil N.

Yield losses due to *Striga hermonthica* may range from 10% to 100% depending on the variety and the environmental conditions (Kroschel 1999). *Striga* infestation is extremely difficult to control and constitutes a major threat to the rapid spread of maize into the WCA savanna. Available *Striga* control measures include host plant resistance and cultural, chemical, and manual methods (Odhiambo and Ransom 1994; Kim et al. 1998). However, the use of host plant resistance or tolerance is considered the most economical, sustainable, and environmentally friendly for resource-poor farmers. Therefore, a breeding program for *Striga* resistance was initiated in Côte d'Ivoire in 1994 by the IITA to develop maize populations, cultivars, and inbred lines with combined earliness or extra-earliness and resistance/tolerance to *S. hermonthica,* drought, and low soil N. High-yielding early and extra-early drought and *Striga*-resistant/*Striga*-tolerant populations, inbred lines, varieties, and hybrids have been developed using drought-tolerant and *Striga*-resistant germplasm from diverse sources identified through several years of extensive testing in WCA (Badu-Apraku et al. 2001).

Genotype x environment interaction (GEI) poses a major challenge to breeders during multilocational evaluation of cultivars under *S. hermonthica* infestation because it may result in lack of consistency in the expression of resistance across environments. As a result, our strategy to ensure that the *Striga* resistance of the genotypes from our program does not break down in other environments has been to use the locations Ferkessédougou and Sinématiali in Côte d'Ivoire, Mokwa and Abuja in Nigeria and Angaredebougou, and Ina in Benin Republic as the principal screening and evaluation sites for *Striga* resistance for the maize populations, derived inbred lines, and cultivars in the program. We have observed in our program that *Striga*-resistant genotypes developed in a particular environment show the best performance in that particular environment. However, there is no reported situation where a *Striga*-resistant genotype in one environment has been found susceptible in another environment in WCA, suggesting that the resistance genes in our program could be durable (Kling et al. 2000). Despite the efforts to reduce GEI and hence improve the stability of performance of the products from our breeding program, recent studies by Badu-Apraku et al. (2006, 2008b) and Badu-Apraku and Lum (2010) have revealed significant GEI for most traits under *Striga* infestation, suggesting that the cultivars responded differently to the environments and that the differential response among cultivars was due to varying climatic conditions, soil type, and crop management practices at diverse test locations, which might have significantly influenced infestation and subsequent growth and development of *Striga*. Even though the test locations used in our screening for *Striga* resistance have provided a broad range of growing conditions, the significant GEI for grain yield and the *Striga* traits suggested that changes in the relative rankings of cultivars could be substantial across the diverse growing environments. This calls for the need to examine the GEI patterns and the consistency of the ranking of the *Striga*-resistant cultivars across the test environments in WCA. Therefore, 16 early-maturing cultivars were evaluated at two locations in Nigeria and three locations in the Republic of Benin from 2007 to 2009 to examine the grain yield, the stability, and the consistency of the rankings of the early-maturing cultivars under *Striga*-infested and *Striga*-free environments, assess the consistency of the rankings of the cultivars based on grain yield and other *Striga* traits under *Striga*-infested and *Striga*-free conditions, and assess the repeatability of measured traits and the test locations in Nigeria and Benin.

The combined analysis of variance showed significant cultivar and cultivar × environment interactions for grain yield and other traits under *Striga*-infested and *Striga*-free environments. The test of concordance was highly significant for grain yield ($W = 0.68$), number of emerged *Striga* plants ($W = 0.74$), and *Striga* damage ($W = 0.56$) under *Striga* infestation, indicating stability of resistance in the cultivars developed from diverse sources under artificial *S. hermonthica* infestation across environments. There was high consistency of the rankings of the cultivars for grain yield and other *Striga*-resistant traits under *Striga*-infested and *Striga*-free environments in Benin and Nigeria. Furthermore, the results indicated that *S. hermonthica*-resistant cultivars developed in Nigeria were also resistant in Benin. The AMMI biplot analysis for grain yield revealed POOL15SR/ACR94TZECOMP5-W/

ACR94TZECOMP5-W and 2004 TZE-Y Pop DT STR C_4 as the most stable cultivars with above average mean grain yield in *Striga*-infested environments and can be combined with other crop management options to control the parasite in the *Striga* endemic environments. Cultivars TZE Comp 5-W $C7F_2$ and TZE Comp5-Y C_6 S_6 (Set B) had less *Striga* damage and number of emerged *Striga* plants across test environments. These cultivars could therefore serve as unique sources of favorable alleles for improving *Striga* resistance in maize in different production environments and farming systems.

17.4 Conclusion

Several international trials are packaged annually by IITA and sent out to NARS partners for evaluation. The test entries are usually composed of newly developed varieties by IITA and NARS scientists, and proprietary varieties developed by seed companies. A standard check variety is included along with field book containing the field design and sheets for data collection. The collaborator supplies a second check variety and carries out the trial in his/her location. At the end of the season, the field books are returned to IITA for analysis. The analysis has consistently showed statistically significant GEI, implying the need to subject the data to further analysis to decompose the GEI. Location effects carry the largest portion of GEI in trials conducted within and among countries in WCA; therefore, management of field trials needs refinement so that specific location factors, such as soil type, timing, rate and composition of fertilizer, weed control, and pest control, are done as precisely as possible. Using estimates of repeatability values, multivariate statistical methods, such as factor analysis, we grouped sites with similar characteristics for maize production. Five mega-environments were identified for evaluating maize germplasm. Sites within each mega-environment cut across several countries in WA, for example, mega-environment 1 had Katibougou (Mali), Angaradebou (Benin), Mokwa (Nigeria), Ejura, and Nyankpala (Ghana) as similar locations for maize growth and productivity. This mega-environment accounted for 22% of the total variation for grain yield in the study; others explained 19, 16, 15, and 15%, respectively. AMMI and GGE biplot were quite effective for identifying stable, high-yielding genotypes for specific locations. This is a definite advantage of GEI analysis.

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Chapter 18
Selection Indices and Use of Secondary Traits

18.1 Introduction

Traits controlled by many genes have their phenotypes and genotypes normally distributed. Selection and recombination of superior individuals result in an advanced population with a higher frequency of favorable genes thereby making the performance higher than the original population. Frequently, breeders observe that selection for one trait often results in changes in some other traits that were not selected. Such changes are referred to as *correlated responses to selection* (CRS), and the non-selected traits are referred to as *secondary traits*. Correlated responses are of interest to breeders for several reasons: (i) they confirm that genes controlling quantitative traits are pleiotropic or tightly linked; (ii) they result automatically from selection for one or several traits; and (iii) they allow changing a trait by indirect selection or changing several traits simultaneously by a method referred to as *index selection*.

18.2 Indirect Selection Using Secondary Traits

The ultimate goal of maize breeding is yield improvement. Grain yield is the product of several traits and the cumulative effect of environmental conditions operating throughout the growing season. Yield is believed to be controlled by many genes, the exact number of which is not known. It is highly influenced by the environment; that is, GEI is often very high, resulting in relatively low heritability estimates. Secondary traits are under the control of fewer genes, have lower GEI, and are characterized by higher heritability estimates. If such traits show consistent genotypic and phenotypic relationships with yield, they may be more effective as

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selection criteria than direct selection for grain yield. A classical example was a study reported by Gardner (1961) in which gain from ten cycles of mass selection for grain yield in Hays Golden resulted in a gain of 3.9% cycle^{-1}. Lonnquist (1967) used ear number as indirect selection criterion for grain yield in the same population and obtained a gain of 6.3% cycle^{-1} in grain yield after five cycles of selection. Although there are reports of selection gains under low N resulting from breeding under high-N conditions (Carlone and Russell 1987; Castleberry et al. 1984; Duvick 1984; Kamprath et al. 1982), little is known about the relative efficiency of indirect vs direct selection in targeting low-N environments. Atlin and Frey (1989) found a very high genetic correlation for yield in oat (*Avena sativa* L.) lines grown under low and high N, resulting in similar predicted responses of grain yield to selection in either environment. Brun and Dudley (1989) and Muruli and Paulsen (1981), on the other hand, found that direct selection may be more efficient than indirect selection for targeting low-N environments with maize.

The predicted response in yield (Y) when selection is for a secondary trait (A) can be obtained from the regression of breeding value of Y on the phenotype of A. If $G(A)$, $G(Y)$ represent breeding values, $E(A)$, $E(Y)$ are environmental effects, and P(A), P(Y) are phenotypic values; r_G = genetic correlation coefficient, $\sigma_{G(A)}\sigma_{G(Y)}$ = genetic covariance of A and Y:

$$P(A) = G(A) + E(A), \tag{18.1}$$

and

$$P(Y) = G(Y) + E(Y), \tag{18.2}$$

with the restriction $r_{GE} = 0$.

The covariance between breeding value for Y and phenotype for A is

$$\operatorname{cov} G(Y)P(A) = \operatorname{cov} G(Y)\left[G(A) + E(A)\right], \tag{18.3}$$

$$\operatorname{cov} \mathrm{G(Y)E(A)} = 0$$

Therefore,

$$\operatorname{cov} G(Y),\, P(A) = \operatorname{cov} G(A)G(Y) = r_G s_{G(A)} s_{G(Y)}, \tag{18.4}$$

with the resulting regression coefficient of

$$b_{G(Y),P(Y)} = r_G s_{G(A)} s_{G(Y)} / s^2{}_A = r_G h_A \left[s_{G(Y)} / s_A \right]. \tag{18.5}$$

Equation (18.5) estimates the change in Y when selection is done based on the phenotypes of A. As is the case with direct selection, the observed change is the product of selection intensity, i; the genetic variability in the trait to be improved,

$\sigma^2_{G(Y)}$; and the accuracy of estimating genotype Y from phenotype A, which is obtained as the product of h_A and $r_{G.}$ The indirect change can be compared with the change expected under direct selection. If selection intensity is the same, the gain in Y, $\Delta G(Y)$ may be obtained as follows:

$$\Delta_{G(Y)} = ih_Y\sigma_{G(Y)}. \tag{18.6}$$

Consequently, at equal selection intensities, the ratio of the indirect or correlated response to the change by direct selection is obtainable as

$$\left[\Delta_{G(Y)}A\right] / \Delta_{G(Y)} = \left[r_G h_A / h_Y\right]. \tag{18.7}$$

18.3 Index Selection

As noted earlier, the total worth of individuals in a population is more important than the end product alone, which is yield in maize breeding. For example, an individual with high grain yield potential may have a tendency to lodge, flower much later than expected, or be too tall. Maize breeders must develop varieties that are not only high yielding but also have acceptable agronomic traits. In performing this task, breeders use three methods to select for several traits, including tandem selection, independent culling, and index selection. In tandem selection, individual traits are improved successively: trait A first, followed by B, etc. When selection is for A, progress for B, C, etc. = 0, if $r_g = 0$ in which case there will be no correlated responses. In independent culling, individuals must surpass a certain minimum value for each trait to be selected. The plants that are outstanding in certain traits may not be selected if they do not meet the required minimum for other traits, whereas individuals that are relatively mediocre in some traits are selected as long as they meet the cutoff value in others.

Index selection is an attempt to correct the weaknesses in tandem selection and independent culling methods. In index selection, each trait is weighted by a score, and the individual scores are summed to give a total score, which is referred to as the index value (I) for the genotype. For example, each trait may be weighted by its narrow sense heritability (h^2), that is,

$$I = h_1^2 P_1 + h_2^2 P_2 + \ldots\ldots + h_k^2 P_k \tag{18.8}$$

This index is then used as the selection criterion. Under the assumption of equal variances, the progress from selection is determined by Eq. (18.9):

$$\Delta_{G(I)} = ih_Y\sigma_{G(Y)} \tag{18.9}$$

By this method, superiority in some traits can make up for the mediocrity in others. One distinction between index selection and indirect selection is that the traits included in the index are not necessarily correlated. Although selection for several traits increases total economic value, progress in individual traits is decreased because of lower selection intensity for each trait. The size of this decrease depends on (i) the magnitude and direction of correlation between traits, (ii) the number of traits in the index, (iii) the weight given to individual traits, and (iv) the selection method used. Theoretically, a selection index should combine the different traits in a way that maximizes the probability of progress in the aggregate economic value. Because the traits of the individual are not of the same economic value, relative values are assigned as weighting factors in place of heritability in the construction of the index. Economic value may be defined as the increment in profit occurring from increasing the particular trait by one unit, independent of the other traits. The economic value of a trait is important for deciding how much consideration the trait deserves in selection.

18.4 Search for Secondary Traits for Indirect or Index Selection

There has been ongoing debate on the effect of selection under stress on yield performance of genotypes under optimal conditions and vice versa among plant breeders for decades. As a result of the presence of genotype × environment interaction (GEI), selection in one type of environment may not carry through in other environments. Genotype × environment interaction results from the varied response of genotypes to different environments and reduces the correlation between phenotypic and genotypic values (Comstock and Moll 1963) under stress environments. In WCA, maize breeders have several abiotic and biotic stresses to contend with, including diseases and insect pests, infestation by parasitic weeds—*S. hermonthica* in particular—drought, and low soil N. Experience has demonstrated that some traits are more sensitive to changes in the environment than others. For example, yield in maize consistently has large GEI in WCA. Furthermore, selection for maize grain yield under severe drought stress or low N has often been considered inefficient because the estimates of heritability of grain yield have been observed to decline with reduced yield levels characteristic of stressed environments (Bolanos and Edmeades 1993). Under these conditions, secondary traits may increase selection efficiency provided they have adaptive value, relatively high heritability, and significant genetic correlation with grain yield and are easy to measure (Falconer 1960; Bolanos and Edmeades 1993).

In maize, the occurrence of drought before and during flowering results in a delay between pollen shedding and silk emergence (Hall et al. 1982; Bolanos and Edmeades 1993). A commonly observed phenomenon in maize is that when maize flowers under drought, there is the delay of silking in relation to pollen shed, giving rise to anthesis–silking interval (ASI) whose duration is highly correlated with kernel set (DuPlessis and Dijkhuis 1967; Chapman and Edmeades 1999). In WCA, drought stress increases ASI and significantly reduces the number of ears per plant in early-maturing maize (Badu-Apraku et al. 2004a). Also, induced stress environments produce significantly lower grain yield, fewer ears per plant, and lower grain moisture percentage than the optimal site (Hall et al. 1982; Bolanos and Edmeades 1993; DuPlessis and Dijkhuis 1967; Chapman and Edmeades 1999; Badu-Apraku et al. 2004a, 2005). Badu-Apraku et al. (2004b) studied the effect of drought on genetic variances in Pool 16 DT early maize population. They found that grain moisture at harvest, ear height, and days to anthesis and silking had positive additive genetic variances but with lower narrow-sense heritability. However, there is limited information on the correlation between grain yield and other traits of extra-early maize under drought stress. This is mainly because the focal point of the IITA Maize Improvement Program has been on drought escape mechanism. Several extra-early varieties were developed such as TZEEW-SR and 95TZEEY-SR that normally complete the critical physiological processes before drought sets in. These and similar varieties developed in the program have been released in those areas of WCA where terminal drought is prevalent. Since 2007, however, IITA maize breeders started searching for genetic control of drought tolerance rather than drought escape in the extra-early germplasm. Genes for drought tolerance at the flowering and grain-filling periods have been identified and incorporated into the extra-early germplasm to develop inbred lines (TZEEI 6, TZEEi 21, TZEEI 29, TZEEI 58), synthetics (2008 syn EEDTSTR-Y and 2008 syn EEDTSTR-W), and hybrids, including TZEEI 29 x TZEEI 21 (Ife Hybrid 6), TZEE–WPop STRC5 x TZEEI 6, and TZEE-Y Pop DT POP STRC5 x TZEE 58. Drought occurs randomly and at any growth stage of development of the maize crop. Under such conditions, particularly in areas of WCA where drought occurrence is erratic, with varying intensity and timing, drought-tolerant rather than drought-escaping varieties are more desirable. Secondary traits can facilitate more precise identification of stress-tolerant genotypes, compared with measurement of only grain yield under stress. Studies by several workers (Bolanos and Edmeades 1996; Bänziger and Lafitte 1997; Badu-Apraku et al. 2004a) have revealed that, under stress, the estimates of heritability of grain yield usually decrease, whereas the heritability of some secondary traits remains high, while at the same time, the genetic correlation between grain yield and those traits remains about the same or increases sharply. Therefore, secondary traits may be used as selection criteria for stress tolerance. Furthermore, studies conducted at CIMMYT (Bänziger et al. 1999) and IITA (Badu-Apraku et al. 2011c) have clearly indicated that improvement for drought tolerance also resulted in specific adaptation and improved performance under low-N conditions, suggesting that tolerance to both stresses has a common adaptive mechanism. Breeders at both institutes have, therefore, been using secondary traits such as EPP, stay-green characteristic, and ASI, along with plant and ear aspects, all of which have strong correlation with grain yield under stress conditions, as selection criteria for grain yield in WCA and East and Southern Africa (Lafitte and Edmeades 1994; Bänziger and Lafitte 1997; Edmeades et al. 1998; Badu-Apraku et al. 2009, 2011c). In addition, because selection for *Striga* resistance is effective when done under low-N conditions, recurrent selection for *Striga* resistance resulted in concommitant improvement in grain yield and some other traits when evaluated under low-N environments in WCA. The implication of these results is that it will be more efficient to carry out selection for tolerance to the three stresses, low N, *Striga* infestation, and drought under low-N conditions (Badu-Apraku et al. 2009).

Three strategies have been adopted for breeding maize for stress tolerance in WCA: (i) selection under stress vs non-stress conditions, (ii) indirect selection using secondary traits, and (iii) index selection. In conducting the studies, maize germplasm (populations, varieties, lines, and hybrids) are evaluated under stress and non-stress environments such as *Striga*-infested vs *Striga*-free, moisture-stressed vs well-watered, and low (30 kg ha^{-1}) vs high level (90 kg ha^{-1}) of N. Badu-Apraku et al. (1997) evaluated cycles 0, 1, 2, 4, and 8 of full-sib recurrent selection for drought tolerance in Pool 16 DT under water-deficit and well-watered conditions in Côte d'Ivoire, using EPP, ASI, and flowering traits, and obtained yield gain cycle^{-1} of 0.02 and 0.14 t ha^{-1}, respectively (Fig. 18.1). Yield gain across environments was 0.06 t ha^{-1} cycle^{-1}. The implication of these results is that stress-resistant/stress-tolerant varieties have added value for improved performance under non-stress conditions. This is quite desirable. For several years, maize researchers at IITA have been using secondary traits along with grain yield to characterize the maize germplasm in WCA, starting with the intermediate/late-maturing maize group (Menkir et al. 2003; Meseka et al. 2006) and later followed by the early- and extra-early maturing groups (Badu-Apraku and Akinwale 2011). Specifically, the traits were used to develop base indices as appropriate for selection for tolerance to *Striga*, drought, or low N. A base index similar to that used by the Maize Improvement Program (MIP 1996) is used for selecting for high grain yield and *Striga* resistance in the early and extra-early groups. The index integrated grain yield, *Striga* emergence counts, *Striga* damage syndrome rating, and EPP measured under infested conditions. The means of the selected traits are expressed in standard deviation units and the index scores computed as

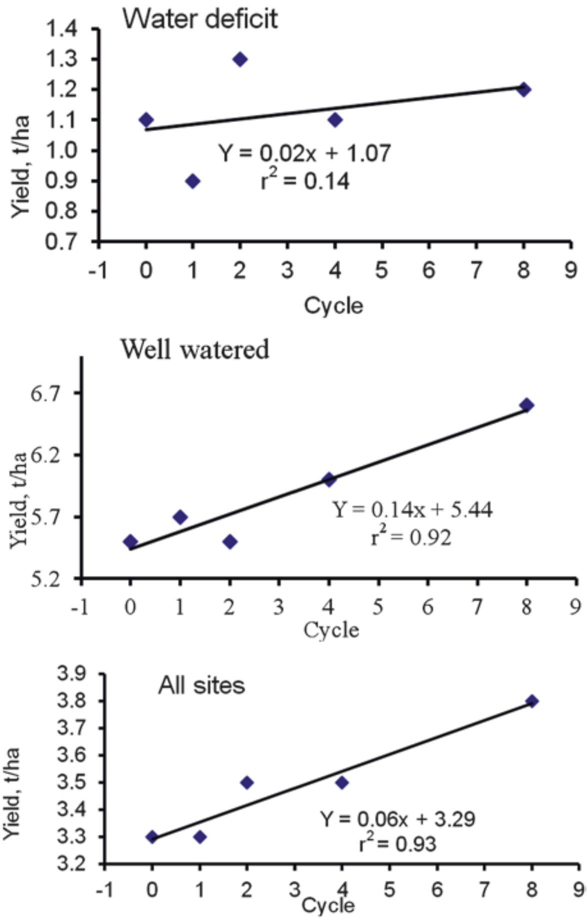
$$I = \left[\left(2 \times \mathrm{YLI}\right) + \mathrm{EPP} - \left(\mathrm{SDR8} + \mathrm{SDR10}\right) - 0.5\left(\mathrm{ESP8} + \mathrm{ESP10}\right)\right],$$

where YLI was the yield of *Striga*-infested plots, EPP is the number of ears at harvest in the *Striga*-infested plots, SDR8 and SDR10 were *Striga* damage ratings at 8 and 10 WAP, and ESP8 and ESP10 were number of emerged *Striga* plants at 8 and 10 WAP. The base index used for selecting for high grain yield under managed drought stress is computed as follows:

$$I = \left[\left(2 \times \mathrm{YL}\right) + \mathrm{EPP} - \mathrm{ASI} - \mathrm{PASP} - \mathrm{EASP} - \mathrm{LD}\right];$$

where YL is the grain yield under managed drought stress, EPP is the number of ears at harvest under drought stress, ASI is the anthesis–silking interval, PASP is the plant aspect, EASP is the ear aspect, and LD is the rating of the stay-green

Fig. 18.1 Response of cycles of full-sib recurrent selection in Pool 16 DT for drought tolerance when evaluated under water-deficit and well-watered environment and across environments (Badu-Apraku et al. 1997)



characteristic. Under both *Strig*a infestation and managed drought stress, each trait is standardized, with a mean of 0 and standard deviation of 1 to minimize the effects of different scales. Therefore, a positive value indicates tolerance of genotypes to the particular stress, while a negative value indicates susceptibility.

Badu-Apraku et al. (2016) proposed a multiple trait base index (MI) that integrated grain yield, EPP, plant and ear aspects, stay-green characteristic, *Striga* damage rating, and number of emerged *Striga* plants to select the entries evaluated across multiple stress environments (drought stress, low soil nitrogen, and *Striga* infestation) for AMMI analysis. Each trait was standardized to minimize the effect of the different scales. A positive MI value was considered an indication of tolerance/resistance to the multiple stresses, while negative values indicated susceptibility. The multiple trait base index was computed as follows:

$$\mathrm{MI} = \left(2 \times \mathrm{YLD}\right) + \mathrm{EPP} - \mathrm{EASP} - \mathrm{PASP} - \mathrm{SGR} - \mathrm{SD8} - \mathrm{SD10} - \left(0.5 \times \mathrm{ESP8}\right) - \left(0.5 \times \mathrm{ESP10}\right)$$

where

YLD = grain yield across environments
EPP = number of ears per plant across environments
EASP = ear aspect across environments
PASP = plant aspect across environments
SGR = stay-green characteristic across drought and low-N environments
SD8 and SD10 = *Strig*a damage rating at 8 and 10 WAP across *Striga* environments

Ensuring that greater response to selection is achieved using secondary traits individually or in combination with the primary trait (grain yield in our case) in a selection index rather than the primary trait per se is an important consideration in maize breeding. Several methods have been used in our program to achieve this goal, including identification of breeding values of secondary traits through determination of their heritability as well as their phenotypic and genetic correlations with grain yield among progenies of single populations, regression analysis, divergent selection, analysis of physiological and morphological changes in varieties that have been consistently selected for performance under stress, simulation models (Bänziger et al. 2000), path-coefficient analysis (Wright 1921), and the genotype × trait interaction (GT) biplot proposed by Yan and Kang (2003). Each of the methods has specific disadvantages, but, in general, the underlying principle is the presence of variation. The correlation coefficient measures the mutual association between a pair of variables independently of all other variables across all genotypes. Regression analysis, including stepwise multiple regression and path analysis, which is a special case of partial multiple regression analysis, as well as multivariate techniques (such as principal component analysis, PCA), examines the association among traits measured on a set of genotypes without identifying individual genotypes superior for specific traits (Fakorede 1979; Badu-Apraku and Akinwale 2011). Contrarily, the GT biplot is an effective statistical tool for evaluating cultivars based on multiple traits and for identifying superior genotypes for specific traits that could be used as selection criteria in a breeding program (Yan and Rajcan 2002; Lee et al. 2003; Yan and Kang 2003; Morris et al. 2004; Ober et al. 2005).

18.5 Trait Relationships Among Tropical Early and Extra-Early Maize in Contrasting Environments

Initially, CIMMYT developed a base index for selecting for drought tolerance. The index integrates grain yield under drought stress, ASI, EPP, stay-green characteristic, and plant and ear aspects and maintains constant number of days to flowering (anthesis in particular). The breeders also considered grain yield under well-watered conditions while selecting for improved performance under drought. The base index used at IITA for improving stress tolerance in early and extra-early germplasm deliberately selected for short ASI while keeping constant plant and ear heights and the number of days to flowering. In some cases, the materials undergoing selection for stress tolerance are also evaluated and selected under non-stress conditions. However, in some other cases such as progeny evaluation where a large number of entries are involved, evaluation and selection are done under stress alone. When evaluated under stress and non-stress conditions, products of stress selections demonstrated equal or better performance under non-stress than stress conditions, a desirable value addition (Badu-Apraku et al. 2004b). Similar findings have also been reported for intermediate- and late-maturing germplasm subjected to improvement for stress tolerance at IITA, using base indices (Menkir and Akintunde 2001).

The aspects of IITA Maize Program covered in this book focused on the development of extra-early and early-maturing varieties, inbred lines and hybrids, and their performance in contrasting environments created by imposing specific stresses and comparing with the non-stress counterpart and natural production conditions. CIMMYT scientists have conducted several studies that confirmed the effectiveness of using secondary traits as selection criteria for low soil N and drought tolerance in Mexico and East and Southern Africa (Edmeades et al. 1998; Lafitte and Edmeades 1994; Bänziger et al. 2000). Similar studies have also been conducted in WCA to evaluate the effectiveness of the base index, selecting for drought and/or low-N tolerance, and to assess the influence of contrasting environmental effects on the effectiveness of the index in selecting low-N and/or drought-tolerant early- and extra-early maturing genotypes.

Maize cultivars were evaluated under low (30 kg ha^{-1}) vs high (90 kg ha^{-1}) N in one experiment and drought vs well-watered environments in the second experiment. Both studies were conducted in four locations for 2 years. Four traits, ASI, EPP, EASP, and PASP, were identified as most reliable for simultaneous selection of drought- and low-N-tolerant genotypes with improved grain yield. Furthermore, GT biplot analysis showed that selection for EPP, PLHT, EASP, and PASP under low-N environments will improve grain yield under N-stress and non-stress environments. The inclusion of stay-green characteristic in the index for selection for yield improvement under drought stress was not justified in this study. The result involving EPP and ASI was not too surprising, particularly ASI which had been identified as an important secondary trait for stress tolerance in earlier studies by CIMMYT scientists. But inclusion of EASP and PASP was surprising, primarily because the traits are relatively easy to determine, are rather subjective, and require experience to minimize the effects of the subjectivity. With more refinements in their methods of determination, both traits, along with ear number, may be effective as selection criteria and consequently reduce the cost of selection programs for varietal improvement under stress conditions.

