

11 Rice Genetic Improvement for Abiotic Stress Tolerance in Africa

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Introduction

In sub-Saharan Africa, biophysical constraints and high reliance on low-input and rainfed agriculture impose various abiotic stresses on rice crops (Defoer *et al.*, 2002). Most of these stresses are associated with water availability (drought and excess water), soil problems (salinity, nutrient deficiencies and toxicities) and extreme temperatures (heat and cold). These stresses fluctuate seasonally and vary spatially. They adversely affect rice growth and productivity, resulting in reduced yields. Abiotic stresses are limiting factors in almost all rice production environments – in both rainfed and irrigated areas (Defoer *et al.*, 2002; Saito *et al.*, Chapter 15, this volume; Table 11.1). They contribute to significantly lower on-farm yields compared to attainable yield. Results of farm-household surveys conducted by the Africa Rice Center (AfricaRice) in 12 sub-Saharan African countries showed that, for example, when drought and flooding occur, they induce average yield losses of 33% (AfricaRice, 2011a). Yield losses due to soil-related problems are higher in the lowlands than in the uplands. In Senegal and Uganda, yield losses due to the soil-related constraints salinity and iron toxicity are as high as 40% and 25%, respectively (AfricaRice, 2011b).

Crop and water management can be improved through efficient irrigation schemes, better infrastructure and hydrological control, and optimal use of fertilizers, which can alleviate some of the effects of abiotic stresses. These measures are effective in reducing yield losses, and most improved varieties are responsive to such measures, consequently stabilizing productivity and narrowing yield gaps (Ismail *et al.*, 2008). However, the costs of adopting these measures are prohibitive for most resource-poor African farmers and local governments. Alternatively, developing rice germplasm tolerant to the prevalent stresses involves no additional costs to farmers and can enhance and stabilize productivity considerably (Ismail and Tuong, 2009). Hence, varietal improvement should be given priority as an entry point for increasing and stabilizing rice production in sub-Saharan Africa. As much as possible, this should be combined with improved management practices to realize the full yield potential of the new tolerant varieties developed. This is all the more important given that the potential impact of research targeted to reduce yield loss due to stresses was estimated at a global cumulative benefit of US\$ 32.9 million for seven countries over 3 years (AfricaRice, 2011b). This means

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Table 11.1. Major rice production ecosystems in Africa: actual and potential yield and limiting constraints. (Adapted from Defoer *et al.*, 2002; Diagne *et al.*, Chapter 3, this volume).

Rice agro-ecosystem	Share of rice area (%)	Yield: Actual / Potential ^a (t/ha)	Abiotic production constraints	Input use
Rainfed upland	32	1.2/2–4	P and N deficiency, acidity, Al toxicity, drought, erosion declining soil fertility, cold in highlands	Very low
Rainfed lowland	38	1.9/3–6	Water control, N and P deficiency, Fe toxicity	Low
Irrigated Sahel/savannah	26	3.7/6–11	N deficiency, salinity and alkalinity, extreme temperatures	High
Irrigated humid/sub-humid zone		1.9/5–8	N deficiency, Fe toxicity	Medium
Mangrove		<1/2–4	Acid sulfate, salinity, Fe toxicity, excess water	Very low
Deepwater/Floating	4	<1/2–4	Salinity, excess water, cold in highlands	Very low

^aLow end of the range refers to potential yield at current input levels; high end refers to potential yields at increased input levels.

additional income for farmers and increased rice production in Africa.

In the rice gene pool – both cultivated and wild species – tremendous genetic variation exists for tolerance to abiotic stresses. This could be exploited to develop improved varieties that are more tolerant to the major abiotic stresses that constrain rice production in sub-Saharan Africa than existing varieties. Progress in developing rice varieties tolerant to abiotic stresses has been slow because of the complexity of the tolerance mechanisms, poor understanding of the inheritance of tolerance, low heritability and lack of efficient screening techniques (Lafitte *et al.*, 2006). However, advances in understanding stress physiology and identification of tolerance genes/QTLs (quantitative trait loci) (Ismail *et al.*, 2007; Jena and Mackill, 2008; Thomson *et al.*, 2010b) offer promising opportunities for rice improvement with regards to abiotic-stress tolerance. Both conventional and biotechnological approaches are being used by AfricaRice to exploit the rich reservoir of genetic resources present in the African germplasm pool, particularly *Oryza sativa* landraces and *O. glaberrima* for the improvement of local rice varieties. In this chapter, we present the major abiotic stresses that constrain rice production in sub-Saharan