Suitable selection criteria are also required in breeding high-yielding maize varieties with effective resistance and/or tolerance to the hemiparasitic weed *S. hermonthica*. Appropriate *Striga* tolerance or resistance indicator traits can improve the precision with which resistant genotypes are selected. At the initial stages of the *Striga*-tolerant/*Striga*-resistant research work at IITA, the program concentrated on the late- and intermediate-maturity groups and used a base index, which combines grain yield under *Striga* infestation, *Striga* damage rating, number of emerged *Striga* plants, and EPP to select for high grain yield measured under *Striga*-infested and non-infested conditions (MIP 1996; Menkir and Kling 2007). The same base index was adopted at the time the research work was expanded to include extra-early and early-maturity groups in 1994. However, the breeders found inconsistent results, depending on traits used and type of germplasm subjected to selection. Using high grain yield under *Striga* infestation, host plant damage rating (*Striga* damage), and *Striga* emergence count (number of emerged *Striga* plants) as components of the base index gave contradictory results on the effectiveness and reliability of *Striga* emergence count as a trait for selecting for *Striga* resistance and improved grain yield under artificial *Striga* infestation. For instance, contrary to the results obtained for the late and intermediate-maturity groups (Kim and Adetimirin 1995; Gethi and Smith 2004; Menkir and Kling 2007; Yallou et al. 2009), Badu-Apraku et al. (2005, 2006, 2007) reported weak phenotypic and genotypic correlations between grain yield and *Striga* emergence count in the early-maturing germplasm. Furthermore, after four cycles of S_1 family selection in an extra-early white population, Badu-Apraku et al. (2012a) found that under *Striga* infestation, yield was not correlated with other traits at C0s but was significantly correlated with EPP, *Striga* damage rating, and emerged *Striga* plants in advanced cycles. Therefore, the value of the traits used in the base index by IITA Maize Program for selecting *Striga*-tolerant and *Striga*-resistant genotypes was in doubt for early and extra-early germplasm and required assessment and confirmation. Several workers have studied the relative importance of secondary traits in selecting for improved grain yield under drought stress and low-N conditions but obtained varying results, with overlapping of identified traits under the different stresses, probably because of the stress factors and type of genetic materials used (Alabi et al. 2001; Bolanos and Edmeades 1996; Bänziger and Lafitte 1997; Bänziger et al. 2000; Badu-Apraku 2006, 2007; Badu-Apraku et al. 2004a, b; 2011b; 2012a; Badu-Apraku and Akinwale 2011). For example, Bänziger et al. (2000) recommended ears per plant (EPP), anthesis–silking interval (ASI), and stay-green character (STGR) as the most useful secondary traits under drought stress and low-N conditions, whereas Badu-Apraku et al. (2011) through genotype x trait (GT) biplot identified ear aspect (EASP), plant aspect (PASP), ASI, and EPP as the most reliable secondary traits under drought stress: days to 50% anthesis (DA), days to 50% silking (DS), STGR, ASI, plant height (PHT), EPP, EASP, and PASP under low N and ASI, EPP, EASP, and PASP across (drought stress and low N) environments. Furthermore, Badu-Apraku et al. (2012a) used both path-coefficient and genotype main effect plus genotype x environment interaction (GGE) biplot analyses to identify EASP, PHT, and ASI as important secondary traits for drought tolerance, whereas EHT, PASP, EASP, and STGR were identified for selection under low-N conditions. Alabi et al. (2001) recommended the use of EPP, STGR, and ASI for selection under low-N environments. Despite the few differences in the reports from these and several other researchers, the IITA Maize Program conducts selection for improved grain yield under drought stress and low-N conditions by using a base index that incorporates high grain yield, increased EPP, reduced ASI, and outstanding expression of EASP, PASP, and STGR (Oyekunle and Badu-Apraku 2013). Thus, further studies are required to validate the reliability of the secondary traits included in the base index of the IITA Maize

Program. The identification and validation of secondary traits for selection for improved grain yield under contrasting stresses remain a relevant research area in maize breeding (Bolanos and Edmeades 1993, 1996; Bänziger and Lafitte 1997; Badu-Apraku et al. 2004a, b). Therefore, Talabi et al. (2017) investigated the inter-trait relationships under drought stress and low-N conditions and across environments, using simple correlations, stepwise multiple linear regression, and path-coefficient analyses. Results showed that EASP, EPP, PASP, STGR, and ASI were identified as the most important traits contributing to the variation in grain yield, suggesting their reliability as secondary traits under drought stress. Using genotype x trait (GT) biplot analysis in an earlier study, Badu-Apraku et al. (2011a) identified EASP, PASP, ASI, and EPP as the important secondary traits for selection under drought stress. Therefore, the inclusion of the traits in the IITA base selection index for improved grain yield under drought stress is well justified. Furthermore, in that study, plant height had indirect effects through all the five first-order traits (EASP, EPP, PASP, STGR, and ASI), whereas DS contributed through four of the five traits, suggesting that they should be considered as traits of potential value in drought experiments. Although EHT and HUSK were identified as third-order traits, EHT had significant effect on grain yield through all the second-order traits, suggesting that EHT is also of potential value in breeding for drought tolerance in maize. Similar results were obtained by Badu-Apraku et al. (2012a), who identified EPP, PASP, EASP, DS, ASI, PHT, and EHT as the most reliable traits in selecting for drought-tolerant genotypes in extra-early maize inbred lines. The authors suggested that DS, PHT, and EHT were additional drought-adaptive traits that should be considered for inclusion in the IITA base index for characterizing extra-early maturity maize for drought tolerance. Similarly, Bänziger and Lafitte (1997) also identified reduced barrenness (increased EPP) and shortened ASI, along with delayed leaf senescence, as reliable secondary traits for selection of superior genotypes under drought stress and low-N conditions. In their study, however, PASP, EASP, PHT, and EHT were not identified as important secondary traits for yield improvement. In our study, traits identified as most reliable indirect selection criteria for maize grain yield improvement under low-N environments included four of the five traits identified under drought (EASP, PASP, EPP, and STGR) plus three others (DS, EHT, and SL). These seven traits were similarly identified as the most reliable indirect selection criteria across environments. Obviously, secondary traits useful as indirect selection criteria for improved grain yield in maize under drought may vary with the type of genetic material and the geographical location of experiments, but some traits appear to be consistent under different research factors. Four traits, namely, PASP, EASP, EPP, and STGR, consistently identified in this study had also been identified by Badu-Apraku et al. (2011a, b), through GT biplot analysis, as the most important secondary traits for selecting superior genotypes under drought stress and low-N environments in genetic materials different from the ones used in the present study. Bänziger and Lafitte (1997) similarly identified delayed leaf senescence (STGR), reduced barrenness (EPP), and shortened ASI as reliable secondary traits for selection of superior genotypes under drought stress and low-N conditions. All of these seemingly important traits for indirect selection for yield improvement are easy to determine because they are based more or less on visual selection or counting. However, there must be caution in the interpretation, application, and extrapolation of research findings on the traits for several reasons. First, determination or quantification of some of the traits, such as PASP, EASP, and STGR, is subjective, and only experienced scientists and research technicians can score them accurately. Although, for many years, these traits have been part of traits determined in maize trials conducted in WCA, maize breeders have paid little or no attention to them as selection criteria perhaps because of the subjectivity in their determination. Breeders are now paying greater attention to these traits, and the need to minimize the subjectivity in their determination cannot be overemphasized. In addition, there is need for more specific studies on these traits using diverse maize types, including OPVs, inbred lines, and hybrids from different maturity groups and subjecting the data to several statistical and biometrical methods of analysis, such as those used in the present study. If the results from such studies are consistent with the findings reported here, maize breeders may need to select for the traits to minimize costs and efforts on selection for yield improvement. Second, results of this and similar studies suggest that selection for EHT and/or PHT should improve yield. This may be done only under the stress conditions evaluated in the studies because the stresses normally reduce both PHT and EHT, which are known to be positively correlated with grain yield in tropical maize. Selection for increased plant height under optimum production conditions will increase lodging, and this will be detrimental to grain production. Third, some ontogenic pairs of traits consistently demonstrated high positive relationships in our present study as well as in those conducted earlier. Some examples in the present study are PHT with EHT and DS with DA, both of which had high positive correlation coefficients ($r > 0.8$) and are either loaded on the same order of traits or one of the traits in a pair acts on yield through the other, with a high positive indirect path coefficient. Selection for improved grain yield using one of the traits in a pair as an indirect selection criterion or as a component in a selection index will suffice. It was concluded based on the results of this study that using simple correlations, stepwise multiple linear regression, and path-coefficient analyses, four traits, namely, EASP, EPP, PASP, and STGR, were important secondary traits, which could be included in a base index together with grain yield when selecting for improved grain yield under drought stress and low-N conditions and across both stress conditions.

The breeding strategy for *Striga* resistance, proposed for maize and sorghum (DeVries 2000; Haussmann et al. 2000) and presently adopted by IITA, is combined resistance/tolerance in individual genotypes with simultaneous selection for low *Striga e*mergence and high grain yield. Maize genotypes which combine low *Striga* damage syndrome ratings and few emerged *Striga* plants have been identified in the IITA program, but also genotypes combining low number of emerged *Striga* plants and severe *Striga* damage syndrome ratings have equally been identified in the program. Badu-Apraku et al. (2007) found that grain yield had a large positive additive genetic correlation with EPP and moderately large negative genetic correlations with flowering traits. Similar results were reported by other workers (Kim and Adetimirin 1995; Akanvou et al. 1997; Menkir and Kling 2007). However, the genotypic correlation between host damage rating and emerged *Striga* plants has been found to be low suggesting that different genes control the two traits (Kim 1994; Akanvou et al. 1997; Badu-Apraku et al. 2007). From the foregoing, the most reliable traits to use in selecting for *S. hermonthica* resistance or tolerance in early and extra-early maize populations needed to be clearly identified. Such traits would have to be combined with grain yield in a base index to maximize yield performance of selected genotypes. Badu-Apraku et al. (2014) evaluated ten *Striga*-resistant extra-early cultivars for 2 years under artificial *Striga*-infested and *Striga*-free environments in Nigeria and subjected the data to GGE biplot and sequential path analyses. Genotype, year, location, and interactions mean squares for most traits were statistically significant. Sequential path analysis identified ear aspect as the only trait with significant direct effect on yield under artificial *Striga* infestation, while GGE biplot confirmed EASP but also picked ears per plant and *Striga* damage rating as the most reliable traits. Another study involving 15 selected *Striga*-resistant/*Striga*-tolerant and *Striga*-susceptible early-maturing cultivars was conducted in 2008 and 2009 under artificial *Striga* infestation at Mokwa and Abuja, both in the southern Guinea savanna (SGS) agroecological zone of Nigeria where *Striga* is endemic. Results showed that EPP, *Striga* damage at 8 and 10 weeks after planting, and EASP were the most reliable traits for selecting *Striga*-resistant genotypes. *Striga* emergence counts at 8 and 10 weeks after planting were not among the reliable traits identified for selection for improved grain yield, and their inclusion in the base index needs to be further verified. EASP had high correlation with grain yield and was one of the most reliable traits for selection for increased grain yield under *Striga* infestation. Results obtained from the several studies are consistent; therefore, *Striga* damage rating, EPP, and EASP are recommended for inclusion, while the number of emerged *Striga* plants has been excluded from the base index for selecting for improved grain yield of early and extra-early maize under *Striga* infestation.

Availability of refined, user-friendly statistical tools continues to facilitate the interpretation of plant breeding studies by simplifying complex data obtained from field experiments. A case in point is the GGE biplot, along with softwares that handle multivariate analysis. A recent review by Akinwale et al. (2014 b) revealed the usefulness, advantages, and disadvantages of the GGE biplot in plant breeding and agronomic studies. Several studies were conducted to assess the efficacy of the traits in the base index presently used to improve the early and extra-early populations. In one of the studies, 90 extra-early inbreds were evaluated for 2 years at 3 locations in Nigeria under low-N conditions and drought to confirm reliability of leaf senescence (LS) for selecting for drought tolerance and EPP and ASI for low N. Data from the studies were subjected to GGE biplot and path-coefficient analyses. Plant aspect (PASP), plant height (PH), and ear height (EH) were identified as the most reliable traits for simultaneous selection for yield (YD) under low-N and drought stress in the extra-early inbreds. Leaf senescence (LS) was found to be unreliable for selecting drought-tolerant genotypes, while EPP and ASI were not identified among the reliable traits for selecting low-N-tolerant genotypes. EH, PASP, EASP, and LS1 were identified by both path-coefficient and GGE biplot analyses as reliable for selecting for low N and EASP, PH, and ASI for drought tolerance. Several useful implications may be deduced from the identification of PASP, EASP, and PH as the most reliable traits for the simultaneous selection for improved YD under low-N and drought stresses. First, the analyses confirmed the results of the earlier studies; second, tolerance of extra-early maturing maize cultivars to both stresses may involve similar adaptive mechanisms; third, the use of the same base index for selecting tolerant genotypes under both stresses is justified; fourth, selecting for reduced PH, good EASP, and PASP under either drought or low-N stress would result in simultaneous improvement in YD under both low-N and drought environments; and fifth, LS is not necessarily a useful trait for indirect selection for high grain yield in maize under stress environments. Most of these findings are consistent with those of several earlier workers (Lafitte and Edmeades 1995; Lafitte and Bänziger 1997; Brancourt-Hulmel et al. 2005; Bänziger et al. 2000). However, effectiveness of LS as an indirect selection criterion for high yield under stress reported by CIMMYT was not corroborated by studies in WCA.

An important result of this study that selections made under one stress environment (e.g., low N) will be equally effective also in the other (e.g., drought) deserves special attention. In this case, selection under low N will be the obvious choice because it is easier and cheaper to accomplish. Badu-Apraku et al. (2011a) had hypothesized that improvement of grain yield under low N indirectly results in improved YD in the other research environments. It is also important to note that the traits, PASP, EA, and PH, were reliable for selecting stress-tolerant early and extra-early genotypes, in addition to late and intermediate varieties, which implies that the same base index could be used for selecting for drought and low-N tolerance in the four maize maturity groups of WCA.

Although grain yield is most often the target parameter in maize breeding programs, field data are normally collected on several other traits in multilocational trials in an effort to identify useful germplasm with specific stress tolerance, desirable agronomic features, and end-use quality attributes for use in breeding programs and for release to farmers. During the analysis of field data, most studies have focused only on grain yield (Fakorede and Adeyemo 1986; Badu-Apraku and Lum 2007; Badu-Apraku et al. 2008, 2009). Genotype x environment interaction (GEI) results from the differential response of genotypes across a range of environments (Allard and Bradshaw 1964; Kang 1998). The GEI reduces the correlation between phenotypic and genotypic values (Comstock and Moll 1963) and complicates the selection of the best genotypes for a relatively large area (Ebdon and Gauch 2002; Magari and Kang 1993). Epinat-Le Signor et al. (2001) reported that identification of a combination of genotypic traits significantly contributing to GEI for grain yield facilitates the biological interpretation of the results of genotype × environment interaction (GEI) analysis and the identification of superior and stable cultivars and inbred lines for hybrid production and development of synthetics. The genotype-by-trait (GT) biplot is a very useful statistical tool for comparing genotypes on the basis of multiple traits and for identifying genotypes that are superior in certain traits and can therefore be candidates for parents in a breeding program. It also allows the investigation of the similarities and differences among genotypes in their response to the environments and allows the nature and magnitude of interactions between any genotype and any environment to be readily visualized (Yan et al. 2000; Yan and Kang 2003). Furthermore, the GT biplot is very useful for genotype-by-trait analysis and has been effectively used in determining the interrelationship among traits and measuring the major traits that contribute significantly to target traits including grain yield and quality (Yan and Rajcan 2002; Yan and Kang 2003). The GT biplot also aids in multiple trait selection because it graphically displays the trait associations across genotypes as well as the trait profiles of the genotypes. A comprehensive multi-trait selection procedure, proposed by Yan and Frégeau-Reid (2008), combines three selection strategies, independent selection, independent culling, and index selection, so that all the aspects in variety or parent line selection are taken into consideration. Badu-Apraku et al. (2010) conducted studies from 2007 to 2009 at three locations in Nigeria under induced drought stress and low-nitrogen conditions. The objective was to identify superior inbred lines based on multiple traits for use as parents for hybrid production and for introgression into maize breeding populations. Both the *multi-trait selection* tool of the GGE biplot and the GT biplot identified the inbreds TZEI 17, TZEI 13, TZEI 23, TZEI 2, TZEI 3, TZEI 22, TZEI 7, TZEI 11, and TZEI 8 as the most promising parents under drought stress (Fig. 18.2). Under low N, TZEI 7, TZEI 11, TZEI 2, TZEI 4, TZEI 10, TZEI 8, and TZEI 22 were selected by the two methods (Fig. 18.3). TZEI 11, TZEI 2, TZEI 8, and TZEI 22 had combined tolerance to drought stress and low N and could be used as germplasm sources for introgression of genes for tolerance to the two stresses into tropical maize populations as well as for the development of drought- and/or low-N-tolerant hybrids. Under drought stress, TZEI 17, TZEI 3, TZEI 23, and TZEI 13 were the closest to the ideal genotype, while TZEI 7, TZEI 2, and TZEI 11 were the closest under low-N conditions (figures not shown).

18.6 Conclusions

Drought occurs randomly and at any stage of growth and development of the maize crop. Secondary traits can facilitate more precise identification of stress-tolerant genotypes, compared with measurement of only grain yield under stress. Therefore, grain yield and secondary traits may be used as selection criteria for stress tolerance. Furthermore, studies conducted at CIMMYT and IITA have clearly demonstrated that improvement for drought tolerance also resulted in specific adaptation and improved performance under low-N conditions, suggesting that tolerance to both stresses has a common adaptive mechanism. Breeders at both institutes have, therefore, been using secondary traits such as EPP, stay-green characteristics, and ASI, along with plant and ear aspects, all of which have strong correlation with grain yield under stress conditions, as selection criteria for grain yield in WCA and ESA. In addition, because selection for *Striga* resistance is effective when done under low-N conditions, recurrent selection for *Striga* resistance resulted in

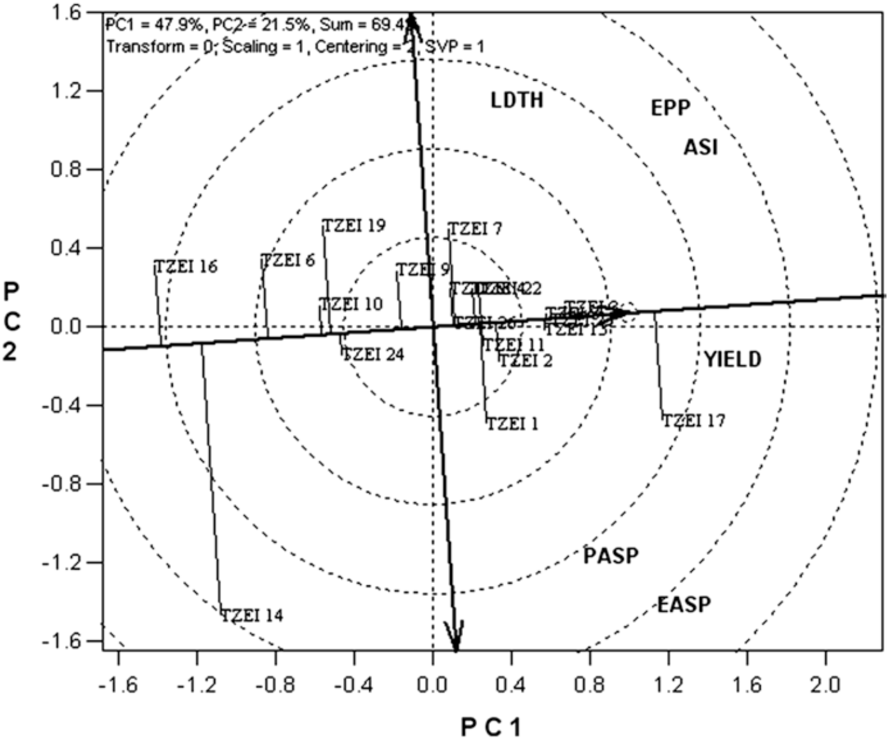


Fig. 18.2 An entry/tester view of genotype × trait biplot of six selected traits of 20 early-maturing maize inbred lines evaluated under managed moisture stress at Ikenne, Nigeria, in 2007 and 2008. The data were not transformed ("Transform = 0"), were standardized ("Scaling = 1"), and trait-centered ("Centering = 2"). The biplot was based on trait-focused singular value partitioning ("SVP = 1") and is therefore appropriate for visualizing the relationships among genotypes. The horizontal line passing through the biplot origin and the average tester, with an arrow pointing to the average tester, and its ordinate passing through the origin and perpendicular to the abscissa is called the average tester axis or ATC abscissa. Principal component (PC) 1 and PC 2 for model 2 explained 69.4% of the variation among traits. Abbreviations: *YIELD* grain yield, *EPP* ears per plant, *PASP* plant aspect, *EASP* ear aspect, *ASI* anthesis–silking interval, *LDTH* leaf death score

concommitant improvement in grain yield and some other traits when evaluated under low-N environments in WCA. It will therefore be more efficient to carry out selection for tolerance to the three stresses, low N, *Striga* infestation, and drought under low-N conditions. It is also important to note that the traits, PASP, EA, and PH, were reliable for selecting stress-tolerant early and extra-early genotypes, in addition to late and intermediate varieties. This implies that the same base index could be used for selecting for drought and low-N tolerance in the four maize maturity groups of WCA.

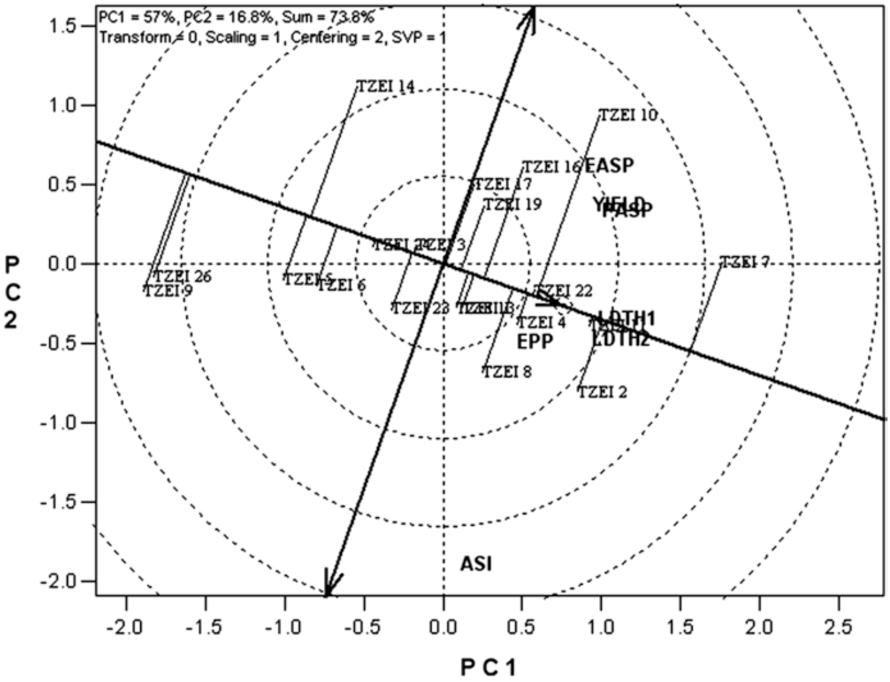


Fig. 18.3 An entry/tester view of genotype × trait biplot of seven selected traits of 20 early maturing maize inbred lines evaluated under low-N conditions at Mokwa, Nigeria, in 2007 and 2008. The data were not transformed ("Transform = 0"), were standardized ("Scaling = 1"), and genotype-centered ("Centering = 2"). The biplot was based on genotype-focused singular value partitioning ("SVP = 1") and is therefore appropriate for visualizing the relationships among genotypes. The horizontal line passing through the biplot origin and the average tester, with an arrow pointing to the average tester, and its ordinate passing through the origin and perpendicular to the abscissa is called the average tester axis or ATC abscissa. Principal component (PC) 1 and PC 2 for model 2 explained 73.8% of the variation among traits. Abbreviations: *YIELD* grain yield, *EPP* ears per plant, *PASP* plant aspect, *EASP* ear aspect, *ASI* anthesis–silking interval, *LDTH1* leaf death score at 56 days after planting, *LDTH2* leaf death score at 70 days after planting

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Part V

Potential Role of Early and Extra-Early Maize in Sustainable Food Security in Sub-Saharan Africa

Chapter 19
Variety Testing, Release, and Registration in West Africa

19.1 Introduction

The benefits of improved varieties are realized, and investment of time and huge resources to breeding justified when improved varieties are released, and a large number of farmers cultivate the variety. Although the process of release of variety differs considerably from country to country, there are similarities. Usually, a body is given the responsibility to authorize the release of newly developed varieties. To ensure that only varieties that have shown outstanding performance are released for cultivation by farmers, the process of variety release involves a list of steps and activities. The plant breeder of an institution that intends to release a variety nominates such a variety for release through the completion of appropriate forms requesting for release. Prior to this, the variety is required to have been tested in several locations over a number of years. The testing is usually done at different levels, viz., on-station and on-farm. During the testing, important agronomic data including yield and reaction to important pests and diseases are collected. A check variety is normally included in such trials for comparison.

In Nigeria, the committee responsible for regulating variety release is known as the National Variety Release Committee (NVRC). The data collected by the researcher or institution intending to release the variety are made available to the NVRC and are considered by a technical subcommittee. The technical subcommittee examines the data and takes a decision on release which is communicated to the NVRC which, thereafter, registers the variety.

The on-farm testing requirement for variety release involves the conduct of variety testing and other new technologies on farmers' fields to verify superior performance obtained on-station and expose the new technologies to farmers. In addition, it helps to generate data that are required for variety release and helps to determine the economic feasibility of new technologies. On-farm trials are conducted in areas with a large number of farmers. The areas for the conduct of on-farm trials must be

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accessible as repeated visits are made to the trial sites during the season to inspect the trials and interact with farmers. The areas selected for the conduct of on-farm trials must be representative of the areas where the new varieties are intended for cultivation. On-farm trials could use the mini-plot technique or the mother–baby approach. The mother–baby trial is twin in nature with one objective. One of the twin trials is researcher managed, while the other is farmer managed. The farmer-managed trial affords the farmer the opportunity to situate the new technology in the context of his environment and socioeconomic circumstances. It is desirable to have a limited number of varieties in the mother trial. The baby trial only evaluates a subset of the entries in the mother trial. Yield data and other important agronomic data are collected on both the mother and baby trials. Socioeconomic data are also collected. Field days are organized at critical stages during the trials to help farmers assess the new varieties compared to their most favored ones. Field days bring farmers together and provide the opportunity for discussions among farmers as well as the opportunity for interaction among all stakeholders which include researchers and seed companies.

Data collected are analyzed statistically. This is possible because the entries being evaluated are sometimes within each farmer's field, but at other times each unreplicated baby trial is considered a replicate. Ranks of varieties being tested by farmers could also be very useful.

Regional Uniform Variety Trials (RUVT) involving extra-early maturing (80–85 days to maturity) and early-maturing (90–95 days to maturity) cultivars have been organized by IITA in collaboration with the NARS partners of WCA during the last two decades. The RUVT which are packaged and dispatched by IITA scientists to collaborators serve as the vehicle for dissemination of germplasm and cultivars among the NARS of the sub-region. The trials offer the NARS partners the opportunity to select promising and stable cultivars for on-farm testing and release or for introgression of favorable alleles into breeding populations of national maize programs to broaden the genetic base.

The RUVT in WCA usually have significant genotype x environment interaction (GEI) due to the differential response of cultivars to varied growing conditions (Fakorede and Adeyemo 1986; Badu-Apraku et al. 1995, 2003, 2007, 2008, 2009, 2011). For example, Badu-Apraku et al. (2011) evaluated 12 extra-early maturing maize cultivars at 17 locations in four countries of WA from 2006 to 2009. Results showed that the effects of genotype (G), environments (E), and GEI were significant ($p < 0.01$) for grain yield. Differences among E accounted for 74.9% of the total variation in grain yield, while the G effects and GEI accounted for 3.4% and 21.7%, respectively. The presence of significant GEI complicates the selection of superior cultivars and the best testing sites that can be used to identify superior and stable genotypes. This calls for extensive testing of cultivars in multiple environments over years before cultivar recommendations.

During the past two decades, recurrent drought, desertification, and global warming have severely reduced the agroecological zones in WCA such as the rainforest agroecology, while the forest–savanna transition zone appears to have blended into the Guinea savanna (Menkir et al. 2003). It is therefore important that the appropriateness of test locations in the various mega-environments in the sub-region is continuously assessed for efficient and successful development of maize cultivars with high-yield potential adapted to the various agroecologies for increased adoption by farmers. Furthermore, a protocol on seed was signed by the Heads of States of ECOWAS member countries in 2009, and the West African Catalogue of Plant Species and Varieties (COAFEV) has been published and is presently available in the sub-region. The seed catalogue which contains the list of varieties whose seeds can be produced and commercialized within the territories of the 17 member countries of the ECOWAS is an aggregate of the varieties registered in the national catalogues of the Member States. The catalogue offers a unique opportunity for movement of good-quality seed of improved maize varieties and hybrids across borders of the ECOWAS countries for production and marketing. As a result of this new development in the seed sectors of the ECOWAS member countries and the implications of the global warming, desertification, and recurrent drought, there was a need for re-examination of the mega-environments and core testing locations in each of the mega-environments in WCA. This was crucial to facilitate the selection of high-yielding and stable maize cultivars for seed production and marketing across countries of WCA. Towards this goal, multi-environment trials (METs) have been routinely conducted by the IITA Maize Program in Nigeria. The information obtained from such trials is invaluable to the national maize programs with similar growing environments in the sub-region. It facilitates the identification and selection of high-yielding cultivars with specific or broad adaptation to their conditions for further testing on-farm and for release to their farmers. In addition, the information helps national scientists to identify appropriate germplasm with specific stress tolerance, desirable agronomic traits, and end-use quality attributes for use in national breeding programs (Badu-Apraku et al. 2009).

19.2 Approaches to Variety Release in West and Central Africa

Constraints to variety release and registration in SSA include lack of functional varietal release systems in some countries, poor efficiency in variety testing, rigid regulations which overlap in variety release protocols, lack of seed laws in some countries, and lack of funds for meetings of varietal release committees. To ensure that distinct, uniform, and stable (DUS) varieties enter the market and that the released varieties have a minimum value for cultivation and use (VCU), stimulate use of better varieties, and enhance development of strong maize breeding programs, a study was carried out by Setimela et al. (2009) under the auspices of the Drought-Tolerant Maize for Africa (DTMA) Project funded by the Bill & Melinda Gates Foundation (B&MGF). The specific objectives of the study were to define the time taken to release elite maize varieties, summarize the variety release requirements and procedures in 13 DTMA Project countries, identify constraints militating against the release of elite maize germplasm to smallholder farmers, and propose

Table 19.1 Estimated number of maize varieties by type released by public and private breeding programs in DTMA Project countries in sub-Saharan Africa, 2002–2006

	OPVs		Hybrids		
Country	White	Yellow	White	Yellow	Total
Angola	9	2	14	6	31
Benin	6	0	1	0	7
Ethiopia	6	0	12	0	18
Ghana	0	0	0	0	0
Kenya	6	0	49	0	55
Malawi	0	0	7	0	7
Mali	0	0	0	0	0
Mozambique	4	0	0	0	4
Nigeria	3	1	2	0	6
South Africa	9	6	134	154	303
Tanzania	1	0	6	0	7
Zambia	5	0	40	6	51
Uganda	0	0	0	0	0
Zimbabwe	5	0	13	1	19
Total	54	9	278	167	508

Source: DTMA National variety testing and release survey 2007/2008 (Setimela et al. 2009)

strategies to accelerate the release of new maize varieties. Results showed that variety testing and release committees differed greatly among the study countries including their composition. In a number of situations, the public sector dominated the variety release committee meetings. The difficulties with existing variety release systems have resulted in delayed access by farmers to new maize varieties. The system has allowed few varieties to be released (Table 19.1); it is costly and duplicative, as the same variety must be tested in all countries where it is being targeted for marketing. The returns on investment are also delayed as seed companies have to wait for a long period before they can enter the seed market, while their variety is undergoing testing prior to release.

19.3 Organization and Structure of Variety Release System in WA Countries

19.3.1 Benin

Maize improvement in Benin is the responsibility of the Insitut National des Recherches Agricoles du Bénin (INRAB). INRAB develops maize varieties and conducts the national multilocation variety trials in all the maize-growing agro-ecologies of the country. The Institute also conducts extensive on-farm trials

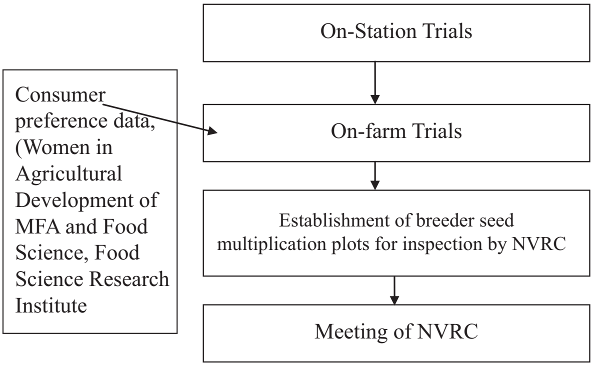


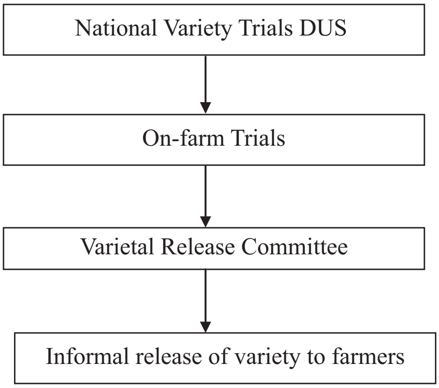
Fig. 19.1. Variety release channel in Ghana

throughout the country in collaboration with the extension services of the Ministry of Agriculture and Rural Development. Even though Benin does not yet have a defined seed law, a formal variety release mechanism has just been put in place and is presently operational in the country. The national scientists of INRAB conduct several on-station and on-farm trials annually. Several varieties have been informally released in the country and are in the hands of Beninois farmers.

19.3.2 Ghana

The Crops Research Institute (CRI) and the Savanna Agricultural Research Institute (SARI) of the Council for Scientific and Industrial Research (CSIR) are responsible for the development and on-station evaluation of maize varieties and hybrids in Ghana (Fig. 19.1). The two institutes have several experiment stations scattered throughout Ghana for extensive multilocation trials. At least 2 years on-station data and 2 years on-farm data, consumer preference data, and physicochemical and economic analysis are required for the release of a variety. The on-farm trials are conducted by the researchers of CRI and SARI in collaboration with the extension staff of the Ministry of Food and Agriculture (MOFA). The consumer preference data are collected by the women staff of MOFA, while the physicochemical analyses are conducted by the Department of Food Science at the University of Ghana and Food Science Research Institute of CSIR. The economic analyses are carried out by the economists at CRI and SARI. Once all the required data for the release of a variety have been assembled, an application for the release of the variety is submitted to the NVRC which is composed of the directors of CRI, SARI, Department of Agric. Extension Services, Women in Agricultural Development, Crops Services Division, Grains and Legumes Development Board, and Plant Protection and Regulatory Services Division, the representative of the universities of Ghana, a plant breeder, a

Fig. 19.2 Variety release channel in Mali



representative of the Seed Growers' Association, a seed technologist, head of the Ghana Seed Inspection Division, head of the National Seed Service, a representative of the seed dealers' association, and a farmers' representative.

The members of the NVRC visit the breeder seed field twice during the growing season. The first visit is at the flowering stage and the second at harvesting. Based on these visits, the committee decides whether or not the process for the release of the variety should go on. If the committee is satisfied with the performance of the variety in the breeder seed plot, then a date is fixed for a committee meeting to consider the release of the variety. The sponsoring breeder of the candidate variety is responsible for the presentation of the necessary data during the meeting of the NVRC to support the release of the variety.

The rate of release of new maize varieties has been poor. However, in the past 5 years, several maize varieties have been released (Table 19.1). Poor rate of variety release may be due to the few seed companies operating in the country. Ghana is the only country that requires an economic analysis for a new maize variety to be released.

19.3.3 Mali

The Insitut D'Economie Rurale (IER) has the mandate for breeding and evaluation of maize varieties in Mali. The Institute carries out the national variety trials at multilocations in the Guinea and Sudan savanna agroecologies of the country (Fig.19.2). In addition, IER carries out on-farm trials and demonstrations in collaboration with the national extension systems, private seed companies, and NGOs such as SG 2000. The seed law is yet to be promulgated. Therefore, there is no formal variety release mechanism, and varieties are informally released to farmers through on-farm trials and demonstrations. Several improved varieties have been released informally by IER and are presently in the farmers' hands.

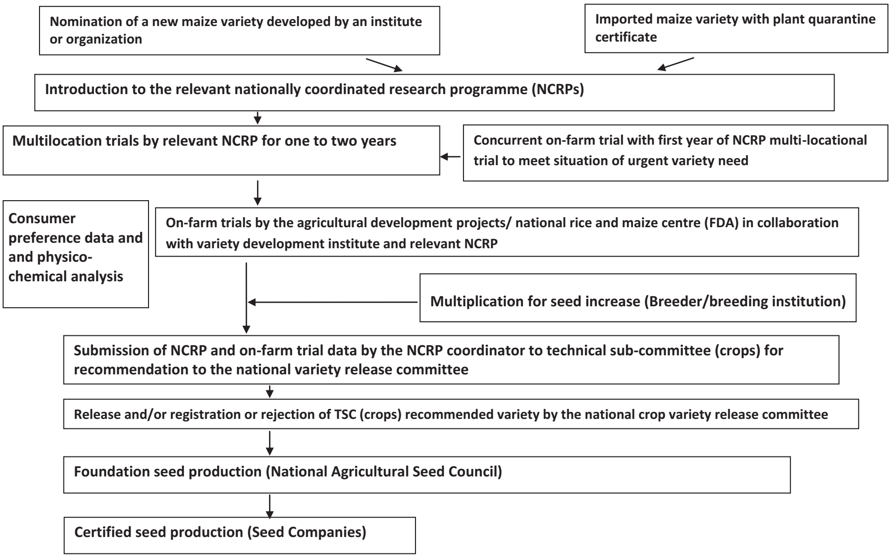


Fig. 19.3 Variety release channel in Nigeria

19.3.4 Nigeria

The Institute for Agricultural Research (IAR) of the Ahmadu Bello University, Samaru, and the Institute of Agricultural Research and Training (IAR&T), Moor Plantation, have the mandate for maize research in Nigeria. In addition to the two institutions, Obafemi Awolowo University, University of Maiduguri, University of Ilorin, and seed companies such as the Premier Seed Company are also involved in maize research and development. The nationally coordinated multilocation trials are conducted throughout the country annually and are a major vehicle for testing maize varieties and identifying promising entries for release in Nigeria (Fig.19.3). In addition to the nationally coordinated trials, varieties earmarked for release are tested on-farm for at least 2 years before release. Apart from the yield and agronomic data required for varietal release, consumer preference data and physicochemical analysis data are also required for the release of varieties. A maize breeder in a public research institute or a private seed company has to go through a number of steps to get a new variety released and registered by the National Crop Varieties and Livestock Breeds Registration and Release Committee (NCVLBRRC). The maize breeder, with the approval of the research institute, submits the variety to the relevant Nationally Coordinated Research Project (NCRP) for researcher-managed nationwide multilocation on-station trials in the appropriate agroecologies. After the first year of the NCRP on-station multilocation trials, if the variety significantly outyields the commercial variety used as check, the variety is submitted to the appropriate national crop center for multilocation on-farm trials which may run concurrently with the second year of NCRP on-station trials to confirm the results of the first year trials. In case there is an urgent need for the release of a variety, the first year NCRP multilocation trials may run concurrently with the on-farm testing of the variety slated for release. If the performance of the variety in the 2 years of NCRP on-station and 1 year on-farm multilocation trials is outstanding for the relevant traits, including yield and farmers' preference, the institution of the breeder in consultation with the national coordinator of the NCRP of the crop may apply to the registrar of NCVLBRRC for consideration of the release and registration of the new variety. The breeder then completes the relevant general and specific descriptor format of the variety and submits it with comprehensive data from NCRP on-station and crop center and/or on-farm trials to the registrar not later than 2 weeks before the meeting of the technical subcommittee (TSC) crops and the NCVLBRRC meeting scheduled to consider the application for the release and registration of the variety. The breeder of the variety under consideration for release has to bring prescribed quantity of seed of the variety for the national gene bank and also make provision for enough breeder seed for the National Agricultural Seed Council for foundation seed production.

The NCVLBRRC comprises the chairman who is appointed by the President of Nigeria; the director of Agricultural Sciences, Federal Ministry of Science and Technology; the director of Federal Department of Agriculture (FDA); the head of the Genetic Resources Unit, Federal Ministry of Science and Technology; the director of the National Agricultural Seed Council; the chairman of the Committee of Deans of the Faculties of Agriculture in Nigerian Universities; the President of Genetics Society of Nigeria; a representative of the Federal Agricultural Coordinating Unit (FACU); two experienced breeders appointed on their personal merit by the Minister; and two general managers representing two River Basin Development Authorities from different ecological areas in rotation appointed by the Minister. The committee was expected to meet annually, but because of fund limitations, the meetings were not regular for several years. For example, six varieties were released between 2002 and 2006 (Table 19.1). However, during the past couple of years, the NVRC has been meeting regularly, twice a year, and several maize varieties and hybrids have been released by the NVRC. Following the release of a variety, it is entered in the National Variety Release Catalogue.

19.4 Results of Survey in West Africa

The results of the survey showed that for any new maize variety to be released and registered for distribution, it must be distinct, uniform, and stable (DUS) and have value for cultivation and use (VCU) (Setimela et al. 2009). The national seed authorities (NSA) determine if the new maize varieties are DUS and meet the criteria for VCU in the respective countries. Lack of an effective variety release system is one of the major constraints to the transfer of available elite maize varieties to smallholder farmers in DTMA Project countries in SSA. The long delay between variety development, registration, and release constitutes a major constraint to increased maize production and productivity. Most of the VRCs lack good coordination and meet only once a year to consider varieties for release. The seed laws are very rigid as data from other countries with similar agroecology cannot be used, resulting in a delay, because retesting has to be done each time a new variety is to be considered for release.

National variety lists are not updated regularly, making it difficult for seed companies to commercialize improved varieties. Only a few countries have Plant Breeder's Rights (PBRs) thus discouraging many private seed companies from introducing their best products, since their products are not protected. White endosperm hybrids dominated the few maize varieties released, followed by white OPVs. The private sector has dominated the varietal release rates in East and Southern Africa, while in West Africa the variety release has been mainly from the public sector, reflecting the few seed companies in WA compared to the other two regions. Besides Southern Africa having the highest varietal release rates, it also has the highest adoption rate of improved maize varieties.

19.5 Recommendations Based on Survey Results

Based on the findings of the study, the following recommendations were made to improve the varietal release rates in the DTMA Project countries in SSA (Setimela et al. 2009):

Promotion of regional standards for PBRs Regional standards for PBR should be promoted to enable plant breeding programs to generate reasonable incomes from the products of their research through royalties. This will allow the private and the public sectors to benefit from the product of research and lead to more investments in variety improvement.

Regional harmonization of seed laws The East, Southern, and West Africa will benefit from free flow of germplasm across national boundaries if the regional variety release process is harmonized. Maize varieties released in one country should be considered automatically released in other countries with similar agroecologies. Mega-environments cut across country boundaries and adaptation zones and are not country specific, so varieties should be released based on mega-environments to create a larger seed market and accelerate the process of variety release.

Promoting the use of data from other countries Only few countries accept data from other countries for variety release. Testing should not be mandatory for varieties already released in other countries if the recommendation domain is the same. Data from other countries should be acceptable for variety release. If this is done, it will eliminate the need for retesting of varieties from country to country thereby saving resources and accelerating the pace of variety release.

Simplifying variety testing and release process A number of agronomic and DUS data are required for variety release. Registration should be simplified so that only important VCU and DUS information would be required to distinguish a new variety from the others. A season's data should suffice for the DUS information since DUS is not affected much by the environment. DUS test should be conducted along with METs to shorten time to variety release.

Promotion of the use of breeders' own data Breeders' own data should be allowed for use to support variety release thereby eliminating the need for NPTs. The number of locations required for release should be few and emphasis should be placed on locations where the variety will be recommended for production.

Production of breeders' seed Breeders should embark on limited breeder seed production and marketing instead of waiting until the variety is fully released as this prolongs the time for a variety to reach farmers.

Variety release guidelines In some cases, the NVRC rejects a variety and asks the breeder to improve a specific trait thus delaying the release of a new variety. The decision to release a variety should be based on merit and uniqueness. The new variety should contribute new trait(s) that the existing one lacks. Therefore, it is important that each country develops variety release guidelines to ensure fairness and transparency in the variety release process.

Request of the meetings of NVRC The variety release committee meetings have been irregular in some countries. It is therefore important that governments provide enough resources to enable the NVRC meet regularly.

19.6 ECOWAS Protocol on Seed Production

A protocol on seed was signed by the Heads of States of ECOWAS member countries in 2009, and the West African Catalogue of Plant Species and Varieties (COAFEV) is presently available in the sub-region. The seed catalogue which contains the list of varieties whose seeds can be produced and commercialized within the territories of the 17 member countries of ECOWAS is an aggregate of the varieties registered in the national catalogues of the Member States. The catalogue offers a unique opportunity for movement of good-quality seed of improved maize varieties and hybrids across borders of the ECOWAS countries for production and marketing.

As a result of this new development in the seed sectors of the ECOWAS member countries and the implications of the global warming, desertification, and recurrent drought, there is a need for reexamination of the current mega-environments and core testing locations in each of the mega-environment in WA to facilitate the selection of high-yielding and stable extra-early cultivars for seed production and marketing across countries of WA.

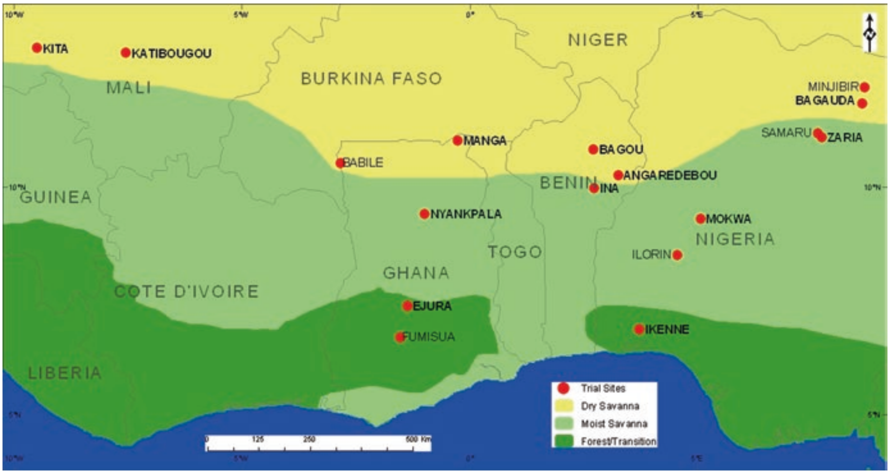


Fig. 19.4 Locations in the major agroecological zones in West Africa used for testing extra-early maize cultivars in the RUVT-extra-early from 2006 to 2009

In support of the ECOWAS Protocol on seed production, a number of studies have been conducted to identify stable and high-yielding maize cultivars with specific or broad adaptation in WA, to validate the existing mega-environments, and to identify core testing sites within each mega-environment for cultivar evaluation, release, and marketing across countries in WA. Badu-Apraku et al. (2011) compared the effectiveness of the GGE biplot and AMMI analysis in identifying maize mega-environments and stable and superior maize cultivars with good adaptation to WA. Twelve extra-early maturing maize cultivars were evaluated at 17 locations in four countries of WA between 2006 and 2009 (Fig. 19.4). The GGE biplot analysis revealed three mega-environments and seven groups for the cultivars, while AMMI biplot clustered cultivars and environments each into four groups but could not identify mega-environments. The two procedures provided similar results in terms of stability and performance of the cultivars. Zaria was identified as an ideal test site for the cultivars by the GGE biplot. The cultivars 2004 TZEE-W Pop STR C_4 and TZEE-W Pop STR C_4 were identified as superior across environments by both methods. Cultivar 2004 TZEE-W Pop STR C_4 was the most stable. GGE biplot was more versatile and flexible and provided better understanding of GEI than AMMI biplot. It identified Zaria, Ilorin, Ikenne, Ejura, Katibougou, Babile, Ina, and Angaredebou as the core testing sites of the three mega-environments identified for testing the RUVT extra early (Fig. 19.5). It was concluded that the research facilities at these testing sites should be upgraded and funds provided for conducting regional trials to ensure collection of reliable data to support the release of improved varieties and hybrids across borders of the ECOWAS countries for production and marketing based on the seed protocol.

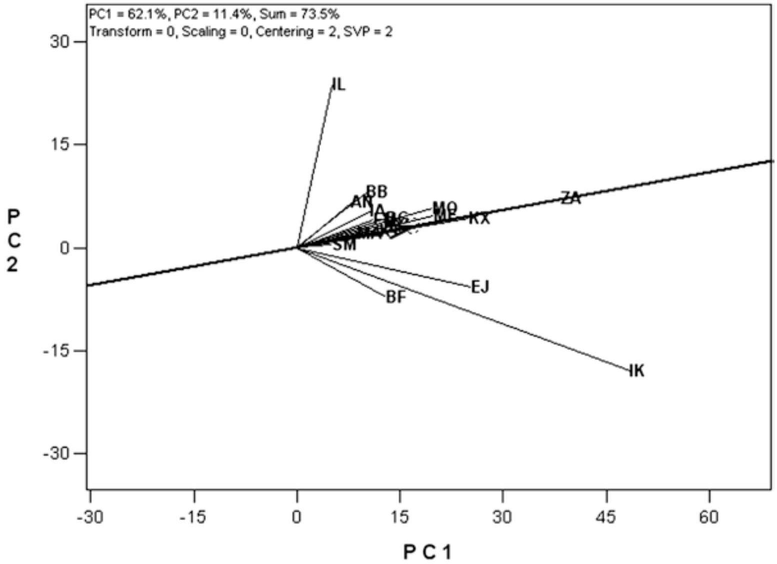


Fig. 19.5 The "discriminating power and representativeness" view of GGE biplot based on a genotype x environment yield data of 12 extra-early maturing maize cultivars evaluated in 17 locations across WA between 2006 and 2009. The data were not transformed ("Transform = 0"), not standardized ("Scaling = 0"), and were environment-centered ("Centering = 2"). The biplot was based on genotype-focused singular value partitioning ("SVP = 2") and is therefore appropriate for visualizing the relationships among environments. Principal component (PC) 1 and PC 2 explained 0.74 of yield variation (see Table 19.1 for the legend)

19.7 Strategies Adopted by DTMA Project to Promote Variety Release and Registration in West Africa

As pointed out earlier in this chapter, constraints to variety release and registration in West Africa include lack of functional variety release system in some countries; long delay between variety development, registration, and release; rigid regulations which overlap in variety release protocols; lack of seed laws in some countries; and lack of funds for meetings of varietal release committees. The weakness of variety testing and release systems is due to several reasons. For a variety to be released, it must be DUS and VCU; a large number of DUS and VCU traits are measured; the quality of DUS and VCU data is poor; there are only a few qualified personnel to conduct the DUS and VCU tests; there is lack of funding to carry out DUS and VCU tests; national variety lists are not updated regularly; there are no functional varietal release committees in some countries; the private sector dominates the varietal releases in WA. There is therefore a need to speed up variety testing and release in order to ensure that DUS varieties enter the seed market, have a minimum value for cultivation and use (VCU), stimulate the use of better varieties, and enhance development of strong maize breeding programs. The end result of all these measures should be adequate protection for the breeder and the farmer. Concerned with the long delay between variety testing and release in West Africa, the DTMA Project has adopted a number of strategies to promote rapid release and registration of drought-tolerant varieties and hybrids in WA. These are discussed in the sections that follow.

19.7.1 Provision of Parental Lines, Hybrids, and Open-Pollinated Varieties of Maize to Private Seed Companies and Community-Based Seed Producers for Production, Distribution, and Marketing

The DTMA Project has since 2007 provided germplasm to seed companies and NARES as follows:

(i) *Provision of breeder seed to partners*

Large quantities of seed of parental inbred lines and seed of drought-tolerant varieties and hybrids have been provided by the DTMA breeders to seed companies and CBOs in WA on request for seed production, testing, and promotion.

(ii) *DTMA Project support to regional and international trials in WA*

The regional and international trials serve as the vehicle for exchange of germplasm among the partner countries of the DTMA Project. The regional and international testing activities are, firstly, to accelerate the process of verification and validation of the performance of technologies under different environmental and socioeconomic conditions; secondly, to publicize the new germplasm and related technologies available in the NARS and international centers; and, thirdly, to identify, test on-farm, and release eventually the varieties evaluated in the NARS trials. Tables 19.2 and 19.3 show the sets of regional/international trials and on-farm trials that have been made available to DTMA Project partners including seed companies on request from 2007 to 2014.

(iii) Financial support has been provided to selected NARS partners for breeder seed and parental line production.

(iv) DTMA Project scientists pay several regular visits to seed companies to encourage their involvement in conducting collaborative trials and in identifying and commercializing maize varieties and hybrids to farmers.

(v) Staff of seed companies are invited each year to visit DTMA maize breeding nurseries and trials in IITA, Ibadan, and to select promising entries for their companies.

(vi) Staff of seed companies are invited to participate in the planning meetings of the DTMA Project to share information on the performance of varieties evaluated.

Table 19.2 Regional trials conducted by DTMA/STMA Project partners, 2007–2016

Country	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Total
Nigeria	36	92	74	195	109	73	142	30	*185*	*79*	*1015*
Ghana	–	21	39	54	74	51	79	62	*62*	*54*	*496*
Benin	24	21	20	48	35	28	37	146	*17*	*20*	*396*
Mali	–	9	21	34	38	35	77	50	*31*	*27*	*322*
Total	*60*	*143*	*154*	*331*	*256*	*187*	*335*	*288*	*295*	*180*	*2229*

Source: DTMA Milestone Report for 2016

Table 19.3 On-farm trials and demonstrations conducted by DTMA Project partners, 2007–2012

Year							
Country	2007	2008	2009	2010	2011	2012	Total
Nigeria	48	166	166	166	170	*122*	*811*
Ghana	–	32	62	70	42	*54*	*230*
Benin	26	26	56	42	39	*39*	*225*
Mali	36	36	36	36	32	*40*	*196*
Total	*110*	*344*	*320*	*314*	*283*	*255*	*1462*

Source: DTMA Milestone Report for 2014

(vii) Information is provided at the end of each year on sources of seed and available improved varieties and hybrids to NGOs.

(viii) Results of multilocation and on-farm trials are summarized each year for the National Agricultural and Extension Services (NARES) and seed companies to promote release of varieties.

(ix) Catalogue of available DT varieties in partner countries are compiled annually and made available to NARS, seed companies, and other seed producers, extensionists and NGOs through emails, CDs, and DTMA website to promote variety release.

(x) Strategies for promoting widespread adoption of DT maize in the respective countries have been prepared and approved.

19.7.2 Backstopping Variety Release of NARS Partners of the DTMA Project

- NARS, seed services, and SMEs and seed companies participate in annual planning meeting of DTMA to share information on the performance of varieties and hybrids.
- Consultation visits paid by DTMA scientists to NARS and seed companies to encourage involvement in conducting collaborative trials as well as in identifying and commercializing maize varieties and hybrids to farmers.
- Seed companies and NARS invited each year to visit breeding nurseries and trials to select promising entries.

19.7.3 Regional Data Exchange

- Data on new maize varieties are exchanged at the regional level, and a variety of information have been linked to GIS environmental characterization data.
- DTMA database has been updated annually with variety and environmental data integrated.
- Database has been made accessible on CD and through the web.
- Characteristics of new maize varieties and their drought tolerance are published annually (web, print).

19.7.4 Facilitation of Foundation Seed Production in Target Countries by Private Seed Companies to Ensure Efficient Delivery of Quality Seed

In Nigeria and Ghana, seed output from the formal sector is not readily available to most small-scale farmers. Moreover, most private seed companies are interested in marketing maize hybrids. To ensure that seeds are available at all times, the DTMA Project is promoting production of foundation seed by NARS, which is then used by community-based seed producers.

The aim of the seed multiplication schemes is to promote on-farm production of quality seeds of maize OPVs through the involvement of individual farmers as well as farmers' groups in community-based seed production schemes. The objectives of the community seed production schemes are to strengthen farmers' capacity in the techniques of good-quality seed production and to encourage the seed certification organizations to work with selected farmers and NGOs in the development of on-farm community-level seed production schemes. In this way, improved seeds of maize are made available readily to the communities. This is expected to enhance access to improved varieties and promote technology adoption on a large scale. Through this scheme, large quantities of foundation seed of maize are being produced at research stations and by selected seed companies under the supervision of DTMA Project staff. Production of quality seed of improved varieties is contracted out to selected farmers or farmer groups. These farmers are given training in seed production and management, provided with all the required inputs on credit basis and are closely monitored by researchers. Special attention is paid to the needs of farmers or farmers' groups constrained by lack of storage facilities for large-scale seed production. These farmers are linked to the seed companies and other institutions for proper storage of their products, better access to seed market, and to ensure sustainability. The resulting seed is bought in the first year of the project and eventually distributed to other farmers or farmers' groups by the second year of the project on credit basis. This approach ensures that farmers have access to improved seeds every year.

19.7.5 Promotion of Community-Based Seed Production by Strengthening Community-Based Organizations (CBOs)

Working with existing farmer groups, CBOs, and encouraging the formation of new ones, building their capacity through technical, organizational, and leadership training will strengthen common interest groups, which will evolve into farmer-owned and farmer-managed organizations that are capable of providing services to members. The support of the DTMA Project to the community-based seed production schemes is through:

(i) Training of farmers and seed producers in techniques of quality seed production
(ii) Strengthening of the capacity and capability of seed producers to produce good-quality seed
(iii) Encouragement of NARS scientists to work with selected farmers and NGOs in the development of on-farm level seed production
(iv) Assistance to NARS scientists to produce breeder seed of released maize varieties in adequate quantities at the research stations

NARS scientists are being provided technical advice, breeder and/or foundation seed, and other inputs to collaborating farmers. At harvest, farmers are required to pay back either in cash or in kind. Each community seed production scheme involves breeder, foundation, commercial or certified seed production, marketing, and distribution.

19.7.6 Supporting the Development of New Seed Enterprises to Either Serve as Satellites to Established Ones or Transform into Smaller Seed Companies for Sustainability

Through the community-based seed production schemes that were supported by WECAMAN, some successful community-based seed production schemes in Benin Republic have evolved into cooperatives which buy seed produced by schemes, process, store, and sell to other farmers. Effort is being made to organize other successful community-based seed producers in the DTMA partner countries into farmer cooperatives. Similarly, a community-based production scheme under the PROSAB Project has evolved into a registered seed company. Efforts are being made to catalyze other successful community-based seed production schemes in partner countries into microenterprises.

19.7.7 Training of Leading Staff from Small and Emerging Maize Seed Companies in Establishing Viable Maize Seed Production, Dissemination, and Business Activities

Small and emerging seed entrepreneurs are being trained in maize-specific know-how, using a modular applied curriculum relevant to the SSA maize seed business environment. It is anticipated that in the short term, small and emerging seed companies will be more effective in establishing viable and growing maize seed businesses in particular as they target new markets in target areas. In the long term, increasing numbers of farmers will have sustainable access to seed of improved maize varieties and hybrids.

19.7.8 Backstopping of Small and Medium Seed Enterprises (SMEs)

The target countries of this project can provide different kind of scenarios for seed system development under the Project. Mali and Ghana have emerging private seed sectors, which need to be strengthened and supported. Ghana has three emerging and several mini private seed companies, with the government providing customized services (processing and storage facilities) for a fee. These companies package seeds of improved varieties and hybrids in different quantities and distribute them to vendors in various parts of the country. The DTMA is providing an opportunity to strengthen the emerging seed companies to evolve into independent, large, and viable seed companies. SMEs are being backstopped and mentored as they build up a seed producer base in a smallholder environment and target new markets in drought-prone areas. Both private and community-based seed entrepreneurs are receiving competent advice on maize seed production and dissemination.

19.7.9 Private Sector Engagement

There is a need to engage the private seed companies to improve delivery of improved seeds to smallholder farmers. To achieve this, the DTMA/STMA Project is working closely with seed companies in partner countries such as Premier Seeds, Maslaha Seed Company, and Seed Project Co. in Nigeria, Faso Kaba in Mali, Savannah Seeds and M&B Seeds in Ghana to improve farmers' access to maize seeds. Strategic incentives are being used to engage seed companies/producers in self-sustainable multiplication, NARS, and NGOs in promotion and dissemination

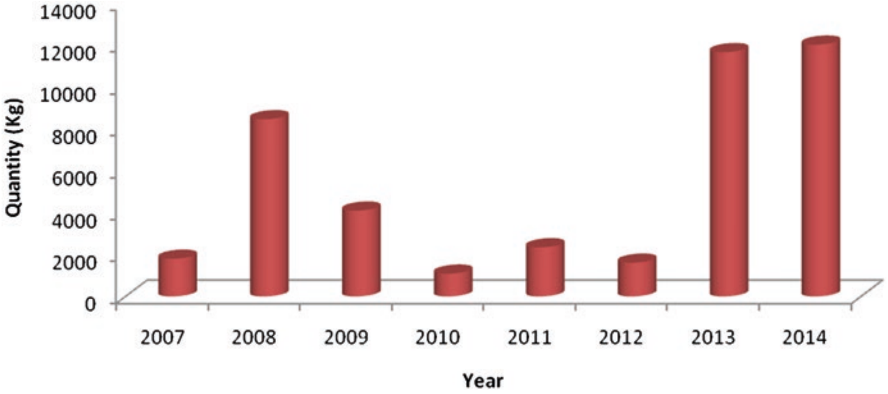


Fig. 19.6 Quantity of seeds of drought-tolerant varieties and hybrids produced and disseminated to DTMA partners in West Africa, 2007–2014 (Source: DTMA Milestone Report for 2014)

of maize seed to reach farmers through two main channels: (i) from seed companies to retail outlets to farmers and (ii) from seed companies to NGOs and government-owned (GO)-assisted seed production and dissemination programs to farmers. Currently it is estimated that 25% of all maize area is planted to seed channeled to farmers. Additional impact will be generated by farmer-to-farmer dissemination of new varieties. Seed companies or producers are being encouraged to invest in elite public maize varieties as long as they have confidence in their adoption potential and agronomic performance in a large target environment/market. Selected private seed companies have been given rights to commercialize distinct varieties with good seed production characteristics and receive sufficient amounts of breeder seed and technical backstopping for rapid scale-up. Hence, agreements for the rights to produce different maize varieties and hybrids will be made with private seed companies/producers either directly or through the NARS. Sufficient breeder seed of new maize varieties (or their parents) is also being produced and provided to seed companies/producers, along with technical backstopping to ensure rapid certified seed production of new drought-tolerant cultivars of maize (Fig. 19.6). The multiplication and distribution of seed will continue to several farmers in the various target areas throughout the life of the project. Seed producer groups have been linked to appropriate markets for the sale of surplus seed in close collaboration with the AGRA/PASS initiative (Fig. 19.6).

19.8 Conclusions

Recurrent drought, desertification, and global warming have severely reduced the agroecological zones in WCA such as the rainforest agroecology, while the forest–savanna transition zone appears to have blended into the Guinea savanna. It is therefore important that the appropriateness of test locations in the various mega-environments in the sub-region is continuously assessed for efficient and successful development of maize cultivars with high-yield potential adapted to the various agroecologies for increased adoption by farmers. Furthermore, the protocol on seed has been published and is presently available in the sub-region. The catalogue offers a unique opportunity for movement of good-quality seed of improved maize varieties and hybrids across borders of the ECOWAS countries for production and marketing. There is a need to engage the private seed companies to improve delivery of improved seeds to smallholder farmers. To achieve this, the DTMA Project is working closely with seed companies in partner countries. Strategic incentives are being used to engage seed companies/producers in self-sustainable multiplication, NARS, and NGOs in promotion and dissemination of maize seed to reach farmers. Mega-environments cut across country boundaries and adaptation zones and are not country specific, so varieties should be released based on mega-environments to create a larger seed market and accelerate the process of variety release.

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Chapter 20
Seed Technology for Sustainable Maize Production in Sub-Saharan Africa

20.1 Introduction

In crop production, *seed* refers to the plant part resulting from the mating of the male and female gametes of a sexually reproducing plant species. Seed is the propagule used to reproduce the plant from generation to generation. In maize, seed is carried by the ear, and it results from the pollination of silks by the pollen grains from the tassel of the same plant or another plant in the plant population. There are two types of agricultural seeds: orthodox and recalcitrant. Orthodox seeds are seeds which can be dried and stored under certain environmental conditions for a long time without losing viability. There is variation in the ability of orthodox seeds to withstand drying and storage, with some seeds being more sensitive than others. Thus, some seeds are considered intermediate in their storage capability, while others are fully orthodox. Maize seed belongs to the fully orthodox category. On the other hand, recalcitrant seeds (also known as unorthodox seeds) are seeds that do not survive drying and freezing during ex situ conservation. These seeds cannot resist the effects of drying or temperatures less than 10 °C; thus, they cannot be stored for long periods like orthodox seeds because they can lose their viability. Desiccation has an adverse effect on the intercellular structure of recalcitrant seeds. Cocoa (*Theobroma cacao*), rubber (*Hevea brasiliensis*), and mango (*Mangifera indica*) are examples of crops with recalcitrant seeds.

In addition to genetic improvement of crops for the ultimate product of human desire in the crop such as grain yield and nutrient quality in maize, seed improvement is also an important area of crop improvement. Seed improvement involves incorporation into the seed all qualities that would ascertain durability in storage, high seed and seedling vigor, and near-perfect-to-perfect stand when planted in the field. Improved seed is vital for significant increase in agricultural production and for successful achievement of national food self-sufficiency programs. Therefore, in addition to high grain yield, seed production goals in WCA include high seed yield,

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maintenance of genetic and physical uniformity and purity, freedom from extraneous matter and organisms, easy storability, longevity in storage, consumer acceptability, and high field emergence.

In this chapter, we summarize efforts made to improve maize seeds for the WCA farmers during the last 30–40 years. Our efforts are concentrated on classes of maize seed, its demand and supply, distribution of breeder seed by IITA, maize seed research, establishment of seed companies, public–private partnership in seed business, and the seed business in WCA. Greater details of these and other topics have been well covered in an earlier publication (Badu-Apraku et al. 2013).

20.2 Classes of Maize Seed

Basically, there are four classes of maize seed: breeder, foundation or basic, registered, and certified seeds.

Breeder seed Breeder seed is produced under the direct control of the plant breeder who developed the variety and/or others in the institution. Breeder seed is usually produced under strict control and maintenance; therefore, it is produced in small plots where a breeder can monitor the plants to ensure that there is no contamination and that the plants are "true to type." Breeder seed is usually of the highest genetic purity and the smallest quantity in the seed production chain. Breeder seeds may be produced in two stages to make available an adequate quantity of seeds required for the production of foundation seeds. Maintenance of genetic purity in OPVs is difficult because of contamination, but its danger may be achieved successfully by adequate isolation, rogueing of off-types, avoidance of volunteers, and using approved source of seed for planting. Seeds of OPVs could be used for two to three generations without too much loss of vigor. OPVs are maintained by open pollination under proper isolation—about 200—400 m around the field.