Africa and the breeding activities to develop rice varieties tolerant of these stresses and adapted to local conditions in Africa. We also highlight the challenges that should be addressed in order to sustainably increase rice productivity in sub-Saharan Africa.

Major Abiotic Stresses Limiting Rice Production in Sub-Saharan Africa

Sub-Saharan Africa is affected by numerous types of environmental stresses related to water availability, soil problems and climatic issues. In many cases, several stresses are experienced simultaneously (e.g. in mangrove-swamp rice fields where submergence, salinity and iron toxicity occur together). Rice production in such areas is severely constrained by abiotic stresses. Specific data on the extent of abiotic stresses in rice-growing areas of sub-Saharan Africa are scarce. Most of the data available are either not specific to rice-growing areas or limited to a few countries. This issue is being addressed by AfricaRice. Insight on farmer perceptions of abiotic constraints is provided by Diagne *et al.* (Chapter 4, this volume).

Drought

Drought is generally avoided in areas where irrigation water is available throughout the season, but it is a consistent feature across much of the 63.5 million hectares of rainfed rice sown annually, most of which is in tropical Asia, Africa and Latin America (Lafitte *et al.*, 2006). It can occur at any stage during the rice cropping season, but it is more devastating when it occurs just prior to flowering than it is during the vegetative stage, with substantial effects on grain yield (Boojung and Fukai, 1996). About 70% of the rice area in sub-Saharan Africa is rainfed (Diagne *et al.*, Chapter 3, this volume; Table 11.1). The spatial and temporal variability of rainfall in this region expose rice plants to frequent drought spells. Regardless of the total rainfall and distribution, the poor physical properties of highly weathered, coarse-textured soils in some parts of sub-Saharan Africa induce low water-holding capacity and establish water deficit as a major constraint to rainfed crop yields in sub-Saharan Africa (Hsiao *et al.*, 1980). This is particularly true for upland rice, which makes up 32% of rice-growing areas in sub-Saharan Africa (Table 11.1). Analysis of farmer perceptions in 18 countries in sub-Saharan Africa across rice environments provided evidence that in 2008 an estimated 10% of rice farmers experienced drought affecting 37% of their rice area, causing 29% of rice yield loss (Diagne *et al.*, Chapter 4, this volume). The diversity of affected production systems, variability of drought in terms of timing and severity, and the multiple traits involved in drought tolerance require strategic research to prioritize and define environment-specific approaches for developing drought-tolerant rice cultivars (Manneh *et al.*, 2007).

Salinity

Irrigation has the potential to ensure high rice yields and is a good strategy to offset recurrent droughts. Unfortunately, soils of most irrigated areas in sub-Saharan Africa have continued to be degraded as a result of poor irrigation practices and the absence of efficient drainage. These have

led to a rapid rise in the water table and an increase in soil sodium/alkalinity and salinity (Bertrand *et al.*, 1993). In the Office du Niger (Mali), 50% of the water table is now saline and occasionally very saline despite low mineral content of the irrigation water (Bertrand *et al.*, 1993). In the Senegal River delta, marine-derived soil salinity is an inherent problem and sodicity is increasing in irrigated flood plains in inland areas due to high evaporation, rising groundwater tables and poor drainage (WARDA, 1993; Matlon *et al.*, 1998). Miézan and Dingkuhn (2001) observed that waters of the Niger and Senegal rivers carry substantial alkalinity, and the salt content of water sometimes increases markedly between the main rivers and the actual irrigation site. However, van Asten *et al.* (2003) show that salt accumulation in the soils of Sahelian countries has more to do with the underlying bedrock than with the irrigation system. Examining soils in the irrigated areas of Foum Gleita (Mauritania) they found that the geographical distribution of salt was not related to the presence of irrigation or drainage canals. Also the alkaline salts present in the upper soil layers in Foum Gleita did not come from irrigation water, but from the underlying bedrock. Additional to the salt stress itself, the high pH resulting from the sodification/alkalinization reduces the availability of plant nutrients such as zinc and increases nitrogen losses through volatilization (Bertrand *et al.*, 1993; Miézan and Dingkuhn, 2001). According to van Asten *et al.* (2004), using data from Sourou Valley (Burkina Faso), this shortage of nutrients in the soil is a bigger problem than soil degradation attributable to irrigation.