After an OPV has been developed, tested, recommended, and released for farmers' use, a system has to be put in place to provide a regular supply of good-quality seed. Plant breeders in WCA maintain the genetic purity and produced breeder seed of OPVs using modified mass selection (grid system), half-sib, or modified half-sib methods. In the mass selection method, the breeder grows seed of the variety in isolation, with four to six border rows, and gives special attention to crop management practices. Random intermating is expected to occur naturally, but the breeder rogues out off-types before flowering, divides field into grids of 4 × 10 plants, and harvests ears from agronomically desirable plants within each grid. Equal number of seed from selected ears within grid is bulked to form or maintain breeder seed. In the half-sib method, the breeder grows $\geq$1000 plants from the variety in isolation, maintains the field agronomically, and rogues out off-types before and after flowering. Here also random intermating occurs naturally. Seed is harvested from individual plants with desirable agronomic characteristics, and seed from selected ears with good ear aspect is bulked to form or maintain the breeder seed. The modified half-sib method involves greater work than each of the other two methods. A sample of ears is taken from the variety chosen for seed multiplication and is grown ear to row in an isolation block as the female rows. Equal seed numbers are taken from each ear and bulked. The bulked seeds serve as the male rows. The male and female rows are planted in a ratio of 2:4 (the most commonly used), 1:2, 1:3, or 1:4. The female rows are detasseled before pollen shed, and selection is practiced among and within progenies before and after flowering. At harvest, the ears are carefully examined, and off-types are discarded. Selected ears from female rows are bulked to form breeder seed.

Foundation or basic seed Foundation or basic seed is the progeny or the first increase of the breeder seed. It is produced directly by growing breeder seed in isolation and harvesting strictly under controlled conditions to ensure that varietal identity and genetic purity are maintained as close as possible to those of the breeder seed, that is, the variety remains true to type. In WCA, foundation seed is usually produced by a seed production expert or under the control of an agricultural experimental station or seed production agency. The maize breeder is usually involved in foundation seed production. About 5–7 kg of breeder seed is planted in 400–500 m^2 field in isolation. Plants not showing characteristics typical of the variety are rogued out. At harvest, the ears are carefully examined and off-types are discarded. The selected ears are bulked, dried, and shelled. Foundation seed production is intended for the production of certified seed.

Registered seed Registered seed is the progeny of the foundation seeds or sometimes the breeder seeds. In its production, the requirements and standards of the seed certifying agency must be met. Ideally, registered seed is an increase of foundation or basic seed. In programs where adequate quantity of foundation seed has been produced from breeder seed, the production of registered seed is usually omitted in the seed production chain.

Certified seed Certified seed is the seed-chain end product made available to farmers for planting. It is usually the progeny of the registered or foundation seed. In some unusual circumstances, certified seed may be produced from breeder seed, provided the desired quantity of the breeder seed is available for planting. Certified seed is produced in commercial quantities by seed companies. Unlike breeder and foundation seeds, certified seed may be produced for seed companies by contract seed growers who are farmers trained to handle seed production. The production carried out by contract seed growers must be certified by the regulatory agency, and this ensures the maintenance of the identity of the variety as well as its genetic purity. In WCA, the national seed certification unit of each country is responsible for the quality control, including proper isolation in time and/or space, rogueing of off type plants, and discarding disease-infected and insect-infested ears.

For a long time, seed production was unorganized in WCA countries. During that period, the seed production chain, along with the different classes of seed, was not in place, and the researchers obviously gave out breeder seed to farmers on demand and without definite records. About the mid-1970s, governments of West African countries started paying attention to seed production. Seed production, certification, and marketing were completely under government control during that period. With time, seed companies have come on board, and this has gradually led to the rationalization of the seed production system in some of the countries. Presently, breeder seed production rests squarely with the breeder and the institution where the variety was developed, and foundation seed production is done by the national seed unit, such as the Agricultural Seed Council of Nigeria and seed companies in Ghana and in Mali. Certified OPV seed is produced by seed companies and some government parastatals such as the Agricultural Development Project (ADP) in Nigeria and seed companies in Benin, Ghana, and Mali. Apart from the publicly bred inbred lines, the hybrid seed production chain rests absolutely with seed companies. Apart from the publicly bred inbred lines, the hybrid seed production chain rests absolutely with seed companies.

20.3 Maize Seed Demand and Supply

Maize grain production has continued to increase in WCA since 1961 when record keeping started, till now. However, accurate data on the demand and supply of seed is hard to come by because a large proportion of farmers obtain seed for planting from the informal sector, that is, farmer's self-saved seed, farmer-to-farmer exchanges, and purchase from the open market where farmers obtain grain as seed for planting. Several approaches have been used to estimate the land area used for maize, the production in million t and the productivity in t ha^{-1}. Principal among the methods is the estimates produced annually by the Food and Agriculture Organization (FAO) of the United Nations for each country in the sub-region. According to the FAO, the area planted to maize (in million ha) was 3.2 in 1961, about 8 in 1987, 8.9 in 2005, and 12 in 2012 (FAOSTAT 2013). This phenomenal expansion of the land area devoted to maize resulted in increased production from 2.4 million t in 1961 to about 22 million t in 2012, valued at about US $11.345 billion. The land area under maize cultivation would need 240, 000 t of certified seed for planting, assuming a planting rate of 20 kg of seed ha^{-1}. A survey conducted by the Drought-Tolerant Maize for Africa (DTMA) Project of IITA on maize production constraints showed that in the 13 DTMA Project countries in East, Southern, and West Africa, maize is grown on more than 17 million ha, with Nigeria accounting for more than 3.6 million ha of the total land area cropped to maize in the sub-region. Mali accounted for the smallest area, about 0.3 million ha. By region, East Africa accounted for the largest area, while Southern and West Africa had equal areas under maize cultivation. The investigations also showed that the estimated demand for maize seeds in the 13 countries was about 425,000 t. Improved OPVs accounted for about 24,000 t; hybrid maize seeds about 83,000 t, and the rest of the seeds were sourced from the informal seed sector through seed exchanges and the recycling of OPVs and hybrids (Abdoulaye et al. 2009). In other words, more than 75% of the maize crop in the 13 countries is planted to seeds from the informal sector, mostly farmer-to-farmer exchanges and grain purchased from the open market. Based on these estimates, the WA countries included in the study needed well over 100,000 t of maize seed annually.

Over the years, IITA has been actively involved in developing early- and extra-early maturing varieties which are both drought escaping and drought tolerant. The varieties mature in time to fill the hunger gap (as green maize early in the growing season) and complete their growth cycle before terminal drought starts in the drought-prone savannas and in the late planting season of the forest agroclimatic zone thereby letting the crop escape drought and tolerate sporadic drought during the growing season. A striking advantage of the early and extra-early varieties is that they give reasonable yields where drought-susceptible intermediate- or late-cycle varieties would fail as a result of drought.

Most of the modern-day developed varieties in SSA have been bred for resistance to the prevalent biotic stresses, notably maize streak virus, *Striga*, rust, downy mildew, stem borers, and gray leaf spot, which are among the major constraints to production. Some varieties have also been developed for high productivity under drought and the low soil nitrogen levels that are cross cutting characteristics of the soils and production systems in the SSA sub-regions. The rising profile of maize and the impact generated by the crop have been aptly described as a revolution (Fakorede et al. 2003), and the crop is considered the vehicle for a green revolution that has already commenced in SSA (Abalu 2003).

Commercial seed producers are faced with the challenge of completely selling their produce every year. In order to mitigate this challenge, seed production planning is a necessity. One primary requirement for seed production planning is accurate information on seed demand which, unfortunately, is not readily available in SSA, especially in WCA where it is not even available in the immediate (local) environment of the seed producer. Therefore, several methods are used to estimate the seed demand by farmers and seed production by the producers, especially seed companies. Seed production is usually undertaken in order to meet the projected seed demand (i.e., seed demand forecasting). The perceived seed demand and the real demand are two completely different concepts. Perceived seed demand is based more or less on the *feelings* and/or *speculations* of the seed producer, and this, more often than not, is a mirage because it is not quantifiable and not based on scientific reality. Market demand, which is the real demand, is the quantified total volume of a class of seed that will be purchased by farmers in a defined location within a specified time period and with minimal marketing efforts because the farmers, without fail, will purchase the seeds for their crop. Successfully forecasting market demand is based on several factors, including the land area covered by the crop, amount of seed per unit land areas, cost of seed to the purchaser, and awareness of the seed quality by the farmers in the area of jurisdiction of the seed seller. Some of the factors are not quantifiable and may be difficult to determine. An example is verbal or written survey of what farmers say they will buy in terms of seed. The farmers may or may not keep their words. In some other cases, forecasting may have to depend on historical data, that is, what people have done—their reaction to adverts of availability of quality seed, container type and size preferred, seed type and size in great demand, desire for seed treatment, and complementary services appreciated by the seed buyers, such as when and how to plant; fertilizer type to use; when and how to apply the fertilizer; control of weeds, pests, and diseases; etc. This is a more dependable approach to successful seed production planning.

Seed supply for marketing must be based on estimated market or real demand. Seeds for marketing are usually produced by the marketing organization on its own land and/or by contract growers. In either case, seeds for marketing require advanced production planning. Seed production planning is usually tied to demand forecast and the marketing plan. In WCA, maize scientists expose seed producers to two methods of seed production planning (Fakorede et al. 1999):

(a) Working backward from the amount of certified seed demanded through foundation seed and breeder seed requirements
(b) Application of regression or trend analysis on historical seed demand and sales data

Working backward The following information will be needed to determine the amount of certified seed to produce for marketing: expected yields and seeding rates of both foundation and breeder seeds, the total land area to be covered by the certified seed to be marketed (total seed demand for the variety or varieties), and the amounts of breeder and foundation seed needed in the certified seed production chain. For example, 200,000 ha of land are to be planted to maize at the planting rate of 20 kg ha^{-1}. That translates to a total of 4000,000 kg or 4000 t of certified seed. There are two possibilities: (i) the seed producer has access to foundation seed, or (ii) the producer has access to only breeder seed. For the first scenario, all the producer needs to know is the seeding rate and yield of the foundation seed per ha. The land area needed to produce the 4000 t of certified seed can then be determined easily. For the second scenario, the seed producer needs to complete and execute the entries in Table 20.1 to produce the required seed.

Calculations are as follows:

(i) For the commercial crop, the seed producer needs to produce 200,000 × 20 kg of certified seed, which is 4000 t for marketing.
(ii) Land needed for planting foundation seed to produce 4000 t of certified seed at 0.8 t ha^{-1} = 4000 ÷ 0.8 = 5000 ha. Foundation seed needed to plant 5000 ha at 15 kg ha^{-1} = 5000 × 15 = 75 t.
(iii) Land needed for planting breeder seed to produce 75 t of foundation seed at 0.5 t ha^{-1}

Table 20.1 Layout of the plan for the production of certified maize seed to cover 200,000 ha of land

Class	Expected yield t ha^{-1}	Area, ha	Seed rate, kg ha^{-1}	Seed required, t
Commercial crop	–	200,000	20	?
Certified seed	1.5	?	15	?
Foundation seed	0.8	?	15	?
Breeder seed	0.5	?	15	–

Table 20.2 Sales of certified seeds of two maize varieties from 2008 to 2017

Year	Year coded	Seed sales in '000 t	
		Variety 1	Variety 2
2008	1	1.4	3.3
2009	2	1.6	3.1
2010	3	1.8	2.9
2011	4	1.7	2.9
2012	5	1.9	2.7
2013	6	2.0	2.7
2014	7	2.1	2.5
2015	8	2.2	2.6
2016	9	2.1	2.4
2017	10	2.3	2.5

= 75 ÷ 0.5 = 150 ha. Breeder seed needed to plant 150 ha at 15 kg ha^{-1} = 150 × 15 = 2.25 t.

The producer needs 2.25 ÷ 0.5 = 4.5 ha of land and 4.5 × 15 = 67.5 kg of breeder seed supply to start the project.

Application of regression analysis to historical demand and sales data In this case, the seed producer has been keeping detailed records of seed demand and sales every year. A hypothetical example is given in Table 20.2. The data in the table may be subjected to linear regression of the sales data on the year of production as shown in Fig. 20.1. From the regression equations, seed demand and sales in 2018 (year 11) may be predicted as

$$\hat{Y}_{\text{Var1}} = (0.0903)(11) + 1.4133 = 2{,}407 \pm 6.25\,\text{t}\,(\text{s.d}) \text{ for variety 1,}$$

and

$$\hat{Y}_{\text{Var2}} = (-0.0897)(11) + 3.2533 = 2{,}267 \pm 5.23\,\text{t}\,(\text{s.d}) \text{ for variety 2.}$$

The coefficient of determination (r2) associated with each model is quite high, an indication that the regression model is about 90% dependable in each case. In addition, the seed producer may use standard deviation (or standard error) to produce a few tons of seed more or less than that estimated by regression. In the case of the hypothetical example considered here, the seed producer may produce about 2,394.5 – 2,419.5 t for variety 1 and 2,256.54 – 2,277.46 t for variety 2, depending on the trends reliably obtained from formal or informal marketing survey by the producing organization. The regression approach may be used every year to predict how much seed to produce for the next year. As the number of historical years increases, the prediction is likely to be more accurate, and the actual demand–sales situation will be close to the predicted. This is a definite advantage of the regression method.

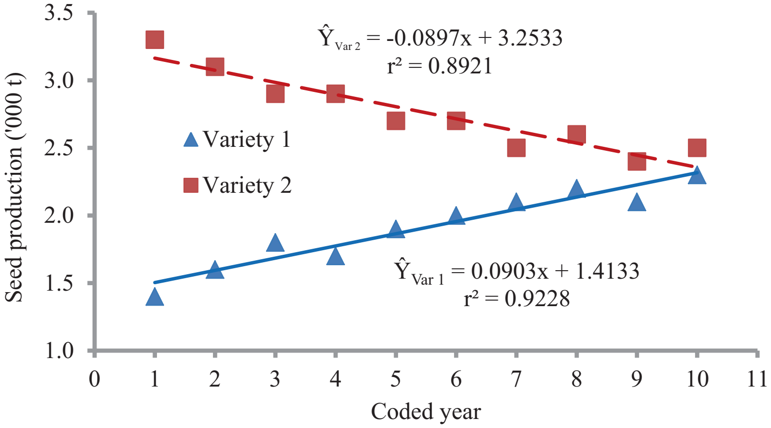

Fig. 20.1 Regression of seed demand and sales induced production for two maize varieties during a 10-year period

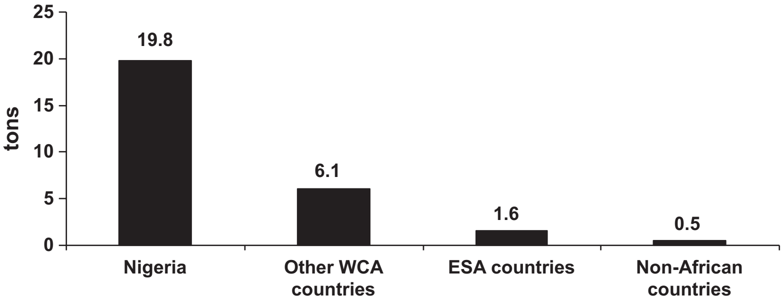

Fig. 20.2 Distribution of breeder's seed of open-pollinated maize varieties produced at IITA, 1988–2000

20.4 Distribution of Breeder Seed by IITA

Following the successful conversion of maize populations to streak resistance (SR) in 1988, IITA has been distributing primarily seeds of SR maize germplasm to African countries and beyond. Similarly, all maize varieties released in WCA countries since then are streak resistant. In 1988, IITA initiated a database on the distribution of breeder's seed (Figs. 20.2 and 20.3, Fakorede et al. 2001a). Over 70% of the breeder's seed of OPVs produced during the 1988–2000 period went into the NARS of Nigeria alone (Fig. 20.2). The supply was about 1050 kg in 1988 with an approximate annual increase of 68 kg thereafter (Fig. 20.3). Much of the breeder's seed supplied from IITA to Nigeria went to the National Seed Service (NSS), the custodian of all crop varieties released in the country. The NSS (now named the National Agricultural Seeds Council, NASC) has the mandate to produce foundation

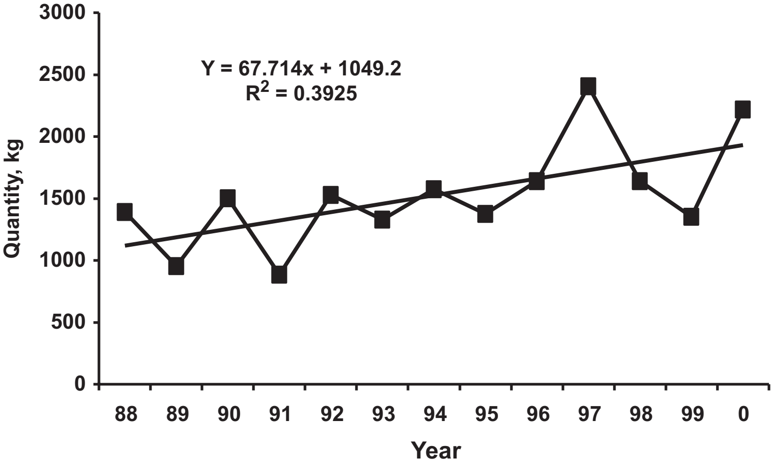

Fig. 20.3 Maize breeder's seed supplied by IITA to Nigeria NARES, 1988–2000

seed and distribute to the Agricultural Development Projects (ADPs) located in every state of the country. The ADPs, in turn, produce certified seed and sell to farmers. If this model of seed production and distribution were properly executed, SR maize varieties would be made available to farmers all over Nigeria.

In an effort to evaluate the extent of adoption of SR varieties, seeds of 416 farmers' varieties were collected during a farm-level survey conducted all over the country in 1992–1994 (Fakorede 2002; Fakorede et al. 1997). The varieties were artificially infested with viruliferous *C. triangula* and scored for resistance on a 1–9 rating scale, as routinely done at IITA. It was hypothesized that farmers having resistant varieties must have obtained the seeds of the SR germplasm originating from IITA. Across the country, about 50% of the farmers' varieties were rated as resistant and intermediate (Fig. 20.4).

Therefore, as at the early 1990s, 50% of Nigerian farmers had not adopted SR maize varieties. However, analysis of the data on state basis showed that, on average, only about 21% of the farmers' varieties from states neighboring IITA were susceptible. The corresponding value for the States further away from IITA was nearly 60% (Fig. 20.4). But that was only about 5 years of the availability of SR maize germplasm in the sub-region.

Distribution records of the early- and extra-early maturing maize varieties at IITA started in 2005. Before then, research and development activities for maize in these maturity groups were anchored at the coordination office of WECAMAN in WARDA (now Africa Rice), Bouaké, Côte d'Ivoire. Maize seed distribution was almost nonexistent at that time primarily because of limited processing facilities and, in any case, it was not part of the network's focus. Because of the Côte d'Ivoire civil war that broke out in 2002, coordination of WECAMAN had to be shifted to IITA-Ibadan, Nigeria, where, fortunately, seed processing facilities were (and still are) available and a database for seed distribution was already in place. Analysis of

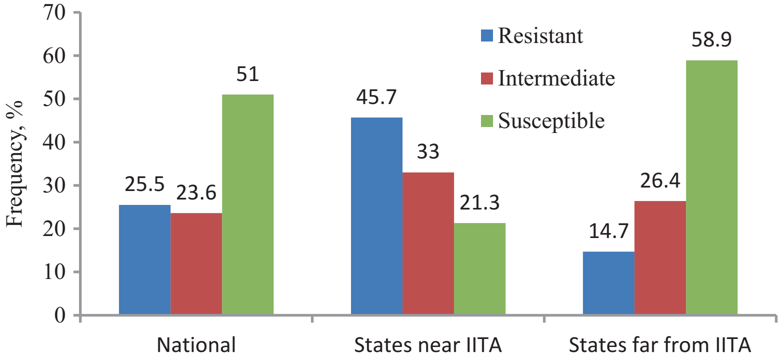

Fig. 20.4 Frequency distribution (%) of the reaction of 416 farmers' maize varieties to artificial inoculation of the streak virus at IITA, 1995. Rating scale of 1–9: resistant = 1–3, intermediate = 4–5, susceptible = 6–9

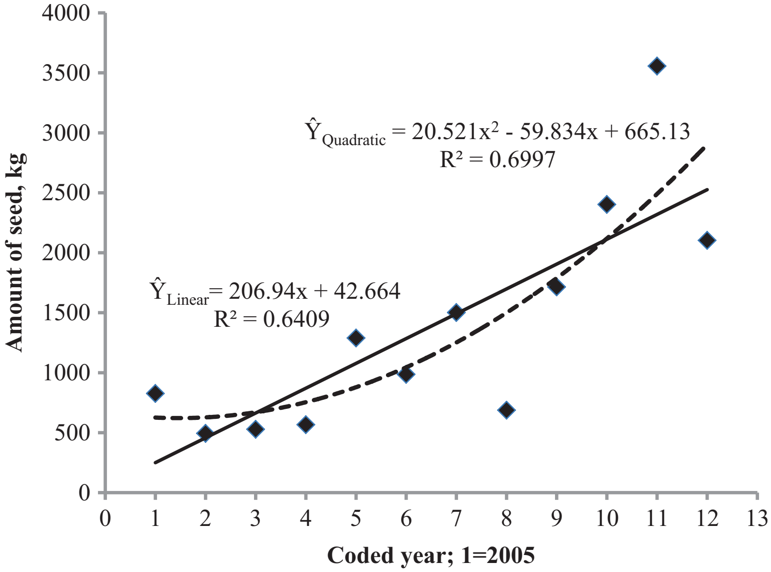

Fig. 20.5 Quantities of seeds of early- and extra-early maturing maize varieties supplied by IITA in response to demands from public and private institutions, 2005–2016

the records showed that at least 200 kg of early and extra-early breeder seed was given out annually from 2005 to 2016 by the IITA Maize Program (b-value in the linear regression model, Fig. 20.5), with much higher amounts in the latter years of that period, as indicated by the positive quadratic b-value in the quadratic regression model in Fig. 20.5.

A similar approach to the seed distribution of SR maize varieties was used for the deployment of downy mildew-resistant (DMR) maize variety seeds. Slightly modified by involving farmers as seed producers, the approach was evaluated in selected downy mildew endemic areas of Ogbomosho in southwestern Nigeria (Ajala et al. 2003). Nine villages were selected for the project during the first season of 1997. Seed and inorganic fertilizers were supplied to three farmers from each village (27 farmers in all), and the farmers were trained to produce high-quality seed on their own. In the following season, each farmer on the project brought in three new farmers from a new village and one from his own village and backstopped them with seeds and technical know-how skill acquired from his earlier training. In 1998, 25 villages and 111 farmers participated in the project. By the third year, 625 farmers in 159 villages had been trained and were producing seed of DMR varieties. In addition, the farmers were trained to produce a healthy maize crop. In the 1998 and 1999 seasons, average yield from the farms of nonparticipating farmers was 1846 kg ha^{-1} compared with 2763 kg ha^{-1}for participating farmers, a 50% yield increase for the participating farmers. Results from the survey conducted at the termination of the project indicated that within 2 years, the farmers observed a drastic reduction in the incidence of downy mildew, acquired skill in seed production technology, and obtained increases in maize yield and annual income.

In addition to seed supply in relatively small quantities to individual researchers, institutions, and seed companies, IITA also supplies large quantities of seed on special demand or request.

20.5 Maize Seed Research

For many reasons, seed research has been much neglected in SSA, and little is known about seed production, processing, conditioning, storage, and distribution in the region. There are many specific research areas that need urgent attention in SSA including the following (Fakorede et al. 2001b):

- Effective seed extension to ensure distribution of new varieties within a short time of release
- Quality control to ensure that true-to-type seeds are sold to the farmers
- Development of methods for maintaining genetic purity of foundation seed and reduced contamination of certified seed
- Effective seed storage to maintain viability for a long time

Seed research facilities and well-trained researchers are not available in nearly all national programs of SSA. Small-scale seed processing unit, standard cold room for seed storage at the right environmental conditions for preservation of seed viability and health, and seed testing laboratories are not available in most crop research institutes and universities. In most cases, seeds are stored under ambient room conditions or in air-conditioned rooms, refrigerators, the freezer compartment of the refrigerator, and deep freezers, all of which have high relative humidity, unless dehumidifiers are installed in them. In a study conducted at the Seed Science Laboratory of Obafemi Awolowo University, Ile-Ife, Nigeria, maize was stored under the five conditions, and germination and root development were monitored bi weekly for 6 months, beginning at the time of storage (Ajayi and Fakorede 2001). For all storage conditions, the value of most traits decreased as the duration of storage increased. For example, root length of resulting seedlings decreased by 0.2 cm day^{-1} relative to significantly higher decreases of 0.28–0.30 cm day^{-1} in the other storage conditions. In addition, Ajayi and Fakorede (2001) found that planting seeds immediately after they were removed from cold storage (deep freezer and refrigerator in this case) reduced germination and increased abnormal seedlings. Equilibrating the seeds with ambient conditions (23–28 °C) up to 14 days before planting maximized germination and minimized the occurrence of abnormal seedlings. The researchers concluded that the effect of the differences between storage and ambient conditions on seeds should be minimized before the seeds are planted to ensure near-perfect emergence in the field. Although Ajayi and Fakorede's study did not include storage in a cold room, which would have served as the standard for purposes of comparison, their results suggest that seed should be removed from cold storage at least a few days before planting in the field.

Apparently in an effort to face the challenge posed by the ineffective seed storage conditions in WCA, the West Africa Seed Development Unit (WASDU), Accra, Ghana, developed a dehumidifier dryer to alleviate the problem associated with long-term storage of maize seed in areas where the ambient temperature and relative humidity could be more than 33 °C and 75%, respectively. These conditions often lead to high rate of seed deterioration in storage with the attendant low germination rate, making the seed unacceptable for marketing. The dehumidifier dryer developed by WASDU was found to be more cost-effective and capable of drying maize seed to 8–9% faster than mechanical dryers (Asiedu et al. 2001). The seed may then be kept in sealed containers, such as polythene bags, for long-term storage under ambient conditions without loss of germination and vigor. In another study, Asiedu et al. (2003) investigated means of reducing storage costs without compromising physiological quality of seed. Using QPM variety, Obatanpa, they dried two batches of seed from the same seed lot to 8.0 and 11.0% representing dehumidified and conventional moisture levels, respectively. The two sets of seed were hermetically sealed in polythene bags and stored under two conditions, the cold room (10 °C/80% r.h.) and the warehouse (21–31 °C/68–86% r.h.) for 18 months. Beginning at the time of storage, germination tests were done on the seeds at 3-month interval till 18 months after storage. Results showed that, for the two storage conditions, high germination %(above 95%) was maintained throughout the 18-month period of storage in seeds dried to 8.0% moisture content and for the seed dried to 11% moisture content and kept under cold storage. For the seeds dried to 11.0% moisture content and stored under the warehouse conditions, however, germination % was below the acceptable level of 85% after 9 months in storage. Economic and financial analyses showed high profitability in opting from cold storage to ambient storage of dehumidified seed. Thus, it was technically feasible and financially cost-effective to dehumidify maize seed to 8% moisture content and store in a warehouse for periods up to 18 months without losing viability and vigor.

Knowledge of cardinal temperatures, consisting of critical minimum, optimum, and critical maximum temperatures, is necessary for successful seedling emergence of corn and is useful in decision-making with respect to optimal sowing. Cardinal temperatures for seed germination, seedling emergence, and early vegetative growth have not been determined conclusively for maize under the tropical environments of SSA. These parameters have been determined to a greater extent for temperate maize, and most maize researchers have applied them when needed. In computing heat units, for example, the 10 °C and 30 °C determined as the critical minimum and maximum temperatures for maize germination in the US Corn Belt were adopted by research workers in SSA (e.g., Abasi et al. 1985; Fakorede and Opeke 1985) to compute heat units. Such estimates may not be accurate because temperatures ≤ 10 °C hardly occur and temperatures much higher than 30 °C occur frequently in the lowland tropics during the cropping season, especially soon after the dry season. In addition, it is generally observed that inadequate moisture affects maize germination rather than high temperatures. Studies have been conducted to solve this problem for tropical maize researchers. Aflakpui (2001) investigated temperature effects on seed germination rates of quality protein maize (QPM) var. *Obatanpa* and normal endosperm maize (NEM) var. *Okomasa* at the University of Reading, UK. To ensure genetic purity, seeds of the two varieties were obtained from the Plant Breeding Division, Ghana Grain Development Program/Crops Research Institute (GGDP/CRI), where they were developed. Because of nonavailability of the necessary infrastructure, the study had to be conducted at the Department of Agriculture, University of Reading, where the temperature gradient plate needed for the study was available. The seeds were subjected to temperatures ranging from 15 to 45 °C, and germination was taken to have occurred at 1–2 mm protrusion of the radicle. Germination rates were then computed with the basic eq. $1/t = [T - T_i]/\theta_i$ where t = number of days to 50% cumulative germination, T = temperature (°C) at germination, T_i =temperature at which $1/t = 0$ (i.e., the intercept of the regression model), and θ_i=number of degree days above i where I = critical minimum temperature required for seed germination, or temperature above optimum but below the critical maximum temperature required for seed germination. Although the results showed statistically significant differences between the two endosperm types of maize, the trends were similar (Table 20.3).

A related study was conducted at the OAU Seed Science Laboratory in 2013, using a binder climatic growth chamber set at 10, 15, 20, 25, 30, and 35 °C (Fasusi 2013). Two varieties each of extra-early NEM (TZEE-YPOPSTR C5 and 2008SYNEE-YPOPSTR) and QPM (TZEE-YPOPSTR QPM C0 and TZEE-WPOPSTR QPM C0) were used for the study. The results also indicated similar trends to those observed by Aflakpui (2001), that is, germination was higher in NEM than QPM, and optimum temperature was about 30 °C (Table 20.4 and Fig. 20.6). The critical minimum and maximum temperatures in the two studies were, however, quite different. For example, whereas germination was about zero at ≤ 15 °C and emergence was much slower at 20 °C than at 25 °C 9 days after planting in Fasusi's study (Plate 20.1), Aflakpui obtained germination at 7–8 °C. Also, Fasusi obtained zero germination at 35 °C (data not shown), but critical maximum in

Table 20.3 Cardinal temperatures for seed germination of normal endosperm (NEM) and quality protein maize (QPM) varieties adapted to the tropical environments of SSA

	Temperature at germination, °C			
Cardinal temperatures	NEM	QPM	Tropical maize[a]	Temperate maize
Critical minimum	7.0	7.6	7.3	8–10
Optimum	30.0	27.5	28.8	28–34
Critical maximum	48.2	43.4	45.8	39–40

Obtained from several studies such as Birch et al. (1998a); Edalat and Kazemeini (2014)
[a]Mean of the NEM and QPM

Table 20.4 Emergence % of four extra-early maize varieties at 7 days after planting in a binder climatic growth chamber at the Seed Science Laboratory, OAU, Ile-Ife, Nigeria, 2013

	Temperature, °C				
Variety	10	15	20	25	30
TZEE-YPOPSTR QPM C0	0	1	57	97	87
TZEE-WPOPSTR QPM C0	0	0	68	85	84
TZEE-YPOPSTR C5	0	3	71	98	89
2008SYNEE-YPOPSTR	0	0	89	97	97

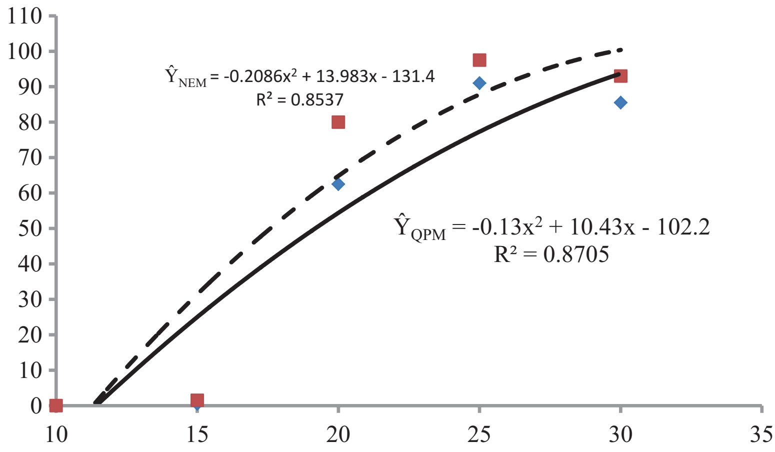

Fig. 20.6 Response of germination % of normal endosperm (NEM) and quality protein (QPM) extra-early maize varieties to temperature in a climate growth chamber at OAU, Ile-Ife, Nigeria, 2013

Aflakpui's study was slightly higher than 40 °C. In addition, differences between temperate and tropical maize were fairly close for optimum temperature but not yet definite for the critical minimum and maximum temperatures (Tables 20.3 and 20.4).

However, results obtained from studies of temperate maize indicated 8, 34, and 40 °C, for critical minimum, optimum, and critical maximum temperatures, respectively, under laboratory conditions (Birch et al. 1998a, b) and 9.4–9.9, 28.9–30.0,

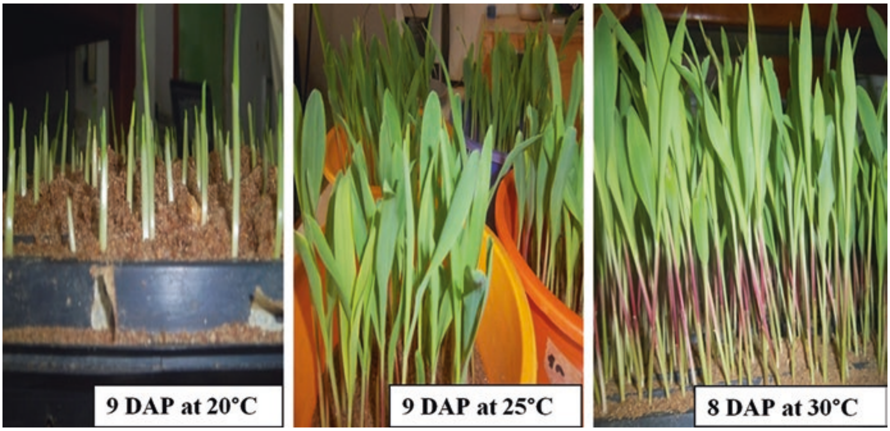

Plate 20.1 Extra-early maize seedling emergence under 20, 25, and 30 °C in a climate growth chamber at the OAU Seed Laboratory, 2013

and 39.1–40 °C under field conditions (Edalat and Kazemeini 2014). Reasons for the contrasting trends are not easy to determine and must await further studies. Under field conditions in WCA, moisture seems to be more limiting to seedling emergence than temperature. Several studies conducted at the Teaching and Research Farm of OAU, a tropical rainforest location, have consistently showed that emergence percentage (E%) increases and emergence index (EI), a measure of the speed of emergence, decreases as rainfall becomes more steady (Fakorede 1985).

Majority of maize farmers in SSA plant saved seed from their farms for the next crop. Asiedu et al. (2007) conducted a study to determine the seed quality and field performance of farmer-saved seed with certified seed of the QPM var. Obatanpa collected from four locations in Ghana. The certified seed showed a higher percentage complete staining of embryos using 2,3,5-triphenyl tetrazolium chloride (TTC) as well as higher 1000 seed weight, indicating higher seed vigor and complete seed development. Field emergence was 91% for certified seed relative to 76% for the farmer-saved seed. The certified seed was also 47% more productive than the farmer-saved seed.

When a new variety or hybrid is earmarked for varietal release and registration, it becomes very imperative to evaluate it for seed production characteristics, including female seed yield, pollen–silk synchrony, agronomic characteristics (tassel exertion, plant and ear heights, standability, disease resistance, and tolerance to biotic and abiotic stresses), etc. In addition, when inbred lines have been identified as potential parents in hybrid production, it is important to evaluate the female and male characteristics under varying environmental conditions. For the seed (female) parent, the characteristics include (i) production of a large number of seeds per ear; (ii) flowering 2–3 days earlier than the male parent; (iii) good, uniform silk emergence; (iv) vigorous plant; and (v) good seed storability (viability). The pollen (male) parent should be characterized by (i) high production of viable pollen,

(ii) pollen production extending over several days, and (iii) flowering 2–3 days later than the female parent and slightly taller than the female parent. This information will be invaluable in deciding whether or not to advance a variety or inbred line to the registration, release, and commercialization stages.

Several studies have been conducted to characterize parental materials for seed production. Because inbred lines were not yet available to an appreciable extent, Ajala and Fakorede (1987) applied flaming, clipping, and a contact herbicide (Gramoxone) at the 3-leaf (stage 1), 5-leaf (stage 2), and both stages combined (stages 1+2) and 5-, 10-, and 15-day delayed plantings, a total of 12 treatments plus a control, to study flowering synchronization in four intermediate/late and one early maize OPVs. The study was conducted in three tropical rainforest environments (E) with four replications. Flaming and clipping at the five-leaf stage produced greater delay in flowering than application of Gramoxone at the same stage. The delayed plantings significantly delayed days to mid-flowering, with the 15-day delay planting producing the longest delay. Application of Gramoxone at stage 1 and stage 1+2 did not produce a practical means of delaying flowering because they both led to severe stand reduction. Although significant genotype (G) × treatment (T) and G × T × E interactions were observed for days to mid-flowering traits (50% tasseling, anthesis, and silking), flaming 1+2, flaming 2, and the three delayed plantings produced consistent flowering delay ranging from about 2 to 20 days, depending on the environment and flowering trait. Although these treatments could be used to synchronize flowering of intermediate/late with early maize varieties, they produced the undesirable effect of 3–94% reduction in seed yield. In another study from Obafemi Awolowo University, Aghughu (1989) used nine inbred lines each from the University (FE lines) and IITA (TZi lines) in line × tester crosses with reciprocal crosses to produce 162 single-cross hybrids. Reciprocal crosses produced nearly 50% more yield in some inbred line combinations, whereas in others, yield reduction up to 35% occurred. Short, intermediate-maturity inbred lines, whenever used as female parents, tended to produce shorter hybrids with little or no lodging. They were also earlier maturing. It was concluded from the study that promising inbred lines should be evaluated in reciprocal crosses to determine their suitability as female or male parent. IITA inbred lines 2097, 9030, 1393, 1368, 5057, and 9091 consistently combined very well with Ife inbred lines FE 0001, FE007, and FE012 and were better as female rather than male parents in crosses with the FE lines.

Presently, IITA maize breeders and their collaborators are focusing a great research attention on combining ability of early and extra-early inbred lines and their characterization as female or male parents in hybrid combinations. Initiated in 2012, the studies were aimed at characterizing early- and extra-early maturing parental inbred lines and their hybrids under stressed and optimal growing environments, determining their producibility for variety release and publication of production recommendations, examining the effects of genotype and environment on grain yield and other measured traits of the hybrids including seed quality, and determining the stability of the parental inbred lines and hybrids under stress and non-stress environments. The trials involving selected early and extra-early inbred lines and hybrids were evaluated in optimal and stress environments at Ikenne, Ile-Ife, Mokwa, Zaria, and Bagauda, which represent the forest and savanna agroecologies in Nigeria. Based on their outstanding performance, a total of 40 and 25 parental lines and their hybrids were selected from the IITA maize improvement program for the early- and extra-early maturity group, respectively, and were evaluated separately under stress environments at Bagauda, Ikenne, and Mokwa and non-stress environments (optimal conditions) at Ikenne, Mokwa, and Zaria during the 2012 and 2013 growing season in Nigeria. For each group, four stable, high-yielding hybrids were identified: TZEI 124 x TZEI 25, TZEI 31 x TZEI 63, TZEI 5 x TZEI 60, and TZEI 161 x TZEI 24 for the early group and TZEEI 112 x TZEEI 29, TZEEI 29 x TZEEI 90, TZEEI 21 x TZEEI 12, and TZEEI 3 x TZEEI 46 for the extra-early group. In each case, the first named inbred line should be used as female, while the second is better as the male parent.

Similar studies have also been conducted by CIMMYT scientists in East and Southern Africa. The objectives of the studies were to (i) evaluate the grain-yield performance of parental elite inbred lines and single crosses developed over the years and (ii) ascertain the flowering synchrony among inbred lines and single-cross hybrid parents in three-way crosses (TWC). Parental inbred lines and single crosses that could be used to produce a total of 98 TWC were evaluated at seven locations in Kenya and Uganda in 2014 (Worku et al. 2016). Some single-cross and inbred line parents showed acceptable flowering synchrony, good producibility, and stable performance across testing environments, suggesting that they had high potential for seed production. In the study, 19% of the 98 TWC hybrids could be produced with minimal synchronization problems as the female flowering of the single-cross parents and male flowering of the inbred line male parents nearly matched (−2 to 2 days). However, some of the inbred line parents flowered later than the parental single crosses. Indeed, seed production of 46% of the TWC hybrids required 6 or more days delayed planting between the male and female, while 35% needed 3–5 days differential planting time between male and female parents.

Research into the flowering synchrony between male and female parents of maize hybrids is relatively new in SSA. Flowering synchrony improves kernel set and seed yield in maize; therefore, delayed planting of the female parent may be used to synchronize flowering at relatively cheaper cost (Ajala and Fakorede 1987). Worku et al. (2016), however, indicated that female delay plantings are undesirable because the seed parent utilizes less of the available growing season resulting in lower potential yield, and there is greater risk of missing flowering synchronization because of potential complications in planting the second parent at the optimal time due to weather or changing seed bed conditions. This risk increases with the duration of the planting time differential. For this reason, some other methods of flowering synchronization, such as clipping, flaming, and application of contact herbicides at the appropriate growth stage (Ajala and Fakorede 1987), may be used. Generally, same-day plantings or female-first planting is, however, much preferred, and that justifies why SSA maize breeders are now increasingly focusing on genotype-dependent flowering synchronization of male inbred lines and single-cross seed parents when advancing new hybrids to national performance trials. This is a good strategy for minimizing synchronization problems and maximizing seed yield from production fields. Further research is needed in this area, and information generated from such studies will likely greatly enhance breeding value of parental germplasm for developing and deploying high-yielding maize hybrids for the benefit of small-scale farmers in SSA.

20.6 Establishment of Seed Companies

Seed industry development started in East and Southern Africa much earlier than in West and Central Africa. In Zimbabwe (formerly Southern Rhodesia), seed business started in 1933 and double-cross maize hybrids were released as early as 1949, and by 1960, single-cross hybrids were already available to farmers (Rusike and Donovan 2008). Similarly in Kenya, seed industry started in the early twentieth century, when the government of Kenya realized the importance of high-quality seed in agricultural production (Sikinyi 2010). This was supported by research on food, industrial, and export crops, which supplied seeds and planting material for the farming community. Kenya Seed Company (KSC), which was established in 1956, initially produced pasture seeds to serve the then dairy farmers but later diversified to other crops, including maize. Seed industry development started in South Africa in the 1940s (Langyintuo et al. 2009), Ethiopia in the 1950s (IFPRI 2010), Uganda in 1968 (Ssebuliba 2010), and Zambia in 1981 when Zamseed Company was established (Smale et al. 2013). In contrast, formalized seed sector activities were not initiated in WCA until the 1970s, and the first seed company in that sub-region, named Agricultural Seeds Ltd., was established in Nigeria in 1984—over 50 years after Zimbabwe. To date, only Nigeria, Ghana, and Mali have seed companies in the sub-region.

Seed industry development in SSA has several factors common among the countries of the region, although at different levels of intensity in each country. The industry has a great involvement of the national government. In some cases, the government started the commercial seed company and eventually liberalized the policy to accommodate private entrepreneurs into the business. In Ethiopia, for example, the Ethiopian Seed Enterprise (ESE) is the lynchpin of Ethiopia's seed industry (Alemu et al. 2008). It is a state-owned enterprise responsible for the multiplication and distribution of improved seed for all major crops, specifically cereals, pulses, fruits, vegetables, and forage. Summarized in Fig. 20.7 are the proportions of land under seed production and quantity of seed produced by ESE out of the total in Ethiopia from 1995/1996 to 2004/2005. ESE-produced seed is distributed to regional and local bureaus of agriculture for onward distribution to farmers. However, since the 2003/2004 production season, the distribution of inputs (including seed) has also been routed through cooperative unions and cooperative societies, thus representing a new channel for seed. Similar trends may be found in several other countries, especially at the initial years of seed industry development. The trend is about the same in WA with slight modifications. In Ghana and Nigeria, for example, seed production, certification, and marketing during the initial years of the

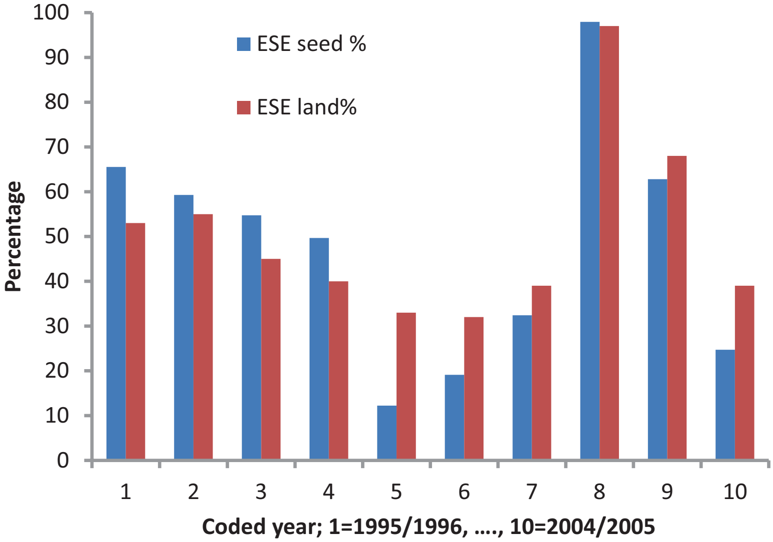

Fig. 20.7 Proportions of land under seed production and quantity of seed produced by Ethiopia Seed Enterprise out of the total in Ethiopia from 1995/1996 to 2004/2005

formalized seed business rested on a government parastatal named National Seed Service in Nigeria and Grains and Legumes Development Board in Ghana. With time, there was liberalization of the sector, and private companies were welcome into the business. The countries adopted the private sector, rather than the public or the joint public–private sector approach, however, with some restrictions.

Established in 1975, the National Seed Service (NSS) was the custodian of all publicly bred varieties in Nigeria. With the advent of hybrid maize, whose parental inbred lines were also publicly bred, NSS was also the custodian of all the inbred lines. In addition, NSS produced, processed, and marketed foundation and certified seeds. The seed companies established at the initial stages were operating primarily on hybrid seed production. For example, 76–94% of the gross income of Premier Seeds Ltd. (formerly Agricultural Seeds Ltd.) for the 1986–1995 decade was from hybrid maize seed alone (Fakorede et al. 2001c). Because of the high demand for improved maize production in Nigeria, rationalization of the seed production system had to be done in the mid-1990s. This made it possible for other corporate bodies such as semigovernmental and nongovernmental (voluntary) organizations to be involved in seed production and distribution. Under the arrangement, inbred line maintenance became the responsibility of the institution that developed the material, NSS produced foundation seed and was still the custodian of all OPVs, and the World Bank financed Agricultural Development Project (ADP) established in every state of the country and which made direct contact with farmers and produced certified OPV seed from foundation seed obtained from the NSS. Hybrid maize seed production was restricted exclusively to registered seed companies.

The seed industry in SSA has the informal and formal sectors. The informal sector is in operation particularly for the small-scale farmers who form the larger proportion of farmers in SSA. The source and quality of most of the planting materials and seed purchased, multiplied, and marketed by the informal seed sector may not be known, yet this is the major source of planting material for the farmers. Some of the informal sources of maize seed include farm-saved seed, farmer-to-farmer exchange, local markets, nongovernmental organizations (NGOs), and community-based organizations (CBOs). The prominence of the informal sector is probably one reason for the low adoption rate of improved seed and hybrid maize, particularly in WCA. As farming is becoming more commercial, the focus is gradually shifting toward the formal seed sector, which involves purchasing certified quality seed from seed companies and registered seed entrepreneurs. The shift may be speeded up by extensive creation of awareness at the level of each country. At the initial stages of the introduction of hybrids in Nigeria, field days were sponsored by the government and organized jointly by the national research and extension systems (NARES) in collaboration with IITA. All national agricultural extension agencies together conducted over 3000 mini-kit trials across the country. The agencies included the National Accelerated Food Production Project (NAFPP), the Agricultural Development Projects (ADPs), and the National Agricultural Extension and Research Liaison Services (NAERLS). Hybrid demonstration plots were planted in farmers' fields, near market places, highways, secondary schools, university farms, home gardens, and other places where people showed interest. Similar approaches were used in Ghana to promote the adoption of improved maize varieties, including Obatanpa, the first QPM variety developed in that country (Gyasi et al. 2003), and in the marginal rainfall areas of Northern Nigeria to create a massive awareness of extra-early maize varieties (Onyibe et al. 2003).

20.7 The Seed Business in WCA

The demand for seed to meet the goal of sustainable food security in SSA has created great opportunities for seed industry development in the region. In WCA, many stable, high-yielding varieties and hybrids, developed for abiotic and biotic stress tolerance by IITA and NARS and adapted to specific agroclimatic zones of different duration of the cropping season, are now available to farmers. There is a great and increasing farmer awareness of the economic benefits of improved seed. Both formal and informal seed systems exist in the sub-region, but improved seed production and rural seed delivery systems are on the increase. In fact, the formal seed system is delving into the informal to ensure that improved seeds reach farmers as far as possible, and, as a result, small and medium seed enterprises are emerging in the region. Several authors (Bänziger et al. 2002; Kamara et al. 2005; Badu Apraku et al. 2011a) have identified recurrent drought and low soil nitrogen as the two most important factors limiting maize production and productivity in SSA. This is because drought and soil nutrient deficiencies do occur simultaneously in farmers' fields, and the combined effects can be devastating (Cechin and Press 1993; Kim and Adetimirin 1997a; Badu-Apraku et al. 2011a). Generally, there is a bright possibility of improvement of regional seed trade and regional agricultural input and market information systems.

Despite the bright future outlook, the seed industry in WCA is still poorly developed due to several reasons. Seed policy is lacking, and there is inadequate funding for seed industry development in most of the countries of the sub-region. The seed industry is presently dependent on publicly developed, registered, and formally released varieties and hybrids. There is a long delay between variety development, release, and registration. In addition, the public seed sector agencies are grossly under-resourced for effective maintenance of varieties and breeder and foundation seed as well as commercial seed production and marketing. The industry is likely to develop fast under satisfactory enabling environment which, unfortunately, is not the case in WCA. There is also a weak regional seed trade development and seed market information systems. The seed companies in WCA depend heavily on contract growers for the larger proportion of the seed they produce and market. Most of the contract growers are unskilled in seed production and must be trained and supervised. Seed companies produce only about 28% of the total seed requirement in WCA. For that reason, public institutions also produce and market improved seeds, as well as the informal sector, which produces seed through recycling of OPVs and hybrids and market their seeds among neighbors and through seed exchanges.

One way to ensure that improved seeds are made available to farmers is to network the public and private seed companies and agencies with community-based organizations (CBOs). One strategy IITA has utilized is called community seed production, a scheme that has worked successfully in WCA and some other subregions of SSA. As at 2013, for example, there were 42 CBO seed producers (about 50% of all maize seed producers) in four WCA countries (10 each in Benin and Ghana, 8 in Mali, and 14 in Nigeria). The CBOs supplement seed production of seed companies even where there are functional seed companies. Predominant varietal types in WCA are improved open-pollinated varieties. Even though the area under hybrid seed production is increasing in WCA, the proportion of hybrid seed is still very low. OPV seed production is about 1.26 m tons, while hybrid seed is estimated to be about 264,000 metric tons in WCA.

The goal of the community seed production (CSP) scheme is to assist farmers and seed producers to develop sustainable seed production systems capable of providing regular supply of high-quality seed of superior varieties to farming communities. IITA's strategy includes making maize seed readily available to countries without seed companies and communities not adequately served by existing seed companies. The specific objectives of IITA's CSP scheme for maize are to:

- Train farmers in techniques of maize seed production.
- Strengthen the capacity and capability of seed producers to produce good-quality seed.
- Encourage NARS scientists to work with selected farmers and NGOs in the development of on-farm-level seed production.

- Assist NARS scientists to produce breeder seed of released maize varieties in adequate quantities at the research stations.

IITA has been executing the CSP scheme through the support of several special projects and donor funding support, including:

(i) West and Central Africa Collaborative Maize Network (WECAMAN)
(ii) African Maize Stress Project
(iii) Nippon Foundation Project
(iv) PROSAB Project
(v) Presidential Initiative for Doubling Maize in Nigeria
(vi) Drought-Tolerant Maize for Africa (DTMA) Project
(vii) Stress-Tolerant Maize for Africa (STMA) Project
(viii) SARD-SC Project
(ix) CORAF/USAID/WASP Project

In general, the CSP scheme has the following characteristics:

- Scientists, extensionists, seed certification agents, farmers, and NGOs work together to provide a reliable and sustainable seed production system for their communities.
- Seed production team helps farmers to plan seed production: the area to be planted, selection of fields, variety to be used, quality control and seed certification, post harvest handling, and marketing.
- NARS scientists provide technical advice, breeder and/or foundation seed, and other inputs to collaborating farmers.
- At harvest farmers are required to pay back either in cash or in kind.
- Each community seed production scheme involves breeder, foundation, commercial or certified seed production, marketing, and distribution.

There are six alternative CSP models from which the community may adopt the most suitable for its facilities (Table 20.5). Model 6 is the most comprehensive and is being used by the DTMA/STMA Project. Under this model, the CBOs that have been linked to seed companies in Nigeria include:

- Three CBOs in northern Guinea savanna (Malumfashi, Ikara, and Antchau) linked to Premier Seed Company
- Six CBOs in Zamfara State (Tazame, Damba GP1, Damba GP2, Fufuri, Bunzubu, and Bela) linked to Maslaha Seed Company
- Three CBOs in Borno State (Sandia, Lokodisa, and Yamtake) linked to the Seed Project Company in Kano

Support is provided by DTMA to NARES, seed companies, CBOs, and NGOs in the deployment of seed of varieties.

- Breeder seeds of inbred lines and varieties are provided to seed companies and CBOs on request.
- Sets of regional and international trials are made available to seed companies on request.

Table 20.5 Community seed production models, their procedures, and countries where they have been adopted in WCA

Model	Procedure	Country where used
1	WECAMAN worked with NARS to produce breeder and foundation seed Researchers provided foundation seed and other inputs to selected farmers through extension services Farmers produced and sold certified seed and reimbursed the input costs to extension	Benin, Burkina Faso, Cameroon, Mali
2	Surveys conducted by national extension services to identify potential contract growers Farmers provided with foundation seed to produce certified seed Certified seed sold directly to extension services which deducted input costs	Benin, Burkina Faso, Mali
3	Farmers received foundation seed once from researchers Farmers purchased and applied fertilizers for certified seed production Scientists provided farmers technical assistance	Benin, Burkina Faso, Cameroon, Nigeria
4	NGOs organized and supplied farmers with improved seed and other inputs for production of certified seed After seed sales, 50% of initial funds were deducted and provided to extension service to encourage seed production by other farmers	Burkina Faso
5	National program produced breeder seed, while foundation seed was the responsibility of a parastatal organization Parastatal organization provided custom services to seed growers and managed national seed stocks Foundation seed was sold to private seed companies and registered seed growers to produce certified seed	Ghana
6	CBOs are linked to seed companies through DTMA Project partners to ensure access to seed market, inputs, credit, and sustainability of the CSP schemes NARS scientists arrange foundation seed and assist CBOs in procurement of inputs Seed companies sign contracts with CBOs and purchase seed at harvest	Benin, Ghana, Mali, Nigeria

- DTMA scientists pay several regular visits to seed companies to encourage their involvement in identifying and commercializing maize varieties and hybrids.
- Seed companies in Nigeria are invited to harvest workshops in Zaria and Bagauda each year in an effort to expose the available promising hybrids to them.
- Staff members of seed companies participate in annual planning meetings of DTMA Project to share information on the performance of varieties.
- Technical expertise and funding are provided to NARES, seed companies, and NGOs for multilocational and on-farm trials.
- Information on sources of seed and available DT varieties has been provided to NGOs.

Table 20.6 DT Seed (in MT) produced by CBOs linked to private seed companies in Nigeria, 2007–2012

Seed company	2007	2008	2009	2010	2012	Total
Maslaha	5	8	21	21	14	69
Premier	6	9	11	7	19	52
Govt./Jikur	–	4	11	17	18	50
Total	11	21	43	45	53	173

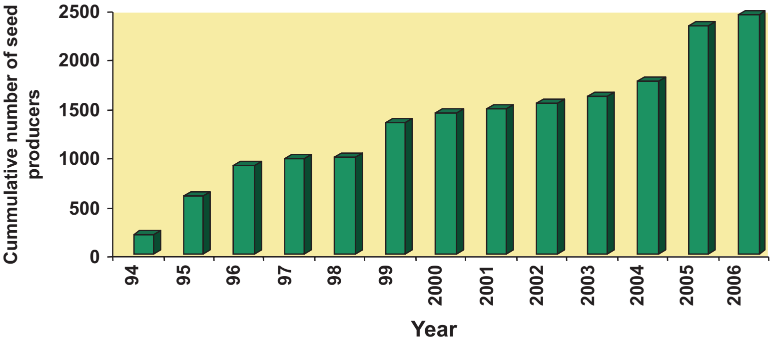

Fig. 20.8 Cumulative number of seed producers trained in seed production in WECAMAN member countries under the community-based seed production scheme, 1994–2006

- Summary of results of multilocational and on-farm trials is provided to NARES and seed companies to promote release of varieties.
- Provision of larger quantities of parental lines and seed of DT varieties to seed companies for seed production, testing, and promotion.
- Financial support to selected NARS partners for breeder seed and parental line production.
- Information on available DT varieties through the DTMA Project website and CDs.

The CSP schemes made impressive achievements over the years of operation in WCA. Annually, training courses have been organized for seed company staff members. The number of participants in the training ranged from 24 to 33 annually. The course is usually held at IITA, and the participants are sponsored. The CBOs linked with seed companies have been productive (Table 20.6). Apart from seed company staff members, several thousands of seed producers have been trained (Fig. 20.8). The CSP scheme has been quite effective in all countries it has been adopted (Fig. 20.9).

Particularly striking is the tremendous increased production of certified seed by seed companies (Table 20.7), especially in Nigeria (Fig. 20.10) that has the largest number of seed companies, the seed business had been in existence longer than other WCA countries, and the intervention into seed production from WECAMAN and the DTMA had been largest. As shown in Fig. 20.10, Premier Seeds Nigeria has

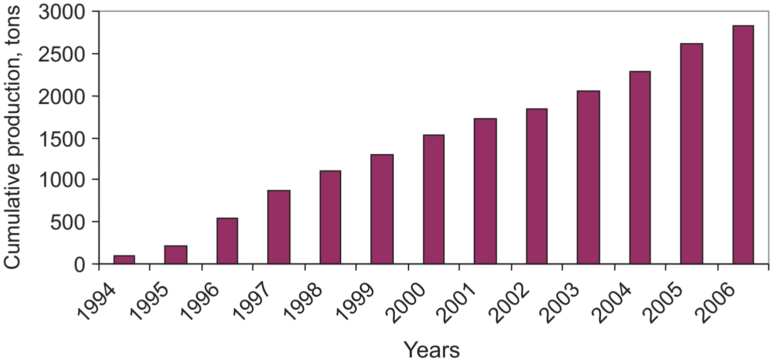

Fig. 20.9 Cumulative commercial seed production in WECAMAN member countries under the community seed production scheme, 1994–2006

Table 20.7 Certified seed production (MT) of drought-tolerant maize varieties and hybrids by seed companies in West Africa, 2007–2013

Country	2007	2008	2009	2010	2011	2012	2013	Total
Nigeria	257	710	138	221	735	3245	3415	8721
Ghana	–	3	79	105	55	79	133	454
Mali	–	3	25	47	80	98	210	463
Total	257	716	242	373	870	3422	3758	

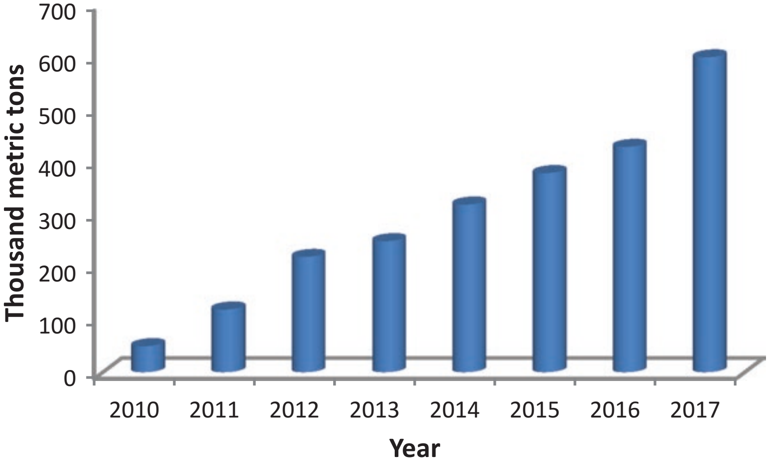

Fig. 20.10 Seed of drought-tolerant maize varieties produced by Premier Seeds Ltd., Nigeria from 2010 to 2017 (Ogungbile 2017)

been producing DT maize seed, starting with about 50,000 t in 2010 with an annual increase of about 70,000 t per year, all of which is sold. In 2017, over 600,000 t was produced and, by April, more than 75% had been sold (Ogungbile 2017).

20.8 Public–Private Partnership in Seed Business

The seed business in SSA has thrived very much on public–private partnerships. In WCA, the partnerships were initiated and facilitated by IITA in an effort to strengthen regional economies by equipping seed companies and entrepreneurs with the necessary skills and raw materials needed for a vibrant seed sector within and across countries of the sub-region. For the seed sector to successfully play its role, there is a need to find innovative and cost-effective ways to ensure that businesses have the skilled workers they need to grow and prosper and that early career seed specialists have the education, skills, and industry-recognized credentials they need to participate fully in the seed sector economy. Both are essential for ensuring robust economic growth, a thriving middle class, and broadly shared prosperity in agriculture. The partnership also aims to accelerate more effective, employer-led regional distribution of quality seed initiatives across each country. IITA started its partnership with Agricultural Seeds Ltd. in 1985 by being actively involved in the supervision and production of the first commercial hybrid in the sub-region on about 150 ha of land. Since then, public–private partnership in the seed business has increased in leaps and bounds. At present, the partnership thrives very well in Benin, Ghana, Mali, and Nigeria.

Sustenance of the public–private partnerships in the seed business has been primarily from funding and other forms of support by regional and international agencies. Prominent among the agencies is the CORAF/WECARD that has initiated and supported the West African Seed Project (WASP). This project has made tremendous contribution to the development of the seed sector in the last decade or so. Through a regional concerted effort, WASP has an objective to expand the availability of quality seeds from the current 12% to 25% by 2017 when its 5-year period will end. The goal of the project is to contribute to sustainable improvement of agricultural productivity. The geographical scope of the WASP for its main activities covers seven countries: Benin, Burkina Faso, Ghana, Mali, Niger, Nigeria, and Senegal. But in the case of the implementation of the Regional Seed Regulation, it covers the 15 ECOWAS plus two CILSS countries (Pouzaa and Okelola 2015).