High rice productivity is also constrained by soil salinity in many mangrove-swamp areas. Mangrove rice is grown on about 200,000 ha of cleared mangrove swamps along the rivers and coastal estuaries of The Gambia, Guinea, Guinea-Bissau, Nigeria, Senegal and Sierra Leone (Matlon *et al.*, 1998). In these areas, rice cultivation depends on the length of the salt-free period, which is an interplay of *in situ* rainfall, the volume of freshwater flow, and salt intrusion from the sea. Swamps located along river banks farthest from the sea experience a salt-free period of 6–9 months during which rice can be grown. Closer to the sea, rice can be grown for only 3–4 months.

Rice is most sensitive to salinity stress at seedling and reproductive stages (Gregorio

et al., 2002). However, salinity tolerance at these two stages is only weakly associated (Moradi *et al.*, 2003). Discovering and combining suitable tolerance traits for both stages is essential for developing resilient salt-tolerant varieties. Moreover, the salt-tolerance level of cultivars depends on environmental conditions (Asch *et al.*, 1997). Generally, salinity effects on rice are more severe in arid climates than in humid ones. For example, salinity levels at an electric conductivity (EC) of 9.5 mS/cm were reported to cause a 50% yield loss in the humid tropics (Flowers and Yeo, 1981), whereas under the arid conditions of the Sahelian dry season an equivalent yield loss was observed at an EC of only 3.5 mS/cm (Dingkuhn *et al.*, 1993).

Excess water

Excess water can be of two types: transient flash floods or submergence that completely inundates the crop for a short duration (up to 2 weeks), and longer-term flooding where water stagnates for up to a few months at different water depths (e.g. 30–50 cm: partial/stagnant, semi-deep; >100 cm: deep-water; up to 3 or 4 m: very deep-water or floating rice) (Mackill *et al.*, 2012). In sub-Saharan Africa, the deep-water area accounts for less than 4% of the whole rice-growing area (Diagne *et al.*, Chapter 3, this volume), mainly in the flood plains of large rivers such as the Niger River. Excess water is also a common constraint throughout the rainfed and irrigated rice-production areas when high rainfall and/or impeded drainage occurs, particularly early in the season (Futakuchi, 2005). In the flood plains, sudden floods can temporarily submerge the rice crop in some areas, and waterlogging can continue through most of the season in others – sometimes both occur within the same season. In savannah and forest zones in West and Central Africa, inland valleys prevail and rice in valley bottoms often experiences waterlogging for several weeks after heavy rainfall (Manneh *et al.*, 2007). Analysis of farmer perceptions in 18 countries in sub-Saharan Africa provided evidence that in 2008 an estimated 5% of farmers experienced flooding, affecting 37% of their farmland, causing a production loss of 27% (Diagne *et al.*, Chapter 4, this volume).

While rice is adapted to waterlogged conditions, complete submergence for several days can be fatal. However, the extent of damage to rice is affected by several factors linked to flood-water conditions, including interference in normal gas exchange and light interception. These factors are largely affected by the duration of the flood, its depth, temperature, and the level of turbidity and turbulence of the floodwater, and vary considerably across locations and seasons (Das *et al.*, 2009). Rice yields in flood-prone areas are very low, mostly averaging below 1.5 t/ha, because farmers usually grow their low-yielding traditional varieties (Haelele *et al.*, 2010); and modern high-yielding varieties tolerant of these stresses are mostly non-existent. In some locations, such as Mopti (Mali) and the Sokoto Rima River flood plains (Nigeria), *O. glaberrima* (African rice) is still cultivated despite its low yield potential relative to the more widely cultivated *O. sativa* (Asian rice) (Jones *et al.*, 1997; Diarra *et al.*, 2004; Sakagami, 2012).