Four key programs which are mutually facilitated by the public–private partnerships are as follows:

(i) Establishment of an Alliance for Seed Industry in West Africa (ASIWA)
(ii) Implementation of a regional seed policy to facilitate trade in seeds among ECOWAS Member States
(iii) Production of sufficient quantities of quality breeder seeds of regional importance
(iv) Strengthening of the private sector and national seed trade associations to increase the quality of the production of foundation and certified seeds

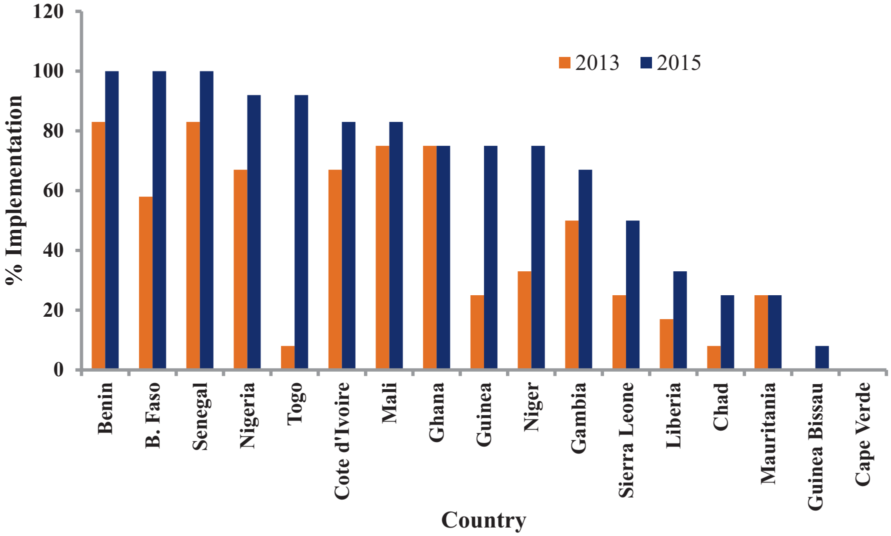

Fig. 20.11 Percentage implementation of ASIWA requirements by West African countries in 2013 and 2015 (Pouzaa and Okelola 2015)

Progress has been made on each of these key programs. Launching of ASIWA was done at Abidjan, Cote d'Ivoire, on August 3, 2015, and the process of harmonized Regional Seed Regulation is being actively pursued. The regulations cover variety release, seed quality control and certification, and phytosanitary certification. The ASIWA concept has been accepted by regional and national stakeholders.

During the period of development of the harmonized Regional Seed Regulation, the CGIAR centers in WA, notably IITA, ICRISAT, and the African Rice Center, were represented at all the meetings organized on the harmonization of the seed regulations in the sub-region and have actively participated in the deliberations on the seed policies and programs that would improve the seed production and supply of good-quality seed in the West Africa sub-region. Across the sub-region, nearly 80% implementation was made by 2015, compared with only 40% in 2013. Also, most of the WA countries have made progress on implementation of the necessary components of the project (Fig. 20.11).

It is envisaged that WASP will continue to collaborate extensively with national, regional, and international partners in the seed sector and rely on broad and combined expertise of a wide range of stakeholders to achieve the expected results.

Capacity building has been one of the main strategies of the public–private partnerships in WCA. Training can contribute to improving smallholder farmers' knowledge and the use of technologies such as seeds. For example, since its inception in 2007, the DTMA (now Stress-Tolerant Maize for Africa (STMA)) Project has intensified efforts to provide an adequate quantity of breeder seeds of parental inbred lines and OPVs as well as foundation seed to partners in Benin, Mali, Ghana, and Nigeria. Efforts are being made to link seed producers to appropriate markets

Table 20.8 Number of IITA early and extra-early germplasm-based maize hybrids and OPVs released by public and private sector entities in West Africa in the last 6 years

Country	Number of hybrids and open-pollinated varieties released per year						
	2012	2013	2014	2015	2016	2017	Total
Benin	–	–	–	6	4	–	**10**
Ghana	11	–	–	10	–	**4**	**25**
Mali	–	2	6	–	6	–	**14**
Nigeria	4	5	4	4	8	**2**	**27**

for the sale of surplus seeds in close collaboration with the AGRA PASS initiative. The results have been achieved through the in-service training in techniques of quality seed production of OPVs and hybrid seeds. Training workshops are organized to build the capacity of support staffs of the seed unit of both the public and private sector institutions in target countries. The individual staff members for training are usually those saddled with the responsibility of multiplying breeder seed and/or foundation seed for in-country and regional use. Seeds and genetic materials used or marketed regionally should conform to the ECOWAS standards. It has been observed that most of the technical staff handling like the multiplication, conditioning, storage, and marketing of seeds do not have the requisite skills and knowledge, particularly in these critical domains as well as in quality control and certification procedures and standards. These together form the basis of the technical know-how for the production and marketing of quality seeds. The lack of this know-how is reflected in the very low quality of seeds traded in the sub-region.

Training is usually aimed at strengthening the capacities of research and seed field technicians at the level of the NARIs, private seed producers, and companies from the WA countries, in collaboration with IITA for maize.

A prominent part of the capacity building plans of the WASP and IITA is to enhance technical competence for the delivery of quality breeder seeds through training and provision of requisite laboratory and processing facilities to the NARS. In addition, technical and agribusiness capacities of the private sector are strengthened to deliver quality foundation and certified seeds and to access credit.

Perhaps because of the lack of necessary competence, the private sector has been reluctant to take up the responsibility or mandate of producing foundation seed in conformity with the ECOWAS Seed Regulation. This has resulted in the creation of a wide gap in the seed production and supply chain and thus constraining the increase in production and supply of certified seeds to farmers. Training helps to build capacities of both the public and the private sector personnel to upscale the supply of these two classes of seed in achieving the goal of increasing the supply of quality seeds from 12% to 25% by 2017.

Seed companies play a key role in enhancing the production and productivity of maize in West Africa (WA) as they provide farmers access to higher-yielding and more stress-tolerant hybrids and open-pollinated varieties (OPVs). For the past 5 years, public and private sector entities have regularly delivered and disseminated seeds of IITA-improved maize hybrids and OPVs that have been formally released in WA countries (Table 20.8). The adoption of these hybrids and varieties has helped improve the lives and livelihoods of farmers, traders, and consumers dependent on maize in the region.

Although access to quality seed of improved maize varieties have been in the upswing in recent years, the production and supply of sufficient quantities of early generation seed (breeder and foundation seeds) still pose a challenge particularly to emerging and small-scale seed companies in WA that rely heavily on varieties bred by NARS and international agricultural research centers. Until such time that policies and scales of production allow for improved efficiencies to address this constraint, public organizations must shoulder part of the responsibility of providing early generation seeds.

To this end, IITA and partners implementing the STMA Project—funded by the Bill & Melinda Gates Foundation through CIMMYT—have been making significant strides. Some of the project's notable achievements in 2016 include the following:

- *Identification of seed companies to produce early generation seeds*. STMA supported the selection of seed companies to produce early generation seed to hasten the production and marketing of stress-tolerant hybrids and OPVs in WA. To this end, Ahmadu Bello University Institute for Agricultural Research (ABU-IAR) Zaria and Premier Seeds Ltd. in Nigeria, M&B in Ghana, and *Institut D'Economie Rurale* (IER) in Mali produced a total of 16,600 kg of breeder seed, while ABU-IAR Zaria, Premier Seeds Ltd., Maslaha Seed Ltd., Value Seed Ltd., and Gawal Seed Ltd. in Nigeria, M&B in Ghana, and Faso Kaba and IER in Mali collectively produced some 230,800 kg of foundation seed.
- *Production of breeder seed of stress-tolerant varieties*. STMA facilitated the production of 4688 kg of seed of 43 promising stress-tolerant extra-early, early-, intermediate/late-maturing inbreds, hybrids, and OPVs for the use in on-farm trials, breeder seed production, and community-based seed production.
- *Production of foundation seed of stress-tolerant parental lines*. Five institutions/seed companies identified and selected by the project in Nigeria (ABU-IAR Zaria, Premier Seed Ltd., Maslaha Seed Ltd., Value Seed Ltd., and Gawal Seed Ltd.), and one each in Ghana (M&B) and Mali (IER and Faso Kaba) produced 231 MT of foundation seed of stress-tolerant parental lines.
- *Production of initial hybrid seed for demos, registration, and promotion*. The project distributed, on request, about 15,000 kg of breeder seed of promising drought-tolerant, extra-early, early-, intermediate-, and late-maturing inbred lines, hybrids, and varieties to NARS partners and seed companies in Nigeria, Ghana, Benin, Mali, Niger, Burkina Faso, Senegal, and Tanzania. These are currently being used in on-farm trials, breeder seed production, and community-based seed production.
- *Maintenance of parental materials*. Under STMA, more than 2000 kg of breeder/foundation seeds was produced in Nigeria by IAR (2 inbred lines) and IITA (15 inbred lines) and in Ghana by M&B (3 inbred lines).
- *Selection and evaluation of new stress-tolerant hybrids and varieties for seed production characteristics*. The project selected 30 early-maturing maize hybrids comprising single, three-way, double, and topcrosses and their parental lines based on their superior performance in the regional trials and other previous evaluations and characterized for seed production under contrasting environments. Similarly, the project characterized 40 extra-early maturing maize parental lines and their hybrids.

Table 20.9 Drought-tolerant maize varieties released in Mali under DTMA, 2009–2015

Release name	Base-genetics	Year of release	Type	Maturity range
Jorobana	EVDT97WSTRC1	2009	OPV	Early
Brico	TZEE -Y Pop STR C4	2010	OPV	Extra-early
Tieba	DT-SR-W C0/ TZL-COMP3-C2-S2–34–4-1-2-BB	2012	Hybrid	Medium–late
Mata		2012	Hybrid	Medium–late
Diambala		2012	OPV	Medium–late
Sanu	TZE-Y DT STR C4 x TZEI 13	2012	Hybrid	Early
Sahel Kaba	TZEE-W Pop DT STR C5 XTZEEI 6	2014	Hybrid	Extra-early
Sosani	TZEE-Y Pop DT STR C5 X TZEEI 58	2014	Hybrid	Extra-early
Dilika	TZEI 24 X TZEI 17	2015	Hybrid	Early
Apraku	TZEI 11 X TZEI 23	2015	Hybrid	Extra-early
Sahel Kaba Blanc	TZEE-W POP DT STR C5 XTZEEI 6	2015	Hybrid	Extra-early
Sahel Kaba Jaune	TZEE-Y POP DT STR C5 X TZEEI 58	2015	Hybrid	Early
Tamalaka	TZEI 124 X TZEI 25	2015	Hybrid	Early
Duba	IITA TZI1717 X IITA TZI 1528	2015	OPV	Medium–late
Kiban	EV DT Y 2000 STR	2015	OPV	Early
Tieblenke	DTSYN 11 Y	2015	OPV	Medium–late
Soden	TZL COMP4C3DT	2015	OPV	Early

20.9 Mali and DTMA: Showcase of Successful Partnerships

For about 10 years, DTMA/STMA and Mali have worked together to generate, promote, and deliver adapted drought-tolerant maize varieties and hybrids to farmers. This partnership has led to the release of several open-pollinated drought- and *Striga*-resistant varieties and hybrids by Malian scientists in collaboration with IITA (Table 20.9). The project has relied on the national agricultural research and extension system of Mali—including IER and *Institut Polytechnique Rural de Formation et de Recherche Appliquée* (IPR/IFRA)—to promote the adoption of improved varieties through national and local communication and extension networks, as well as worked with local seed companies such as Faso Kaba, Comptoirs 2000, Coprosem, Coop Kolokoani, and DNA to actively scale up and distribute seeds of improved drought-tolerant maize hybrids and OPVs.

Additionally, through the project, 12 IITA-developed drought-tolerant early-, extra-early, and intermediate-maturing hybrids (Table 20.9), as well as 6 drought-tolerant OPVs, have been released in Mali and are now in the hands of farmers or seed companies and community seed producers. These efforts have contributed to increased maize productivity in Mali, making the country one of the top maize producers in Africa today.

Together, Mali and IITA, through DTMA, have used a mix of delivery pathways to sustain and scale up seed production and dissemination to smallholder farmers in the country. In some areas of Mali that are not served by seed companies, the project supported community-based seed production schemes to ensure continued supply of good-quality seed of improved drought-tolerant maize varieties to farmers. Eventually, these schemes are envisioned to evolve into full-blown private seed enterprises or be linked to small-scale seed production start-ups.

Annually, IITA produces and makes available adequate quantities of breeder seed to Malian scientists through the project to produce breeder and foundation seed, with the end goal of meeting the demand from seed producers. To this end, IITA works with Mali partners on seed demand creation strategies to ensure sustainability of seed production such as conducting awareness and information campaigns to spur interest among potential development entities, especially seed suppliers. IITA has also helped build the capacity of national partners to facilitate the release, promotion, and dissemination of drought-tolerant varieties. Through the project, IITA has conducted regular training courses on related areas such as breeding techniques, seed production, and seed marketing involving partners from both the public and private sectors in Mali. Additionally, the DTMA Project has also conducted several on-station and on-farm demonstrations and maize field days and designed and implemented a variety of communication strategies and tactics to generate greater interest and adoption of improved maize seed among stakeholders such as farmers, farmers' organizations, seed companies, and policymakers.

20.10 Conclusions

The demand for high-quality seed is on the increase in SSA and is being met by collaborative efforts of public institutions, private seed companies and entrepreneurs, NGOs, and CBOs. International donor agencies have greatly facilitated formal sector seed production technology, an effort that has triggered maize production revolution in SSA, especially in WCA. Problems of quality maize seed technology in the region are being researched, and the research outcomes are utilized in developing improved seeds by seed companies. The community seed production models have been effective in making quality seeds available in countries where commercial seed companies have not been established and have led to micro-scale seed enterprises springing up. The DTMA/STMA Project sponsored by Bill & Melinda Gates Foundation adopted one of the models to greatly boost the availability of maize varieties and hybrids tolerant/resistant to drought and some other stresses to farmers. This approach has been successful beyond expectation. Hybrid maize seed is steadily replacing OPVs, and research in synchronization of flowering of parental materials for hybrids is now receiving the attention it deserves in the region. That breeding and seed technology produce undisputable synergistic effects on maize production is clearly demonstrated in Mali (the growth rate of maize production in that country is now one of the highest in the world) and in West Africa (the country has the highest maize yield per unit land area and is the second largest producer of maize grain).

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Chapter 21
Commercialization of Early and Extra-Early Maize and Impact on Maize Production and Productivity in Sub-Saharan Africa

21.1 Introduction

Maize (*Zea mays*) is one of the most important staple foods as well as cash crops in sub-Saharan Africa and has the potential to mitigate the present food insecurity in the sub-region. Maize production, apart from its role in improving food security, is a source of employment and income for farmers and other entrepreneurs, providing diversified uses as human food, livestock feed, industrial raw materials, and source of energy. Over 30 kg of maize are consumed per capita per year in WCA because of its suitability for the preparation of local dishes including gruels, porridges, and pastes. Green maize, boiled on the cob or roasted, is an important vegetable crop and plays an important role in bridging the hunger gap after the dry season. In many African countries, maize is widely fed as porridge to weaning children, although unfortunately, often without a protein supplement such as milk, meat, or beans. This can lead to diseases such as kwashiorkor from protein deficiency. This has prompted the development of quality protein maize (QPM), such as Obatanpa, which has gone a long way in WCA to reduce protein-deficiency problems (Vivek et al. 2008; Agbonika 2015). Varieties of QPM can also make significant contributions to the food and livestock industries. More recently, maize has acquired a new role as a raw material in the food beverage industries, providing additional markets for maize farmers.

Promotion and wide adoption of early- and extra-early maturing normal endosperm and quality protein maize (QPM) (with high levels of lysine and tryptophan) developed by IITA and partners have significantly contributed to the rapid spread of maize into the savannas of WCA, making it the most important cereal crop after rice (*Oryza sativa* L.) (Akande and Lamidi 2006; Adefris et al. 2015). Early (90–95 days to physiological maturity) and extra-early (80–85 days to physiological maturity) play a unique role in filling the hunger gap in July in the Sudan savanna and the northern Guinea savanna zones after the long dry season. The early and extra-early

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maize are also preferred to the traditional sorghum (*Sorghum bicolor* (L.) Moench) and millet (*Pennisetum glaucum* L.), for their better responsiveness to fertilizer and improved productivity. The cultivars are also used for late plantings when the rains are delayed; for intercropping with cassava, millet, and sorghum; and as "green maize" in the forest agroecology where they allow early access to the market for a premium price. Maize production in WCA is carried out largely in the savannas because of the high-potential grain yield due to high incoming solar radiation, low cloud cover, and reduced incidence of pests and diseases as a result of low humidity and low night temperatures. The availability of the early and extra-early varieties and hybrids has resulted in improvements in the productivity of maize, income, and well-being of people in the sub-region (Badu-Apraku et al. 2004, 2011, 2012a, b).

However, during the last two decades, maize production and productivity have lagged behind population growth because the production in the savanna agroecology is severely constrained by *Striga hermonthica* (Del.) Benth. parasitism, low soil nitrogen (low N), and recurrent drought (Badu-Apraku et al. 2016). Drought and *Striga* infestation constitute the most important factors frequently limiting maize production, food security, and economic growth in sub-Saharan Africa. Drought at any stage of crop development reduces production, but the greatest damage occurs when it coincides with the flowering and grain-filling periods. Effects of drought stress include delayed silking and female sterility caused by abortion reduction in amount of pollen and number of kernels per plant (Hall et al. 1982; Barazesh and McSteen 2008), resulting in severe grain-yield reduction. Annual maize yield losses due to drought may approach 24 million tons, equivalent to 17% of a normal year's production in the developing world (Edmeades et al. 1992; Ray et al. 2013).

The incidence of drought stress during the last two decades has increased, probably due to the combination of global climate changes, displacement of maize to marginal environments by high-value crops, decline in soil organic matter, reduced soil fertility, and water-holding capacity (Bänziger et al. 2000). Edmeades et al. (1995) reported an annual maize yield loss of 15% from drought stress in the savanna of WCA and indicated that localized losses might be much higher in the marginal areas where the annual rainfall is below 500 mm and soils are sandy or shallow. However, the grain-yield losses could be higher if drought occurs at the flowering and grain-filling periods (NeSmith and Ritchie 1992; Farooq et al. 2009). Yield losses due to *Striga hermonthica* may range from 10% to 100% depending on the variety and the environmental conditions (Kroschel 1999; Atera et al. 2013). *Striga hermonthica* infestation is extremely difficult to control and is a major threat to the rapid spread of maize into the WCA savanna. Available *Striga* control measures include host plant resistance, cultural, chemical, and manual methods (Kim et al. 1998; Teka 2014). Of these, the use of host plant resistance or tolerance is considered the most economical and environmentally friendly for resource-poor farmers. In addition to the losses due to recurrent drought and *Striga*, the soils of WCA are inherently low in N, and farmers do not have ready access to inorganic fertilizers because of nonavailability, high cost, or lack of credit. As a result, most farmers produce maize under low-N conditions (Oikeh and Horst 2001). Estimated yield losses from nitrogen stress alone can be as high as 50% (Wolfe et al. 1988). Low-N-tolerant cultivars are superior in the utilization of available N, either because of enhanced N-uptake capacity or more efficient use of absorbed N for grain production (Lafitte and Edmeades 1994).

Thus far, all the chapters in this book have covered the science and technology aspects of genetic enhancement of early and extra-early maize for WCA in the last few decades. The beneficial aspect of the science and technology is realized only when the technology is available to and actualized by farmers and end consumers. Summarized in this chapter are the strategies used to transfer early- and extra-early-maturing maize technologies to farmers in SSA, especially in WCA where, for many years, farmers' and consumers' adoption of the technologies has resulted in unprecedented improvement in production and commercialization of maize and its products. Details of the different strategies have been well documented in an earlier publication (Badu-Apraku et al. 2012b). Additional information that accrued to our program since that publication are also included in this chapter.

Technology transfer is a dynamic continuum from the researcher to the farmer and finally to the consumer. For this reason and perhaps several others, maize research has been primarily demand driven in WCA. Apart from being a source of human food and a major component of livestock feed, maize has become an indispensable industrial raw material for the production of grits, flour, breakfast cereals, baby foods, baked foods, alcoholic and nonalcoholic beverages, and other products in WCA. For example, of the estimated 5.7 million t total maize grain produced in Nigeria, about 1.5 million t (over 26%) are used by the brewery and bakery industries, where maize has replaced imported barley and wheat (FAO 2012; Adesoji et al. 2016). In addition, the results of the evaluation in Mali of two improved varieties, Sotuba, a yellow maize, and Tuxpeno, a white maize, have shown that wheat flour can be replaced by 20% of maize flour in baking bread, 40% in croissants, and 60% in chocolate cake (IITA/WECAMAN 1996; IITA 2010). This has a significant potential to make large savings in the amount of imported wheat flour.

Global maize production is estimated at 785 million tons, and Africa produces 6.5% of this total (IITA 2016a). Although the availability of food per person increased worldwide during the last four decades, it went down by about 7% in Africa, while annual maize production in WCA is estimated at about 11 million tons. The challenge presently facing Africa, therefore, is to feed a population that is growing annually at 2.3% compared with the per capita agricultural GDP of 3.1% (United Nations Statistics Division 2008). Maize has good prospects for rectifying the food deficit in SSA because it is the number one staple food crop for rural and urban consumers.

Over 650 million people in SSA consume on average 43 kg of maize per year (FAOSTAT 2006). The International Institute of Tropical Agriculture (IITA) in collaboration with the National Agricultural Research Systems (NARS) has developed extra-early and early maize varieties that fit the conditions of the savanna agroecology. Availability of the extra-early and early varieties has made it possible for maize to spread fairly rapidly into the savannas, replacing the traditional crops such as sorghum and millet, especially in the Sudan savanna and the northern fringes of the northern Guinea savanna where the short duration of rainfall had hitherto precluded maize cultivation. Extra-early- and early-maturing maize varieties are more responsive to fertilizer application, mature more quickly, and can be harvested much earlier in the season than the traditional sorghum and millet crops (Badu-Apraku et al. 2013a, b, c).

The maize varieties are thus used for filling the hunger gap in July in the savanna zone when all food reserves are depleted after the long dry period. There is also a high demand for the early and extra-early maize in the forest zone for peri-urban maize consumers because they allow farmers to market the early crop at a premium price in addition to being compatible with cassava for intercropping (IITA 1992; Badu-Apraku et al. 2004, 2015). Another important advantage of the early and extra-early maize is that they provide farmers in the various agroecological zones with flexibility in the dates of planting.

The extension systems in WCA countries have not been well developed, and this prevents improved maize crop technologies from reaching a large proportion of the farmers (Fisher et al. 2015). It is not unusual to find farmers in close proximities to research station approach such stations for seed of improved varieties which they have seen on research plots of the institutions. Therefore, maize improvement efforts in WCA in the last three to four decades have given much consideration to technology transfer-related activities, including regional trials, on-farm trials, demonstration plots, and field days. Between 1987 and 2007, WECAMAN (West and Central Africa Collaborative Maize Research Network) offered on annual basis improved early- and extra-early-maturing maize varieties to NARS in WCA through the Regional Uniform Variety Trials (RUVT): RUVT-early and RUVT-extra-early. The network also collaborated with the IITA Maize Program in the distribution of trials for the intermediate- and late-maturing open-pollinated and hybrid maize varieties. Each NARS received, on request, one to three sets of any of the trials for in-country evaluation at appropriate locations. The NARS followed up with request for seed of one or two varieties identified as promising in their respective countries for further experimentation on-farm and prospective adoption. The Network also provided funds in support of on-farm trials and demonstrations in member countries. Since 2007, the DTMA (Drought-Tolerant Maize for Africa) Project has also supported the regional early and extra-early drought-tolerant trials as well as on-farm trials in the partner countries, including Ghana, Nigeria, Mali, and Benin Republic. This approach has promoted collaboration among national and international scientists in the sub-region to develop, test, and transfer to farmers high-yielding and adapted maize cultivars and accompanying agronomic practices. The regional trials have provided an important vehicle for a wide testing of the varieties and for exchange of germplasm among all participating countries in the sub-region. Also through the regional trials, less endowed member countries, with respect to technology development, have been offered the opportunity to identify varieties for their target ecologies.

As a result of the availability of improved maize varieties and hybrids of various maturity groups with resistance to the important biotic and abiotic stresses, and the intensified promotion for adoption, maize production has been expanding very rapidly in WCA to the extent that it has now become the most important food crop for urban and rural consumers (Byerlee and Ficher 1997; Badu-Apraku et al. 2001; FAOSTAT 2015). The sub-region has witnessed remarkable success stories as the use of new seed, and improved technologies have increased smallholder maize production. Trends in land area under maize, total maize production, and yield per unit land area have shown dramatic increases in most of the WECAMAN member countries. Total maize production in the sub-region has increased from about 2.74 million tons in 1980 to 10.5 million tons in 2000, representing a 384% increase. According to FAO, the area in WCA planted to maize increased from 3.2 million ha in 1961 to 8.9 million ha in 2005. Between 1987 and 2007, this area increased from 7,958,927 to 11,752,136 ha (FAO 2009). Maize production has caught up with or surpassed sorghum and millet in much of the savanna areas of WCA. This expansion has been attributed to the adoption of new maize germplasm, development of road infrastructure in rural areas, relatively good extension services, and urban demand (Smith et al. 1997; Kennedy and Reardon 1997; Fakorede et al. 2003). For example, FAO data show that during the period 1998–2000, 70% of the area grown to maize in sub-Saharan Africa (SSA) was in WCA, a dramatic increase from the 22% recorded about 30 years ago (1968–1970). In 2000, 43% of the total maize production in SSA was from WCA compared to 17% in 1970. Yields increased by 41%, from an average of 858 kg ha^{-1} in 1970 to about 1210 kg ha^{-1} in 2000 (FAO 2001, 2012).

Thus, through networking involving national and international research programs, regional constraints to increased maize production were tackled by scientists in WCA. The effort gradually ushered in a maize-based green revolution in the sub-region (Fakorede et al. 2003). However, a full-blown maize revolution would be achieved when farmers practiced intensive maize production. For farmers to do this, policy impediments to higher production and trade inefficiencies negating the realization of the full potential of maize in the sub-region needed to be critically examined. CORAF/WECARD (*Conseil Ouest et Centre Africain pour la Recherche et le Développement Agricoles*/West and Central African Council for Agricultural Research and Development) as the regional research coordinating body had a critical role to play in this respect. CORAF/WECARD in collaboration with WECAMAN needed to energize the NARS in each country to encourage the creation of appropriate national policy environments for greater maize production and improved trade. CORAF/WECARD needed also to become actively involved in advocacy at the national and sub-regional levels to influence national governments to support public research systems and investment in public goods.

21.2 Progress in Breeding for Multiple Stress Tolerance in Early and Extra-Early Maize

Under field conditions, drought, *Striga*, and soil nutrient deficiencies can occur simultaneously, and the combined effect can be devastating. Drought and low soil N aggravate *Striga* parasitism on maize (Badu-Apraku et al. 2004). Studies conducted in WCA by Badu-Apraku et al. (2004, 2010) on the combined effects of these stress factors showed 44–53% grain-yield reduction because of drought, 42–65% from *Striga* infestation, and 40% from low soil N. Therefore, a major strategy of IITA's Maize Improvement Program is to breed cultivars that are *Striga*-resistant and drought and low-N-tolerant to increase and stabilize maize yield production in the sub-region. The germplasm used for breeding multiple stress-tolerant, early, and extra-early cultivars in the IITA program were from diverse sources identified through many years of extensive testing in WCA and included (i) local and exotic germplasm, (ii) introduced temperate inbred lines found to exhibit resistance and tolerance to *Striga*, (iii) African landraces pool formed from selected landraces evaluated under artificial infestation with *S. hermonthica* and found to possess resistance to the parasite, and (iv) backcross progeny from crosses with *Z. diploperennis*. Using the available germplasm and carefully designed strategies, including reliable and uniform artificial *Striga* infestation methods, recurrent selection, inbreeding, and hybridization, IITA, in collaboration with the National Agricultural Research Systems of WCA, has developed several early and extra-early maize cultivars that combine resistance to *Striga* with tolerance to drought and low soil N. During three breeding eras, 1995–2000, 2001–2006, and 2007–2012, considerable efforts were devoted to breeding for stress-tolerant, extra-early maize. Through this program, a number of extra-early maturing cultivars that are not only *Striga* resistant and tolerant but also drought escaping or have genes for tolerance to drought at flowering and grain-filling periods have been developed. Similarly, three generations of *Striga*-resistant early cultivars have been developed in the maize program. The first-generation cultivars were developed through the introgression of *Striga* resistance/tolerance genes into available early populations and varieties, using inbred lines from IITA (1368 STR and 9450 STR) as the sources of resistance/tolerance. A second generation of cultivars was developed from two broad-based populations with white and yellow kernel colors formed by intercrossing promising local and adapted germplasm followed by the introgression of drought tolerance and *Striga* resistance/tolerance genes from selected inbred lines. The populations were subjected to recurrent selection under artificial *Striga* infestation without intentionally selecting for drought tolerance to develop early white and yellow maize cultivars resistant to *Striga* and are drought tolerant (Badu-Apraku et al. 2008, 2009). Additional cycles of recurrent selection were conducted during the period 2007–2010 to further increase the frequencies of favorable alleles for tolerance to drought and resistance/tolerance to *Striga* in the two populations, TZE-W Pop STR C0 and TZE-Y Pop STR C0. Through this program, a third generation of the early-maturing drought and *Striga* resistant/tolerant was developed.

Two approaches have been adopted for breeding for drought tolerance in the early- and extra-early maturing maize. The first is to breed for extra-early and early-maturing cultivars that are drought escaping. These cultivars are adapted to drought-prone environments in WCA; they mature and complete their life cycles before severe moisture deficit occurs or before the onset of terminal drought. The second strategy is to breed drought-tolerant early and extra-early cultivars with better adaptation to drought-prone environments under induced drought stress. This is achieved by introgressing or introducing into extra-early cultivars the genes for drought tolerance to enable them withstand mid-season drought when it occurs during most drought-sensitive flowering and grain-filling periods. Using the two strategies, IITA has, during the last three decades, capitalized on naturally available mechanism for drought escape and drought tolerance in the germplasm and the prevailing production environments in WCA to develop a wide range of high-yielding drought-tolerant or drought-escaping early and, since 2001, extra-early *Striga*-resistant populations (white and yellow endosperm), inbred lines, and cultivars to combat the threat posed by *Striga hermonthica* and recurrent drought in the savannas of WCA. In 2011, the extra-early program identified extra-early white and yellow inbreds with genes for tolerance to drought at the flowering and grain-filling periods thus allowing the development of extra-early hybrids that do not only escape drought but can also tolerate drought that occur randomly during the flowering and grain-filling periods. Edmeades et al. (1995) reported similar gains under low N and drought for selection programs conducted at CIMMYT, indicating that there was a close correspondence between the performance of maize genotypes under drought and low-N environments. The authors concluded that drought environments caused variation in the partitioning of N to the ear at flowering and identified genotypes with higher harvest indices. Thus, selection for improved partitioning of assimilates to the developing ear using drought stress at flowering as the selection environment can simultaneously improve tolerance to drought and low N. Studies at IITA (Badu-Apraku et al. 2009, 2010) also showed that selection for *Striga* resistance, which is normally done under low N, resulted in concomitant increase in tolerance to low N. Furthermore, the early-maturing drought and *Striga*-resistant cultivars, EV DT 97 STRC1 and TZE-W DT STR C_4, and the drought-tolerant cultivar, TZE Comp3 C_3, were tolerant to low N although they were not consciously selected for tolerance to low N. Guided by these results, IITA scientists have made selection under low N an important strategy for developing low-N-tolerant cultivars. The early and extra-early source populations have been subjected to improvement for tolerance to drought under managed drought stress, low N, and resistance to *Striga*, resulting in the development of several extra-early cultivars with combined resistance and/or tolerance to the three stresses (Badu-Apraku et al. 2013a, b, c). Furthermore, genes for low N and/or drought tolerance from selected extra-early inbred lines were introgressed into the drought-tolerant, *Striga*-resistant, and low-N-tolerant extra-early maturing populations undergoing the recurrent selection programs to enhance the levels of tolerance of the populations and the derived cultivars to multiple stresses.

21.3 Releases of Maize Varieties in WCA

In collaboration with the NARS of WCA, a total of 41 open-pollinated early and extra-early varieties and hybrids have been released and registered in Nigeria, Ghana, Mali, and Benin Republic during the period 2007–2016 (Table 21.1) following extensive multilocational and on-farm trials in the respective countries. Two extra-early hybrids Ife Hybrid 5 and Ife Hybrid 6, with genes that can tolerate drought during the flowering and grain-filling periods, *Striga hermonthica* parasitism, and low soil nitrogen, were released by the National Variety Release Committee (NVRC) of Nigeria in 2013. This was the first report of the availability of extra-early

Table 21.1 Maize varieties developed by IITA and released by NARS partners, 2007–2016

No.	Release name	IITA name	Year of release	Cultivar type	Releasing institutions	Maturity	Yield range (kg ha^{-1})	Suitable agroecologies[a]	*Additional traits*[b]
Nigeria									
1	Sammaz 27	EV DT-W 99 STR	2009	OPV	IAR/IITA	Early	4500–5500	SGS and SS	STR
2	Sammaz 28	TZEE-Y Pop STR C_3	2009	OPV	IAR/IITA	Extra-early	4000–5000	SGS and SS	STR
3	Sammaz 29	2000 Syn EE-W STR	2009	OPV	IAR/IITA	Extra-early	4000–5000	SGS and SS	STR
4	Sammaz 32	99 TZEE-Y Pop STR QPM C_0	2011	OPV	IAR/IITA	Extra-early	4000–5000	SGS and SS	DT and STR and QPM
5	Sammaz 33	2000 Syn EE-W STR QPM C_0	2011	OPV	IAR/IITA	Extra-early	4000–5000	SGS and SS	DT and STR and QPM
6	Sammaz 35	2000 EV DT-Y STR C4	2011	OPV	IAR/IITA	Early	4500–5500	SGS and SS	STR
7	Ife-Maizehyb5	TZEEI 29 × TZEEI 21	2013	Hybrid	IAR and T/IITA	Extra-early	5000–6000	SGS and SS	LNT, DT, and STR
8	Ife-Maizehyb6	TZEE-W Pop STR C_5 × TZEEI 6	2013	Hybrid	IAR and T/IITA	Extra-early	4500–5500	SGS and SS	LNT, DT, and STR
9	Sammaz 41	TZEI 124 × TZEI 25	2014	Hybrid	IAR/IITA	Early	5000–7000	NGS and SS	DT and LNT and STR
10	Sammaz 42	TZE-Y Pop DT STR × TZEI 13	2014	Hybrid	IAR/IITA	Early	5000–7000	NGS and SS	STR and DT and LNT
11	Sammaz 46	TZEI 60 × TZEI 86	2016	Hybrid	IAR/IITA	Early	7500–9500	NGS and SS	DT and LNT and STR
12	Sammaz 47	ENT 3 × TZEI 65	2016	Hybrid	IAR/IITA	Early	8000–10000	NGS and SS	DT and LNT and STR
13	Sammaz 48	2011 TZE-W DT STR Synthetic	2016	OPV	IAR/IITA	Early	5500–7500	NGS and SS	DT and LNT and STR
14	Sammaz 53	TZEE-W STR 104 BC2	2017	OPV	IAR/IITA	Extra-early	7500–8500	SGS and SS	LNT and STR
15	Sammaz 54	2013 TZEE-W Pop DT STR	2017	OPV	IAR/IITA	Extra-early	7000–8000	SGS and SS	LNT and STR

Benin									
1	Ku Gnaayi	2000 Syn EE-W	2007	OPV	IITA/INRAB	Extra-early	2500–3500	SS	DT and STR
2	Mougnangui	EV 97 DT STR W	2007	OPV	IITA/INRAB	Early	3000–4000	SGS and SS	DT and STR
3	2000 EV DT STR QPM-Y	2000 EV DT STR QPM-Y	2014	OPV	IITA/INRAB	Early	3000–4000	SGS and SS	DT, STR, and QPM
4	2008 SYN EE DT STR W	2008 Syn EE DT STR W-Y	2015	OPV	IITA/INRAB	Extra-early	2500–3500	SGS and SS	DT and STR
5	2008 SYN EE DT STR-Y	2008 Syn EE DT STR Y-Y	2015	OPV	IITA/INRAB	Extra-early	2500–3500	SGS and SS	DT and STR
6	TZEE POP STR QPM Y	TZEE Pop STR QPM-Y	2015	OPV	IITA/INRAB	Extra-early	2500–3500	SGS and SS	DT and STR
7	TZEE POP STR QPM-W	TZEE Pop STR QPM-W	2015	OPV	IITA/INRAB	Extra-early	2500–3500	SGS and SS	DT and STR
8	2008 EV DT STR-Y	2008 EV DT STR-Y	2015	OPV	IITA/INRAB	Early	3000–4000	SGS and SS	DT and STR
9	TZE POP DT STR QPM-W	TZE Pop DT STR QPM-W	2015	OPV	IITA/INRAB	Early	3000–4000	SGS and SS	DT, STR, and QPM
Ghana									
1	Bantam	TZEE-Y Pop STR QPM C_0	2010	OPV	CRI/IITA	Extra-early	4500–4700	SGS, CS, F, FT, and SS	STR and QPM
2	Omankwa	TZE-W Pop DT STR QPM C_4	2010	OPV	CRI/IITA	Early	4500–4700	SGS, CS, F, FT, and SS	DT, STR, and QPM
3	Aburohemaa	EV DT-W 99 STR QPM C_0	2010	OPV	CRI/IITA	Early	4500–4700	SGS, CS, F, FT, and SS	DT, STR, and QPM
4	Wang Taa	TZE-Y DT STR C_4	2012	OPV	SARI/CRI/IITA	Early	4500–4700	SGS, CS, F, FT, and SS	DT and STR

(continued)

Table 21.1 (continued)

No.	Release name	IITA name	Year of release	Cultivar type	Releasing institutions	Maturity	Yield range (kg ha^{-1})	Suitable agroecologies[a]	*Additional traits*[b]
5	Bihilifa	TZE-W DT STR C_4	2012	OPV	SARI/CRI/IITA	Early	4500–4700	SGS, CS, F, FT, and SS	DT and STR
6	Kunjor-wari	TZE-Y Pop DT STR C_4 × TZEI 17	2015	Hybrid	SARI/CRI/IITA	Early	5500–5700	SGS, CS, F, FT, and SS	DT, LNT, and STR
7	Suhudoo	TZE-W Pop DT STR C_4 × TZE 7	2015	Hybrid	SARI/CRI/IITA	Early	5500–5800	SGS, CS, F, FT, and SS	DT, LNT, and STR
8	Afriyie	TZEEI 6 × TZEEI 4	2015	Hybrid	CRI/SARI/IITA	Extra-early	5500–5700	SGS, CS, F, FT, and SS	DT, LNT, and STR
9	Obotantim	TZEEI 15 × TZEEI 24	2015	Hybrid	CRI/SARI/IITA	Extra-early	5500–5800	SGS, CS, F, FT, and SS	DT, LNT, and STR
10	Nkabom	TZEE-Y Pop STR C5 × TZEEI 82	2015	Hybrid	CRI/SARI/IITA	Extra-early	5000–5200	SGS, CS, F, FT, and SS	DT, LNT, and STR
11	CSIR-Similenu	TZEI 60 × TZEI 86	2017	Single-cross hybrid	CRI/SARI/IITA	Early	6.0–6.50	SGS, CS, F, FT, and SS	DT, LNT, and STR
12	CSIR-Denbea	TZEI 124 × TZEI 25	2017	Single-cross hybrid	CRI/SARI/IITA	Early	6.5–7.0	SGS, CS, F, FT, and SS	DT, LNT, and STR
13	CSIR-Kom-naaya	TZEE-W Pop STR C5 × TZEEI 29	2017	Topcross hybrid	CRI/SARI/IITA	Extra-early	5.5–6.0	SGS, CS, F, FT, and SS	DT and STR
14	CSIR-Wang-Basig	TZEE-W Pop STR C5 × TZEEI 21	2017	Topcross hybrid	CRI/SARI/IITA	Extra-early	5.5–6.0	SGS, CS, F, FT, and SS	DT and STR
Mali									
1	Jorobana	EV DT 97 W STR C_1	2009	OPV	IER/IITA	Early	5000–6000	SGS and SS	DT
2	Brico	TZEE-Y Pop STR C_4	2010	OPV	IER/IITA	Extra-early	4000–5000	SS	DT and STR

4	Sanu	TZEI 60 × TZEI 86	2012	Hybrid	IER/IITA	Early	5000–6000	SGS and SS	DT, LNT, and STR
5	TZE-Y DT STR C4 × TZEI 13	TZE-Y DT STR C_4 × TZEI 13	2012	Hybrid	IER/IITA	Early	5000–6000	SGS and SS	DT, LNT ,and STR
6	Dilika	TZEI 24 × TZEI 17	2014	Hybrid	IER/IITA	Early	5000–7000	SS	DT, LNT, and STR
7	Apraku	TZEI 11 × TZEI 23	2014	Hybrid	IER/IITA	Early	7000–8000	SS	DT, LNT, and STR
8	Sahel Kaba	TZEE-W Pop DT STR C_5 × TZEEI 6	2014	Hybrid	IER/IITA	Early	5000–6000	SGS and SS	DT and STR
9	Sosani	TZEE-Y Pop DT STR C_5 × TZEEI 58	2014	Hybrid	IER/IITA	Early	5000–6000	SGS and SS	DT and STR
10	TAMALAKA	TZEI 124 × TZEI 25	2014	Hybrid	IER/IITA	Early	6000–7000	SS	DT and STR
11	KIBAN	EV DT-Y 2000 STR	2015	OPV	IER/IITA	Early	4000–5000	SS	DT and STR

[a] SGS = southern Guinea savanna; SS = Sudan savanna; NGS= northern Guinea savanna; CS= coastal savanna; F= forest; FT= forest savanna transition

[b] STR = *Striga* resistance; DT= drought tolerant; QPM= quality protein maize; LNT= low nitrogen tolerant

hybrids with combined tolerance to drought that occurs at the flowering and grain-filling periods (most critical stage of grain production), resistance to *Striga*, and tolerance to low N. In addition, two early-maturing hybrids, SAMMAZ 41 (TZE-Y Pop DT STR × TZEI 13) and SAMMAZ 42 (TZEI 124 × TZEI 25), were released by the NVRC in December 2014. In 2016, two additional early white hybrids, ENT 3 × TZEI 65 and TZEI 60 × TZEI 86, were also released in Nigeria. Also, in collaboration with the national maize program of Mali and the Faso Kaba Seed Company, seven hybrids (TZEI 60 × TZEI 86, TZE-Y DT STR C_4 × TZEI 13, TZEI 24 × TZEI 17, TZEI 11 × TZEI 23, TZEE-W Pop DT STR C_5 × TZEEI 6, TZEE-Y Pop DT STR C_5 × TZEEI 58, TZEI 124 × TZEI 25) and three open-pollinated varieties (EV DT 97 W STR C_1, TZEE -Y Pop STR C_4, and EV DT-Y 2000 STR) were released in Mali between 2012 and 2015. The hybrids possess genes that can tolerate drought during the flowering and grain-filling periods, *Striga hermonthica para*sitism, and low soil nitrogen. Five early- and extra-early maturing drought-tolerant and *Striga*-resistant hybrids, TZE-Y Pop DT STR × TZEI 17, TZE-W Pop DT STR × TZEI 7, TZEE-Y Pop STR C_5 × TZEEI 82, TZEEI 6 × TZEEI 4, and TZEEI 15 × TZEEI 24, were released in Ghana in 2015. Nine early and extra-early *Striga*-resistant and drought-tolerant maize varieties have been released in Benin Republic. Among the extra-early and early open-pollinated varieties released in Nigeria, 2000 Syn EE-W, 99 TZEE-Y STR, and EV DT-W 99 STR have been widely adopted in the Guinea and Sudan savanna zones with the Premier Seed Company Nigeria Ltd, Maslaha Seed Co., and Seed Project Co. actively involved in the production of the commercial seed of the varieties. The varieties are presently covering several hectares of land in Northern Nigeria where they are playing a very important role in filling the hunger gap in July. The varieties have also been released in Togo, Chad, and Senegal. The extra-early *Striga*-tolerant variety, 2000 Syn EE-W, and the early drought-tolerant and *Striga*-resistant white variety, EV DT 97 STR C_1, developed in our program, have also been released in Benin, Togo, Chad, and Mali. Furthermore, EV DT-W 99 STR released in Nigeria is presently the most widely marketed open-pollinated variety by the largest seed company in Nigeria, Premier Seed Company. The two extra-early, drought-tolerant, and *Striga*-resistant QPM varieties, TZEE-W STR QPM and TZEE-Y STR QPM, and the early *Striga*-resistant and drought-tolerant variety, TZE-W Pop DT STR QPM, are among the latest IITA varieties released in Ghana and Nigeria.

A study of total annual production across the eight countries between 1990 and 2014 showed a mean grain-yield increase from 1.2 t/ha in 1990 to 1.6 t/ha in 2014, an increase of 36%, although there were large variations among countries. The greatest yield/ha increases were noted in Mali (110%), Côte d'Ivoire (66%), Nigeria (42%), Ghana (35%), and Senegal (27%) and the lowest in Cameroon (8%), Togo (14%), Chad (16%), and Burkina Faso (17%).

21.4 Impact of Maize Research in WCA

As a result of the increasing scarcity of funds in WCA, it was imperative to justify further investments in maize research in the sub-region by demonstrating the early impact of the research (Badu-Apraku et al. 2012a, b). WECAMAN therefore sponsored NARS social scientists from Burkina Faso, Togo, Benin, Ghana, Nigeria, Cameroon, Côte d'Ivoire, and Mali to attend impact assessment training workshops organized by Purdue University and INSAH, a regional NGO. After these workshops financial support was provided to undertake impact studies in these countries.

Although increased maize production in the sub-region resulted from the collective effort of many players, WECAMAN was a central component of the team effort. Results of impact studies funded by the Network in most of the member countries clearly justified the investment in maize research, training, and development activities in the sub-region (Badu-Apraku et al. 2003, 2004). For example, in Burkina Faso, an economic model used to determine the impact of maize research and extension in improving social welfare showed an IRR of 35.3% during the period from 1982 to 1998 (Laraba 2001; Badu-Apraku et al. 2012a, b). The study revealed a high rate of adoption of improved and released maize varieties.

In the Northern Province of Cameroon, a farm-level survey of 345 farm households in 16 villages showed that maize was quickly replacing sorghum in the diet and cropping systems of rural households. This was found to be linked to several factors, including mainly early maturity, high yield, better taste and color, high market prices, and availability during the hunger period (Enyong et al. 1999). Results indicated that maize technology adoption rates, social rates of return, and social gains from the maize research and extension had been positive and that investment in maize research and development during the period was justified. WECAMAN had clearly stimulated national scientists to solve production problems with significant returns on investment in maize programs estimated to be 74% in Ghana, 78% in Burkina Faso, and over 100% in Mali over the past decade (Oehmke 1997; Badu-Apraku et al. 2011).

The increasing availability of new maize varieties adapted to the savanna zones, with high-yield potential and increased tolerance to multiple biotic and abiotic stresses together with fertilizer subsidies and improved infrastructure and support services, changed the status of maize from a minor crop in the 1970s to one of the most important food and cash crops in the 1990s (Smith et al. 1994; Badu-Apraku et al. 2012a, b). However, there was little empirical evidence on the impact of maize research in WCA. The economic and poverty reduction impacts of maize research were estimated in Benin, Burkina Faso, Cameroon, Côte d'Ivoire, Ghana, Guinea, Mali, Nigeria, Senegal, and Togo, which together account for about 85% of maize production in WCA, using data on variety release, adoption, and yield gains as well as research investments (Alene et al. 2009). Both IITA and WECAMAN contributed to the recorded impact of maize in the sub-region.

Future research accounting for the non-yield benefits of modern varieties, such as early-maturing drought-tolerant varieties that avert possible hunger and QPM varieties that improve nutrition and health, is likely to reveal even greater benefits from maize research. The results suggest that poverty in the region would have been substantially worse had there been no research to increase, or at least maintain, maize yields in the face of pest and disease pressure, soil fertility decline, and area expansion onto marginal lands. There is no sign of any decline in the benefits from modern varieties of maize in the region, suggesting that maize research will continue to be a factor in reducing poverty. If there is any decline in variety adoption and benefits, this would likely be due to constraints outside the research system. For example, the benefits from maize research stagnated during the late 1990s when area planted to maize declined, and the area under modern varieties stagnated after the removal of fertilizer subsidies and the collapse of support services. High fertilizer prices and poor access to credit together reduce the profitability of modern varieties and limit further adoption. For Nigeria, which actually accounted for much of the decline in maize area during the late 1990s, the fertilizer liberalization policy adopted in 1996 effectively ended the heavy subsidies of up to 85% and resulted in a sharp decline in fertilizer use from over 500,000 t in 1994 to about 100,000 t in 1999 (Bumb et al. 2000; Morris et al. 1999; Akinwale et al. 2014). The evidence points to the fact that the impacts of research investments are conditioned by farmers' physical and economic access to a number of complementary inputs. High rates of return to agricultural research are difficult to sustain in an environment where farmers do not have accessible or affordable inputs.

The development and adoption by farmers of high-yielding, disease- and pest-resistant maize varieties and crop production technologies specifically adapted to the various agroecologies and socioeconomic situations and the enhancement of the research capacity of NARS through training courses and workshops, research project development and implementation, scientific monitoring tours, consultation visits, and visiting scientist scheme have been central to the green revolution in WCA. Trends in land area under maize, total maize production, and yield per unit land area have shown dramatic increases in most of the WECAMAN member countries. Total maize production in the sub-region has increased from about 2.74 million tons in 1980 to 10.5 million tons in 2000, a 384% increase. Maize production has caught up with or surpassed the traditional staple crops, sorghum, and millet in much of the savanna areas of WCA (Fig. 21.1). Independent impact studies conducted in most of the member countries without reference to the FAO data showed that maize was quickly replacing sorghum in the diet and cropping systems of the rural dwellers. Also, the impact studies showed that some of the countries in the sub-region experienced high annual growth rates in maize production far above the 3% population growth observed for the sub-region as a whole.

Estimated annual growth rates in total maize production for the period covered in our study were Benin 9.5%, Burkina Faso 4.7%, Cameroon 8.2%, Côte d'Ivoire 3.7%, Ghana 13.3%, Mali 3%, Nigeria 27.6%, and Togo 18.9%. Results of the impact studies (Laraba 2001; Phillip 2001; Sanogo et al. 2001; Manyong et al. 2000; Enyong et al. 1999; Awotide and Tonsta 2011) clearly justified the investment

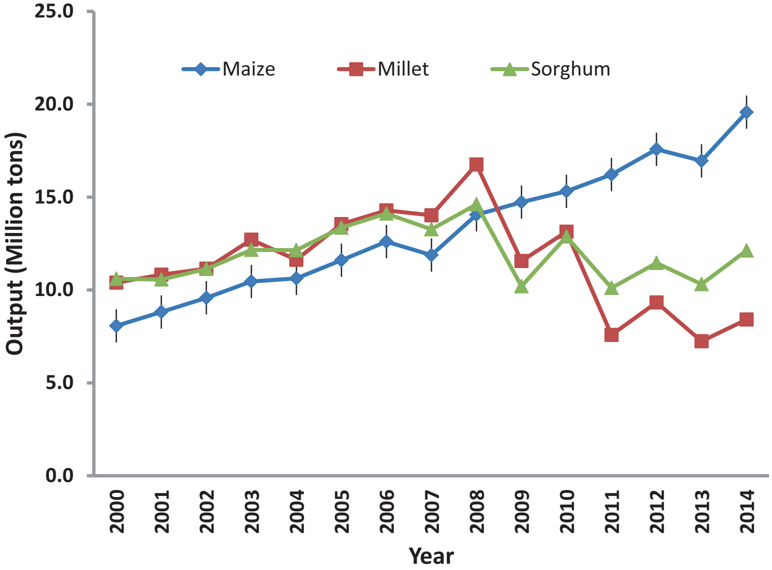

Fig. 21.1 Total maize (with standard error), millet, and sorghum grain production in eleven West and Central African countries, 2000–2014 (Source: FAO Statistics 2014)

in maize research, training, and development activities in the sub-region. The most recent studies showed even greater growth rates in total maize production with the production growth rate ranging from 58.23 in Mali to −6.28 in Cape Verde. Although the adoption of improved varieties has progressed well in the sub-region, there is a need for accelerated pace of adoption if the revolution is to be sustained. Average yield in the sub-region has only increased modestly from the long-standing <1.0 t ha^{-1} to about 1.3 t ha^{-1}. Average yield in researcher managed trials is about 6 t ha^{-1}.

Therefore, the yields obtained in farmers' fields are far from the potential yield of maize in WCA (Fakorede et al. 2001; Olaniyan 2015). A major factor that has seriously constrained a full-blown green revolution in WCA therefore is the gap between research and farmers' yields. Factors responsible for the differences in yield between research and farmers' fields are lack of availability of improved seed, weeds, pests, diseases, low soil nutrient supply, damage by S*triga*, low plant density, late planting, late first weeding, and several other factors that constitute poor crop management practices (Carsky and Kling 1997; Fakorede et al. 2001; Olaniyan 2015). Realization of attainable maize yields must, therefore, combine availability of good-quality seed, appropriate variety, and soil management, along with appropriate and sustainable crop management practices. Some of the open-pollinated and hybrid cultivars released to WCA farmers under the DTMA Project during the period 2007–2013 are presented in Table 21.2. The rate of adoption of improved early and extra-early maize cultivars in the savannas has gone far beyond the expectation of WECAMAN partners and has revolutionized maize production in WCA

Table 21.2 Maize production trends through adoption of improved technologies in selected WCA countries, 1990–1992 and 2012–2014

Country	Area harvested ('000 ha)			Production ('000 t)			Yield (t/ha)		
	1990–1992	2012–2014	% increase	1990–1992	2012–2014	% increase	1990–1992	2012–2014	% increase
Benin	464	971	109	433	1285	196	0.9	1.3	41
Burkina Faso	196	836	326	305	1524	399	1.6	1.8	17
Cameroon	276	883	219	465	1665	258	1.7	1.9	8
Chad	48	319	553	54	402	635	1.1	1.3	16
Côte d'Ivoire	397	318	−19	498	665	33	1.3	2.1	66
Ghana	560	1028	83	738	1825	147	1.3	1.8	35
Guinea	117	510	332	124	655	426	1.1	1.3	22
Mali	182	674	269	215	1653	668	1.2	2.5	110
Nigeria	5156	5787	12	5806	9302	60	1.1	1.6	42
Senegal	104	150	44	116	214	83	1.1	1.4	27
Togo	275	712	159	264	783	195	1.0	1.1	14
Total/mean	707	1108	189.7	820	1816	282	1.2	1.6	36

Compiled from several sources (Badu-Apraku et al. 2012a, b; FAOSTAT, 2014)

(Fakorede et al. 2003; Onyibe et al. 2003, 2006). With the availability of these cultivars, green maize is now produced throughout the year in most of WCA, using hydromorphic soils or irrigation during the dry season.

In a study to determine farmers' adaptations to climate change over the past 20 years, the respondents indicated that they had made adjustments in their farming activities in response to the perceived changes in temperature and rainfall (Ndamani and Watanabe 2016). Although many farmers perceived changes in temperature, about 46% had not undertaken any adaptation measures. Among those that did, most of the respondents took up measures in order to adapt to decreasing volumes or changes in the timing of rainfall. Only 15% of the 184 farmers who perceived changes in rainfall did not take up any form of adaptation. The main adaptation methods were the use of drought-tolerant early-maturing varieties (52%) and a shift in dates of planting (47%). The high use of these two adaptation measures could be attributed to activities of two projects, the Drought-Tolerant Maize for Africa (DTMA) and Promoting Sustainable Agriculture in Borno State (PROSAB), in the study area. These projects identified drought as one of the main problems of farming in the study area and have assisted farmers with early-maturing drought-tolerant varieties of some crops, particularly maize (Tambo and Abdoulaye 2012). As a result of the availability of drought-tolerant and early-maturing varieties, most of the farmers are able to delay the time of planting until there is stable rainfall.

The generation and adoption of improved, higher-yielding maize varieties is one of the outstanding success stories of technological change in food crop production in WCA countries. The increasing availability of new maize varieties adapted to the savanna zones, with high-yield potential and increased tolerance to multiple biotic and abiotic stresses together with fertilizer subsidies and improved infrastructure and support services, has changed the status of maize from that of a minor crop in the 1970s to one of the most important food and cash crops from the 1990s.

As a result of research undertaken by IITA, DTMA, WECAMAN, NARS, and other institutions, a large number of improved maize varieties have been developed, and the area planted to these varieties continues to expand. Studies show that in 2005, of the 7 million ha planted to maize in nine WCA countries, over 4 million, representing about 60% of the area, had been planted to improved varieties. Over half of this impact has been attributed to maize research.

21.5 Gains in Productivity and Impacts of Stress-Tolerant Maize Varieties and Hybrids in West Africa

Since the inception of the Drought-Tolerant Maize (DTMA) Project in 2007, there have been successes in the development and dissemination of drought-tolerant maize varieties (DTMVs) including the multiple stress-tolerant early and extra-early varieties developed under the DTMA Project. About 160 DTMVs have been developed between 2007 and 2014 (IITA 2016b). Most of these varieties have been successfully disseminated to maize farmers in 13 African countries including

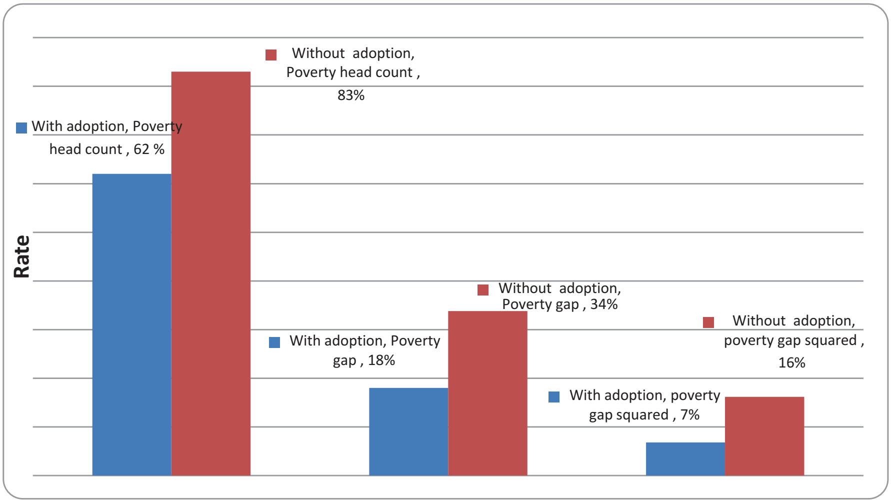

Fig. 21.2 Poverty headcount, poverty gap, and poverty gap squared with and without adoption (Source: Abdoulaye et al. 2016.)

Nigeria. Awotide et al. (2015) conducted a household survey in Nigeria from November 2014 to February 2015 to examine the productivity and welfare impacts of adoption of DTMVs. Results indicated that adoption of the DTMVs resulted in a 268 kg/ha gain in maize productivity and ₦ 10683 per annum in welfare benefits as measured by the gain in annual per capita food expenditure. In terms of poverty reduction, a 21% reduction in poverty was observed as a result of adoption (Fig. 21.2). Overall, an estimated 370,000 households (equivalent to 2.7 million individuals) managed to move out of poverty as a result of adoption of the DTMVs. Further estimated impacts on productivity gains suggested that the program was more beneficial to female-headed households compared to male-headed households. However, estimated results on poverty outcomes suggested that the project targeted better-off female-headed households. In the future, there needs to be a more targeted intervention for addressing disadvantaged groups such as poor female-headed households. In particular, constraints related to DTMV seed access and other barriers associated with adoption have to be addressed.

It may be concluded that the availability of the early and extra-early varieties and hybrids has created niches for maize production, consumption, and improved food security in WCA and has resulted in improvements in the productivity of maize, income, and well-being of people in the sub-region. The release and commercialization of the stress-tolerant early- and extra-early maturing varieties developed in IITA and promoted by the NARS and the private sector have contributed to phenomenal increase in maize production and productivity through movement of maize into new frontiers, replacing sorghum and millet in the savanna zones of WCA (Fig. 21.1) resulting in the high annual growth rates of maize production as summarized (Fig. 21.3).

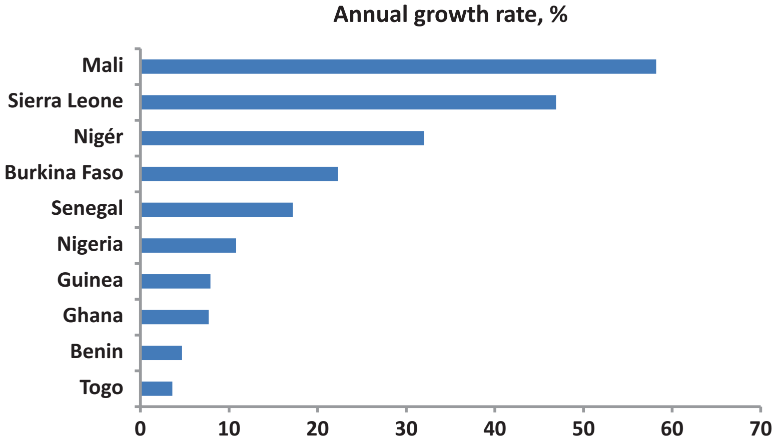

Fig. 21.3 Annual growth rates of maize production in ten West African countries (Source: Abdoulaye et al. 2016)

Linear regression of production on years gave the statistically significant equation:

$$\hat{Y} = 7.086 + 0.765x, \text{with } R^2 = 0.975.$$

In other words, maize production in WCA, on average, has been increasing at the rate of 0.765 million ton per annum since 2000. In the earlier portion of this period, maize production lagged behind millet and sorghum until about 2007. Annual growth rate at the early stage was 0.72 million ton. At the latter stage, however, annual growth rate was 0.93 million ton. Maize production during this latter period was significantly higher than millet and sorghum production. During the latter part of this period, early and extra-early maize varieties were being adopted and cultivated in areas where the cropping season was regarded as too short for maize production.