Phosphorus deficiency

Phosphorus (P) deficiency is one of the major limiting factors for crop production in highly weathered soils in the humid tropics. Total soil P is generally low, with only 2–4% of the total P available to plants. This is because of the high P-fixing capacity of fine-textured soils found in humid and sub-humid zones (Abekoe and Sahrawat, 2001). About 5.7 billion hectares worldwide lack sufficient plant-available P (Batjes, 1997) and 50% of potential arable land worldwide has acid soils, which are widely distributed in sub-Saharan Africa. The bioavailability of inorganic phosphate is reduced in acid soils.

Phosphorus deficiency can be corrected through fertilizer application, but the lack of locally available P sources and the high cost of importing and transporting fertilizers prevent many resource-poor rice farmers from applying P. Furthermore, some rice soils can quickly fix up to 90% of the added P fertilizer into less-soluble forms (Dobermann *et al.*, 1998) that cannot be used by plants. This tight binding of P in the soil is frequently the primary cause of P deficiency, rather than a low total P content.

Insufficient plant-available soil P is a major constraint for rice production. This is particularly apparent in sub-Saharan Africa under upland conditions, which are commonly characterized by infertile, highly acidic, P-fixing soils, usually in areas where little or no fertilizer is applied. Under lowland conditions, where P is more available than in drier areas, P deficiency is still a major factor limiting performance of modern rice varieties (Defoer *et al.*, 2002). Phosphorus deficiency is likely to become an increasingly important constraint, as P is removed from soils under intensive rice production (De Datta *et al.*, 1990) using high-yielding modern varieties.

Iron toxicity

Iron (Fe) toxicity is widely distributed in tropical lowlands and is frequently reported in many inland valleys (mangrove swamps, rain-fed and irrigated lowlands) of sub-Saharan Africa (Masajo *et al.*, 1986). It is usually associated with poor drainage and the presence of iron in the parent rock or in the soils of adjacent slopes through which groundwater flows into the lowland (WARDA, 1988). A wide range of soil types can be Fe-toxic, including acid-sulfate soils, acid-clay soils, peat soils and valley-bottom soils receiving interflow water from adjacent slopes (Becker and Asch, 2005). A survey conducted during 2000–2001 in three West African countries (Côte d'Ivoire, Ghana and Guinea) showed that more than 50% of the lowlands studied and about 60% of the cultivated rice plots were affected by Fe toxicity, and 10% of lowland crop fields were abandoned due to high Fe-toxicity stress (Chérif *et al.*, 2009).

In anaerobic conditions and acidic conditions (pH <5), as found in waterlogged soils, the ferrous form is stabilized and readily taken up by plants. Rice is particularly sensitive to Fe toxicity at two growth stages – soon after transplanting up to tillering, and during heading/flowering (Prade *et al.*, 1990). Depending on the variety and the intensity of the toxicity, yield losses average about 30% and can accrue up to levels that can cause complete crop failure of susceptible varieties (Masajo *et al.*, 1986; Abifarin, 1989;

WARDA, 1997). Excessive uptake of Fe is often accompanied with other nutrient deficiencies, especially potassium, phosphorus, calcium and magnesium (Benckiser *et al.*, 1984; Prade *et al.*, 1990). However, Sahrawat *et al.* (1996) report cases of Fe toxicity without apparent deficiency in other nutrients.