21.6 Success Story of Collaboration Between Mali and DTMA: When Partnerships Work, Farmers Benefit

For the past 9 years, DTMA/STMA and Mali have worked together to generate, promote, and deliver adapted drought-tolerant maize varieties and hybrids to farmers. This partnership has led to the release of seven open-pollinated drought- and *Striga*-resistant varieties and ten hybrids by Malian scientists in collaboration with IITA (Table 20.9). The project has relied on the national agricultural research and extension system of Mali—including IER and Institut Polytechnique Rural de Formation et de Recherche Appliquée (IPR/IFRA)—to promote the adoption of

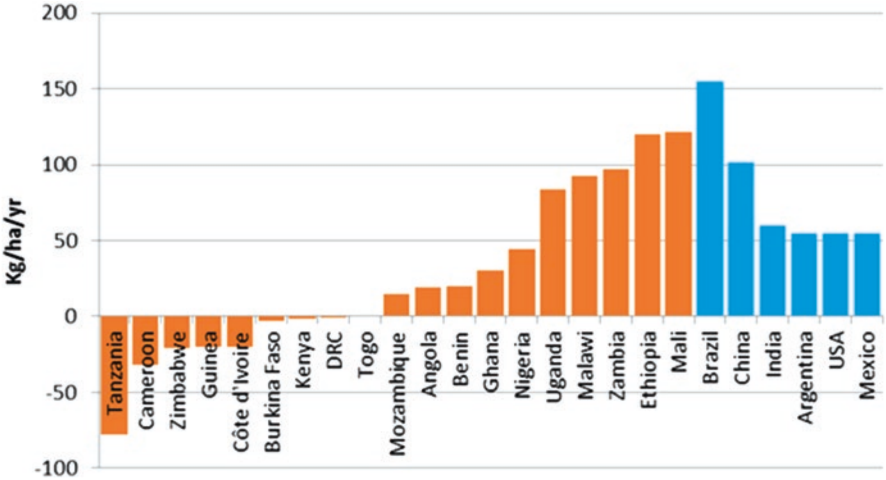

Fig. 21.4 Productivity gains in the top 20 maize-growing countries in sub-Saharan Africa compared to other major global maize-producing countries, 2000–2013 (After Abate et al. 2015)

improved varieties through national and local communication and extension networks, as well as worked with local seed companies such as Faso Kaba, Comptoirs 2000, Coprosem, Coop Kolokoani, and DNA to actively scale up and distribute seeds of improved drought-tolerant maize hybrids and OPVs.

Additionally, through the project, 12 IITA-developed drought-tolerant early-, extra-early, and intermediate-maturing hybrids (Table 21.1), as well as 6 drought-tolerant OPVs, have been released in Mali and are now in the hands of farmers or seed companies and community seed producers. These efforts have contributed to increased maize productivity in Mali, making the country one of the top maize producers in Africa today (Fig. 21.4).

21.7 Challenges

The predominance of maize in many farming systems and diets in WCA implies that yield gains have the potential to jump-start a green revolution. Although considerable progress has been made toward achieving this potential, food insecurity for millions of rural households persists even where progress in maize production has been achieved. With domestic maize production often not keeping up with the requirements of expanding urban populations for food, there is increased consumption of rice and wheat, much of which is imported. At the same time, the demand for maize for industrial use and as a feed for livestock continues to grow rapidly. International and regional research needs to continue to support national programs through regional alliances that build on the comparative advantages of the NARS in developing full scientific capabilities in WCA. Many technical, ecological, institutional, and policy issues needed to be addressed if maize is to contribute its expected share to the alleviation of poverty in WCA. A vibrant and efficient functioning seed sector is required to ensure the wide distribution of the new multiple stress-tolerant varieties needed to increase farmers' incomes, reduce food prices for consumers, and improve the profitability and sustainability of the seed industry.

Although the West African maize seed sector is being strengthened through the emergence of local seed businesses, it is still limited by inadequate access to improved seeds for farmers, and most countries in the region still have difficulties in coping with seed supply, especially during emergencies. Despite the tremendous progress made in developing and promoting maize varieties, over one-third of the maize area in WCA is still planted to low-yielding varieties (Alene et al. 2009). At the same time, many farmers continue to use farm-saved seeds because improved varieties are either not accessible or are regarded as too costly. Since maize is an open-pollinated crop, farm-saved seeds can quickly lose its genetic purity. Farmers who wish to grow improved varieties must replace their seeds regularly, annually, for hybrid varieties and every 2–3 years for OPVs. The adoption of improved maize varieties is strongly conditioned by the policies that affect access to knowledge, input supplies, credit, and market infrastructure. High rates of return to agricultural research are difficult to sustain in an environment where inputs are either not accessible to farmers or not affordable. Integrated knowledge access systems, credit, and input supply systems with an improved market infrastructure are needed to achieve a greater impact from maize research and technology development that is relevant to end users' needs.

Looking to the future, maize will remain crucial for food security in sub-Saharan Africa. The predominance of the crop in many farming systems and diets implies that yield gains have the potential to jump-start a Green Revolution. Although considerable progress has been made towards achieving this potential, food insecurity for millions of rural households persists even where progress in maize production has been achieved. With domestic maize production often not keeping pace with the requirements of expanding urban populations for food, there is increased consumption of rice and wheat, much of which is imported. At the same time, the demand for maize for industrial use and as a feed for livestock continues to grow rapidly.

International and regional research needs to continue to support national programs through regional alliances that build on the comparative advantages of the NARS in developing full scientific capabilities in WCA. Many technical, ecological, institutional, and policy issues needed to be addressed if maize is to contribute its expected share to the alleviation of poverty in WCA. These include the following:

- Ongoing enhancement of NARS capacity to develop and transfer technology through training, infrastructure development, use of biotechnology, geographic information systems, other new tools, and innovative approaches
- Development of micronutrient dense and quality protein maize varieties that are stress (drought, low soil nitrogen, *Striga*, stem borers, and nutrient depletion) tolerant, to improve the income-generating capabilities and nutritional status of farmers

- Increasing the capacity of farmers and farmers' organizations to drive the research agenda and use the products of research
- Development of sustainable farming systems that increase the productivity of land and labor in the face of climate change and land degradation
- Ensuring that the varietal release processes across countries and agroecological zones are efficient and effective
- Developing effective partnerships between the public and private sectors in the development of effective seed production and distribution systems
- Ensuring that input and output markets and the rural infrastructure that support them are capable of providing farmers with access to efficient services
- Developing market information systems to guide and link farmers, traders, end users, input dealers, and policymakers
- Development of existing and new maize technologies for new products, specific markets, production areas, and processing methods to diversify the utilization of maize
- Stimulation of regional trade by promoting appropriate agro-enterprise
- Advocacy in the development of appropriate policy reforms for sustained maize production and productivity

In summary, maize is widely grown in many agroecological zones in West and Central Africa. It is a highly suitable crop, especially well adapted to the savanna zones with their monomodal rainfall distribution. The southern Guinea savanna (SGS) and northern Guinea savanna (NGS) are characterized by adequate moisture, relatively low disease pressure, high solar radiation, and low night temperatures, all favoring maize production. Traditionally, maize had been cultivated as a minor crop in the Guinea savanna zones, grown near household compounds, where it received the regular application of household refuse and organic manure. However, the availability of early and extra-early varieties has subsequently pushed the boundaries of suitability, and maize is now widely grown in the drier areas of the NGS and Sudan savanna (SS) as well as to a lesser extent in the more humid areas of the derived savanna (DS) and humid forest (HF). At the same time, increased availability of inorganic fertilizers has encouraged a considerable expansion in the area planted to maize, making maize an increasingly important cash crop. Over 50% of the maize is now grown in the savannas, whereas in the 1970s it was only a minor crop.

By 1990, nearly 9 million ha of maize were being cultivated in WCA with average grain yields of just over 1 t/ha, varying from 0.9 t/ha in Benin to 1.7 t/ha in Cameroon (FAOSTAT 2014). Nigeria was responsible for producing over 50% of the total grain output with other significant contributions also coming from Congo (10%), Ghana (9%), Cameroon (7%), and Côte d'Ivoire (6%). Between 1980 and 2000, the total maize harvested increased from less than 3 million to more than 10 million t (Fakorede et al. 2003; Badu-Apraku et al. 2012a, b), although much of this increase was due to an increased area under cultivation rather than to higher productivity per unit land area. For instance, Nigeria increased its area under maize by more than 2.5 million ha during the 1990s, which increased maize grain production from 1.8 million to 5.4 million t. Many other countries in the sub-region experienced similar increases. Much of this expansion occurred northward into drier areas where there were fewer serious diseases or pest problems, with maize often displacing sorghum and millet. The development and increased availability of early (90–95 day) and extra-early (80–85 day) varieties developed and disseminated in large part through Semi-Arid Food Grain Research and Development (SAFGRAD) and WECAMAN/IITA made this expansion possible. This wide acceptance of maize was due in part to its versatility, providing a food source early during the hungry period, when it is consumed as green maize as well as grain for making flour for traditional foods for the rest of the year. There was also an increasing demand for maize for industrial uses, such as processed food, livestock feed, and malting for beer.

Over 85% of the rural population of WCA now grow maize because of its ability to fit into the different farming systems and its great potential for increasing yield under improved management practices compared with other grain crops. The new maize varieties made available to farmers have had a considerable impact including a large expansion in the maize area at the expense of sorghum and millet. This has been due to the better response of maize to fertilizer and the availability of high-yielding, disease- and pest-resistant varieties, which have had a major impact in stimulating production, especially into the savanna areas since the 1980s. The production of early and extra-early maize varieties that can be consumed either as green maize or grain has helped in addressing seasonal and transitory food insecurities. At the same time, increased maize production has helped to overcome chronic food insecurity, increasing the availability of food for the most vulnerable groups including women, children, and the poor. The promotion of maize, which is cultivated by rich and poor alike, is proving to be an important step in achieving food security in WCA.

21.8 Conclusions

A large rural population of SSA now grows maize because of its ability to fit into the different farming systems and potential for increasing yield under improved management practices compared with other grain crops. The new maize varieties available to farmers have had a considerable impact including a large expansion in the maize area at the expense of sorghum and millet in the savannas. This is largely due to the better response of maize to fertilizer and the availability of high-yielding, multi-stress-tolerant varieties, which have had a major impact in stimulating production, especially into the savanna areas since the 1980s. The production of early and extra-early maize varieties that can be consumed either as green maize or grain has helped in addressing seasonal and transitory food insecurities, has increased maize production, and has helped to overcome chronic food insecurity, increasing the availability of food for the most vulnerable groups. However, a vibrant and efficient functioning seed sector is required to ensure the wide distribution of the new multiple stress-tolerant varieties needed to increase farmers' incomes, reduce food prices for consumers, and improve the profitability and sustainability of the seed industry. The results of the impact assessment study showed that adoption of improved maize varieties on productivity and household welfare outcomes (food security and poverty) in rural Nigeria shows that adoption improves productivity and welfare outcomes of adopters significantly. The adoption of improved maize varieties increased maize productivity and per capita expenditure by 32% and 22%, respectively. It was observed that the prevalence of subjective food insecurity would have been higher by 6% and 50%, respectively, without adoption of improved maize varieties. The results of this paper revealed that investments and policy measures to increase and sustain adoption of improved maize cultivars are important in agriculture-based economies including Nigeria.

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Chapter 22
Future Outlook and Challenges of Maize Improvement

22.1 Establishment of the West and Central Africa Collaborative Maize Network (WECAMAN)

Maize is one of the most important staple crops in sub-Saharan Africa. Its role in the nutrition and food security of the peoples of West and Central Africa (WCA) has increased tremendously during the last four decades. Consequently, research to improve the yield potential has been high in the agricultural agenda in the sub-region, initially on an individual country basis. However, most of the constraints to maize production were too formidable for individual countries to overcome. Because the constraints were crosscutting, there was an opportunity to pool the available resources to tackle the constraints and minimize duplication of efforts. Unfortunately, the different national governments of the sub-region did not really come together as an entity to address this and other agricultural research problems. The establishment of IITA in Nigeria in 1967 provided an avenue and a unique opportunity for establishing such an entity. The Institute's research efforts were initially limited to Ibadan and environs from where it gradually fanned out to other parts of Nigeria, moved on to other WCA countries and now to much of Africa south of the Sahara desert. Mandatorily, IITA must work in collaboration with NARS thus making it possible for the Institute, within a short time of its existence, to identify the research strengths and weaknesses of the WCA countries in particular. As had been known to the NARS researchers, IITA soon discovered that the savanna agroecology, particularly the northern Guinea savanna, had the greatest potential for maize production in WCA. IITA's scientists started maize research in the Nigeria savanna zones in 1980 and clearly targeted maize varieties of different maturities to the agroecology. Intermediate-to-late maturing varieties were available for the lowland savannas, but much of the savannas needed early and extra-early varieties, while the mid-altitude agroecology needed specific varieties, all of which, unfortunately, were not available. Therefore, breeding efforts were initiated along

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these lines, and it became necessary to cover the whole of WCA. In 1977, foreign ministers of WCA met to discuss and proffer solutions to the problem of recurrent drought which was plaguing the sub-region. One of the outcomes of the meeting was the establishment of the Semi-Arid Food Grain Research and Development (SAFGRAD) Project comprising several commodity networks, including maize. Research on early and extra-early maize was devolved on the maize network of SAFGRAD, and in 1987, the maize network became autonomous and was named West and Central Africa Collaborative Maize Research Network (WECAMAN). The Network served as an effective mechanism for all stakeholders in maize production and productivity to tackle the regional constraints from 1987 to 2007. These included national and international scientists, extension workers, farmers, seed technologists, industrialists, and policymakers.

WECAMAN's approach to maize research and development has been unique and is worthy of adoption in future endeavors for maize improvement in WCA. The strategy, achievements, and challenges of WECAMAN are highlighted in the rest of this chapter to serve as a guide into the future direction for the improvement of maize production and productivity in the sub-region. An important strategy of WECAMAN was to designate the national research programs that were relatively stronger than others in specific subject matter areas as lead centers (LCs). Constraints to maize production were identified in a participatory manner by all stakeholders and prioritized. An ad hoc research committee screened research proposals and allocated funds to the LCs for research projects to address the constraints. Technologies emanating from the research conducted in the LCs were made available to other member countries through Regional Uniform Variety Trials (RUVTs), on-farm trials, and demonstrations. Using this strategy, scientists from WECAMAN member countries identified within a short period the technologies in high demand by maize farmers in their respective countries. For example, farmers in the northern fringes of the northern Guinea and Sudan savannas could not grow maize because early and extra-early varieties that would mature in the relatively short rainy season were not available. In addition, at about the time farmers in these areas were planting the new maize crop in June/July, most food reserves were depleted, leading to a period of low food supply, referred to as the *soudre* or hunger gap. The WECAMAN coordinator/breeder and national maize scientists developed early and extra-early maize varieties that have mitigated this problem and opened new frontiers for maize production. The early and extra-early varieties are also planted by farmers in the forest zones, especially in peri-urban areas, to provide green maize before the main crop matures. The rate of adoption of improved early and extra-early maize varieties in the savannas has gone far beyond the expectation of WECAMAN collaborators and has revolutionized maize production in WCA (Onyibe et al. 2003; Fakorede et al. 2003). With the availability of these varieties, green maize is now produced throughout the year in most countries of WCA, using hydromorphic soils or irrigation during the dry season. Despite the progress made so far, the problem of recurrent drought in the savannas as well as some parts of the forest zone is far from solved. Rather, it has been aggravated by climatic change, which is now negatively impacting maize production in the sub-region (Fakorede and Akinyemiju 2003).

In addition to earliness and extra-earliness, WECAMAN scientists have developed drought-tolerant varieties, especially for the savannas but also for the second season in the forest agroecological zone.

22.2 Breeding for Stress-Tolerant Maize and Improved Agronomic Practices in West and Central Africa

The single most important factor limiting the production of maize in the savannas is recurrent drought with production worth several billion US dollars lost annually. Global warming and the accompanying drought that have increased unpredictability of the intensity and frequency of rainfall patterns call for a more effective improvement of maize yield under drought stress (Badu-Apraku and Fakorede 2013). Two strategies have been adopted since 1995 for developing drought-tolerant extra-early varieties in WCA. These are the development of extra-early maturing cultivars that complete the life cycles before severe moisture deficit occurs and development of drought-tolerant cultivars under controlled drought stress. Selection for extra-earliness has been carried out in the savannas, and several varieties have been developed, some of which have been released to the farmers after extensive testing in the different countries of the sub-region.

Farmers in the Guinea savanna also urgently needed *Striga*-tolerant varieties to combat infestation by the parasitic weed that had compelled them to abandon their farms. The weed is particularly difficult to control because it attaches itself to the roots of the host plant and causes a lot of damage before it emerges from the soil. Host plant resistance has been found to be the most effective control method, with little or no cost to the farmer. Therefore, the strategy of the Network was to develop *Striga*-resistant varieties and hybrids. Introgression of sources of *Striga* resistance into existing early and extra-early maize populations and elite varieties has led to the development of varieties with good levels of resistance/tolerance to *Striga*. The populations are presently being further improved, and the research needs to be sustained until *Striga* is no longer a threat to maize farmers.

In addition to *Striga*, poor soil fertility has been one of the constraints to maize production in WCA. Generally, inorganic fertilizers are not easily available and, when available, are too expensive for most farmers. WECAMAN researchers have approached the problem in three ways: incorporation of legume–maize rotation into the farming system, development of improved cultural practices that efficiently utilize the native soil fertility, and use of low-N tolerant varieties. Early and extra-early maize inbreds, varieties, and populations have been screened for low-N use efficiency, and breeding for low-N tolerance is presently an important strategy of the maize improvement programs in national and international research centers in the sub-region. Improved cultural practices have been developed, including optimal plant populations and time of fertilizer application (topdressing) for increased yield of early and extra-early varieties, the use of local sources of fertilizer and organic matter for soil improvement, appropriate number of maize rows to legume (e.g., groundnut) rows in maize–legume association, and appropriate dates of planting in maize–legume intercrop. Maize–legume rotation has also been used to control *Striga*, improve soil fertility, and increase maize grain yield.

An important lesson learnt from WECAMAN that may be emulated for future maize research activities in the sub-region is the equitable allocation of funds to research and development activities. During the 12 years reviewed by Fakorede et al. (2007), funds were allocated to 11 research and development projects. Technology transfer (about 27%) and community seed production (about 20%) received the largest proportion of the available funds. The more traditional technology-generating project areas, such as breeding, agronomy, and *Striga* control, also received substantial proportions of the available funds. The more recent research areas, such as DNA markers, forage maize, and maize for agro-industries, received the least. The lesson here is that a holistic approach to solving the research, production, and utilization problems of the maize sector is the most appropriate for the sub-region. Fakorede et al. (2007) concluded that, during the period under review, maize production increased in the traditional maize belts of the sub-region and was extended to new areas. Average productivity of maize increased by about 30%, while total grain production in the region increased by nearly 400% during the two decades of WECAMAN's existence. Other benefits derived from the Network were improved research capacity of the NARS and capability of the research technicians and scientists, better research–extension–farmer linkage, improved research management and communication skills of the scientists, and improved interpersonal relationships, with enhanced trust and confidence among maize scientists in the sub-region. WECAMAN's success has resulted from the effective and efficient collaboration of the three major players, the NARS, IARCs, and donors.

Funding for WECAMAN's activities ended in 2007, but maize research and development activities have come to stay in the sub-region. Individual NARS have continued to carry out the activities, although at a relatively lower level than under WECAMAN funding. Some of the aspects that are no longer in place include:

(i) RUVTs, which afforded the scientists the opportunity to identify new technologies (improved germplasm in particular) that they could adopt or adapt
(ii) Exchange of germplasm with relative ease
(iii) Biennial maize workshops that afforded the collaborating scientists opportunity to present the results of their research and development activities, interact among themselves, take an overview of their corporate achievement during the preceding two years, identify the lessons learnt and challenges faced during the preceding two years, and plan activities for the following two years
(iv) The lead center concept that made it possible for research and development funds to be spent judiciously and avoid duplication
(v) Capacity building for both scientists and research technicians
(vi) Agronomic research and on-farm demonstrations conducted in agroecological zones that cut across countries
(vii) Monitoring and evaluation tours consisting of participants drawn from all member countries

A few subregional maize research and development programs are still in place in SSA, including the Drought-Tolerant Maize for Africa (DTMA)/Stress-Tolerant Maize for Africa (STMA) projects funded by Bill & Melinda Gates Foundation and the Agricultural Revolution for Africa (AGRA) also funded by Bill & Melinda Gates Foundation along with Rockefeller Foundation. The DTMA/STMA Projects support maize research and development activities in only four countries: Benin, Ghana, Mali, and Nigeria. The DTMA Project has a 9-point objective:

- Broaden the genetic base for drought-tolerant maize.
- Develop/use new tools to accelerate breeding progress.
- Promote variety testing and release.
- Scale up seed production.
- Overcome bottlenecks to increase farmers' access to drought-tolerant maize in drought-prone areas.
- Build capacity of breeders from NARS and seed companies.
- Target and assess impact.
- Increase advocacy and promote adoption.
- Improve project management and communication.

22.3 Future Strategies for Improvement of Maize Production and Productivity in Sub-Saharan Africa

Although the projects focus primarily on drought, research and development work on tolerance or resistance to some other stresses such as *Striga* infestation, and low soil N was entrenched into the projects. All of these stresses are the main focus of maize research in WCA, and we propose that the following important strategies must be sustained:

- Incorporation of multiple stress resistance has been and *must* continue to be a major enhancement strategy of the germplasm for release to farmers in the subregion. This strategy was initiated by the individual NARS maize breeders and has been greatly improved upon by IITA scientists along with WECAMAN and now the DTMA/STMA project collaborators. The experience of these scientists over the years clearly indicates that this is quite possible. For example, varieties released in WCA in the last two to three decades basically have the streak resistance gene block along with tolerance to other specific stress factors such as drought, *Striga* infestation, and low soil N.
- Genes controlling stress tolerance/resistance need to be stacked in the varieties using marker-assisted selection and other molecular approaches. Relative to conventional breeding methods, the molecular approach fast-tracks the development of stress-tolerant/stress-resistant varieties. To a limited extent, the DTMA/STMA supports research on genotyping the available maize germplasm, and there is a laboratory at IITA for NARS-DTMA/STMA project collaborators to access for

that purpose. Work on this aspect must continue, and the NARS need to be strengthened for the work, which has already been initiated in the four DTMA countries in WCA with the initial focus on drought-tolerant maize.

- Future maize improvement activities in SSA must intensify efforts in the development of hybrids, which is the ultimate goal of maize research programs in the most developed countries. The hybrid maize technology, developed essentially in the USA, has revolutionized maize production in many countries of the world, including most of the East and Southern African countries. While work on hybrid maize started long time ago in East and Southern Africa, hybrid maize research started only recently in WCA, and only Nigeria, Ghana, and Mali have made quantifiable progress in developing and releasing hybrids to farmers. Necessarily, seed companies must be available to produce and market hybrids in commercial quantities. Inbred–hybrid maize development activities are important aspects of maize research in SSA, and donors of the DTMA/STMA projects expect that by 2016, 95% of varieties released to WCA farmers should be hybrids. Over the years since hybrid maize research started at IITA in WCA, a large number of inbred lines have been developed in the different maturity groups, many of which have been evaluated in hybrid combinations. The inbred lines are available to national programs and private seed companies in the sub-region for testing in hybrid combinations to kick-start or sustain hybrid maize development efforts.
- Strengthening the capacity and capability of NARS researchers has been an important strategy for maize improvement in the sub-region, and it must continue. The main focus of AGRA in the sub-region has been along this line. This body identified the acute shortage of well-trained plant breeders; consequently, it established in Ghana a center for higher-degree training of breeders in collaboration with universities in the sub-region. This center, named West African Center for Crop Improvement (WACCI), has produced an impressive number of PhD graduates in plant breeding within the few years of its establishment. This type of arrangement for training should be expanded, sustained, and improved upon.

An important area that needs urgent attention is the estimation of total grain production as well as grain yield per unit land area in the sub-region. A lot of investment in terms of human, material, and financial resources has been sank into maize improvement activities in the sub-region, and it is desirable to ensure that there is progress toward achieving the set goals. Fakorede et al. (2007) emphasized the need for researchers in the sub-region to come up with ways and means of collecting actual data on these aspects. Presently, only FAO data on these aspects are available which, at best, are rough estimates and are far from accurate. Analysis of these data showed discouragingly low estimates of the trend of improvement in yield/ha in the sub-region.

Considering the effectiveness of WECAMAN, we recommend that future efforts on the improvement of maize should be through the networking approach. Although a baseline database for research facilities and training maize researchers is urgently needed, the facilities presently available in the different institutions may be pooled and used collaboratively for training purposes. Some of the constraints of maize research in the sub-region are:

- Lack of human resources, including scientists and technicians
- Lack of infrastructure and equipment
- Problems in maintaining existing equipment
- Limited access to information in journals and on the Internet
- Insufficient funding from government, external donors, and private sector
- Difficulties in obtaining consumables and reagents.

The challenges outlined above could be addressed by taking the following steps:

(i) *Increasing gains from selection using molecular approaches*: Molecular technologies offer the opportunity to expand the size of a breeding program and improve the selection intensity without increasing phenotyping requirements. Genotypic information can be used to preselect germplasm prior to phenotyping stages, and the capability to increase this untested layer will allow the total number of lines within a breeding program to be expanded (Cooper et al. 2014). Results of studies using both biparental and association mapping panels have identified many small-effect QTLs (e.g., Almedia et al. 2014). Meta-analysis of QTLs reduced the number of QTLs for grain yield to 59 (Semagn et al. 2013). However, only a few mQTL were detected across well-watered and drought stress conditions and/or multiple genetic backgrounds, with each explaining a very small proportion of the phenotypic variance. Similarly for low-N, many small-effect genomic regions, which are unlikely to be suitable for marker-assisted backcrossing, have been identified (Coque and Gallais 2006; Semagn et al. 2015). In contrast, trait-linked markers for low-N tolerance have just been identified by Adofo-Boateng (2017) and are presently at the validation stage, while linked markers identified and validated by CIMMYT are being employed for improvement of low-N tolerance of tropical maize in sub-Saharan Africa. A major QTL for MSV (msv1) resistance on chromosome 1 has been identified in several populations (Welz et al. 1998; Pernet et al. 1999; Nair et al. 2015). Subsequent fine mapping of msv1 identified three SNPs within a haplotype block with an accuracy of 0.94 in predicting the disease reaction in a collection of breeding lines with known responses to MSV infection. High-throughput KASP assays have been developed for these three SNPs to enable routine marker screening in the breeding pipeline for MSV resistance. In the last year, 30,000 double haploid lines from the CIMMYT ESA breeding program were screened for the favorable haplotypes at msv1 prior to advancing to field screening (Nair et al. 2015).

Markers for turcicum leaf blight (TLB), gray leaf spot (GLS), and MLN are currently in the validation stage at CIMMYT. A mapping population for *Striga* resistance has been developed in IITA, and QTLs are presently being identified through collaborative research between IITA and Cornell University

(I. Akaogu, unpublished). It is anticipated that the use of these markers in forward breeding programs in CIMMYT and IITA to screen for tolerance/resistance in breeding materials before expensive multilocation field testing is initiated will allow resources for yield testing to be focused on materials with acceptable levels of resistance/tolerance thereby increasing selection intensity for yield, and hopefully to increase the rate of genetic gains. Genome-wide selection is a more recent molecular approach that incorporates all available marker information within a genome into a predictive model, for computation of the genomic estimated breeding value used for selection of top-ranking individuals to serve as parents of the next generation. A major advantage of the genome-wide selection over the conventional marker-assisted recurrent selection is that both major and minor effects genes are used as putative QTLs during selection; thus, the approach is considered more effective in selecting for quantitative traits which are under the control of polygenes. Beyene et al. (2014) obtained accelerated gains through the use of genome-wide selection for improvement of grain yield and drought tolerance in eight maize populations.

(ii) *Increased heritability in field trials*: There is the need for strategies to reduce the effects of field variability in order to increase the genetic signal-to-noise ratio and enable detection of real differences between lines. Reducing the size of the residual relative to the genetic component of variance and/or increasing replication would have a positive impact on heritability levels and expected genetic gains (Cairns et al. 2012, 2013).

(iii) *Reducing breeding cycle time using double haploid technology*: Furthermore, doubled haploid (DH) technology provides another avenue to increase genetic variance and reduce breeding cycle times. DH allows completely homozygous lines to be rapidly developed from heterozygous parents in two seasons, permitting greater selection efficiency since DH lines do not change from one testing season to the next. This combined with higher between-entry variation compared with early generation testing (EGT) methods would improve overall realized heritability, resulting in higher genetic gain. Tropically adapted maize inducer lines with a haploid induction rate of up to 10% and a new marker system have been established in Kenya to allow the routine incorporation of DH into breeding programs in ESA (CIMMYT 2014). The current haploid induction rate is 5.5%, production capacity of over 50,000 haploid lines per year (S. Bumagat, 2016, unpublished). However, current costs (~30 USD/line) limit further utilization of this technology. There is a need to reduce DH production costs through more efficient haploid induction, more efficient chromosome doubling, optimization of protocols to more closely reach production targets, and more efficient haploid discrimination systems. Furthermore, there is a need to establish a DHL facility in IITA, Ibadan, to serve WCA.

(iv) *Speeding up breeding cycles*: Maize hybrid breeding begins by crossing two inbreds. Progeny is then advanced by either selfing or doubled haploid technology and evaluated in testcross trials to determine general combining ability

> (GCA). Testcross selection within a biparental cross is based on phenotypic information and requires one season of field trials (Hallauer 1990). Genomic selection offers a faster way to predict general combining ability (GCA) without phenotyping. Jacobsen et al. (2014) successfully developed a GCA model for GS within A/B crosses. The GCA model relies on information from previously phenotyped and genotyped crosses with inbreds A and B as one of the parents and can be used in advanced breeding programs that use elite inbreds as the parents of new breeding crosses. The ability to predict GCA has the potential to significantly reduce time and costs in inbred development and thus speed up breeding cycles.

In conclusion, the network approach of WECAMAN has clearly demonstrated that collaborative research projects with a multidisciplinary approach are effective in enhancing research productivity in WCA, despite these constraints. Incidentally, this approach is very attractive to external donors. For example, the need for advanced laboratories will continue to increase in the sub-region, and it will be difficult for each country, whether from its resources or from external donations, to put all the needed facilities in place. For this purpose, it may be possible, instead of trying to enhance the capacity of all NARS in the sub-region, to develop central, well-equipped laboratories in selected places to be the focal points for specific aspects of maize research in the sub-region. The need for cooperation between such advanced laboratories, wherever they are located and other countries that do not have such facilities in the sub-region, is obvious. Presently, IITA has been filling the gap of advanced laboratory for NARS programs in the sub-region. But this is far from adequate. This collaboration should be beneficial to all stakeholders, that is, the NARS, the focal centers, and the donors. Here again, using the case of WECAMAN as an example, it was not only the NARS that benefitted. Fakorede et al. (2007) noted that the IARCS and the donor agencies also derived some benefits from the activities of the Network. Duplication of research efforts, especially in the face of dwindling financial resources, has been greatly reduced through networking with NARS. WECAMAN member countries have collaborated very actively with both IITA and CIMMYT in conducting evaluation trials of promising varieties and breeding materials such as progeny trials from which experimental varieties have been developed. Indeed, some of these varieties have been named after the NARS sites from which their parent materials were selected. Identification of fairly strong NARS, which have been designated lead centers, along with availability of screening sites for specific abiotic and biotic stresses, has greatly facilitated IARCs' efforts for breeding for stress tolerance. *Striga*, low soil N, and stem borers are endemic in certain locations so that escapes are hardly possible when screening maize germplasm for resistance to the stress factors in such locations. IARCs did not only have access to these facilities but have also devolved some of the breeding activities on competent NARS partners to allow the international scientists to concentrate on some more basic research that requires relatively more advanced laboratories. In addition, IARCs have trained NARS partners to finalize specific technologies as most appropriate to their specific situations. For example, inbred lines have been developed at IITA and made available to NARS partners who have developed open-pollinated (synthetic) varieties or hybrids best suited to their countries. WECAMAN has provided an overall framework and greatly facilitated the implementation of projects targeted to WCA. Two examples are the AMS and the NF projects which have been executed by member countries of WECAMAN and administered in the same manner as the USAID-funded projects of WECAMAN. The success of WECAMAN, including the AMS and NF projects, is not only in technology generation but also in technology transfer, which actually was given a high priority over the years. This has led to increased maize production, improved food security, and positive move toward poverty alleviation in the sub-region, thus achieving, to a large extent, the goal of donors in funding the activities of the Network. Herein lies the benefit of the Network to the donors, that is, the assurance that the funds they have provided have been judiciously utilized to achieve the desired goal of food security and poverty alleviation in the countries of WCA.

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Index

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