Extreme temperatures

Low-temperature stress is common for rice grown in temperate regions and at high elevations in the tropics. In Africa, cold temperatures occur in the highlands of East and Southern Africa and in some areas of the Sahel region of West Africa during the cold, dry harmattan season, which extends from November to February. For example, in Madagascar, mean temperatures at 1500 m vary from 17°C in October, the rice-sowing period, to 20°C during the reproductive stage (Zenna *et al.*, 2010). Minimum temperatures can fall below 10°C during early vegetative stage and below 14°C during reproductive stage (Zenna *et al.*, 2010). In the Sahel, there are significant temperature fluctuations during the year with low temperatures during panicle initiation in the wet season and high temperatures around flowering during the dry season. In both cases, spikelet sterility may occur, leading to substantial yield loss (Dingkuhn, 1995). In this region, day minimum temperatures fall below 20°C during November to March, while maximum temperatures regularly rise above 40°C from April to June (Fig. 11.1). Planting rice between mid-September and mid-November in the Sahel is generally associated with near total spikelet sterility, since the reproductive phase of the crop coincides with periods of low night temperatures (Dingkuhn, 1995; Manneh *et al.*, 2007). Moreover, crop duration increases with low temperatures, considerably limiting the possibility of double-cropping in areas where water control is possible (Coly, 1980; Matlon *et al.*, 1998). However, the introduction of short-duration varieties can make double-cropping feasible. Dingkuhn and Miezán (1995) used a simulation model based on photothermal constants to show that short-duration genotypes with high plasticity of duration perform best

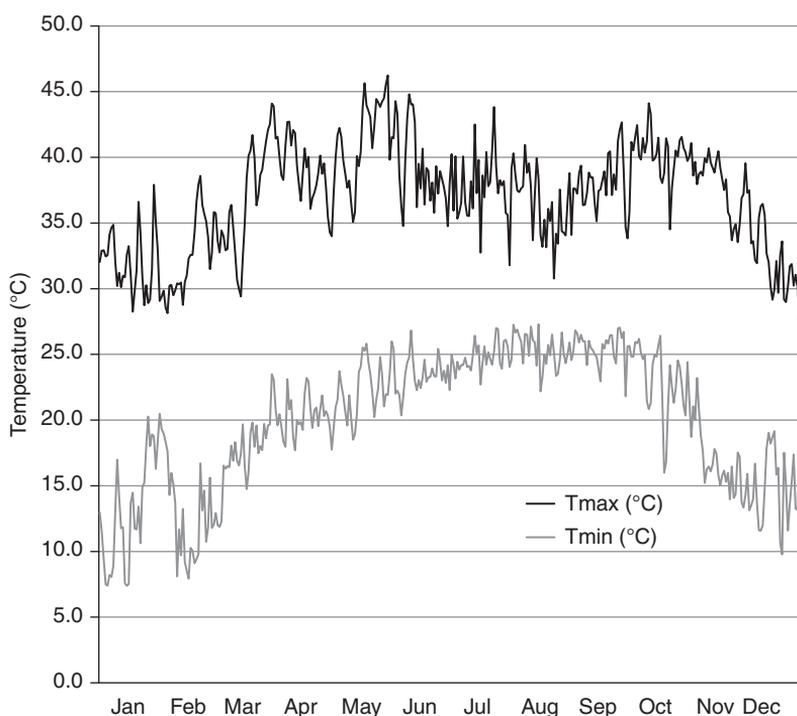


Fig. 11.1. Example of seasonal and diurnal temperature variations during two major cropping seasons in the Sahel (case of Fanaye, Senegal River valley, northern Senegal, 2011). Tmax, maximum temperature; Tmin, minimum temperature.

in the dry season, while medium-duration types with high plasticity perform well in the wet season, and short-duration types with low plasticity of duration perform well in both seasons. Rising temperatures, as a consequence of climate change, could have positive effects on the flexibility of cropping calendars, but the vulnerability of rice to high temperature is also expected to increase. Global mean temperatures have already risen by around 0.6°C over the last century and are projected to increase by 1.4°C to 5.8°C over the next century (IPCC, 2001).

Rice is sensitive to temperature fluctuations, but its sensitivity depends on the developmental stage. Flowering stage and 9–11 days before heading are the most sensitive stages to extremes of temperatures, with very cold or very hot weather leading to high spikelet sterility (Yoshida *et al.*, 1981; Andaya and Mackill, 2003a; Manneh *et al.*, 2007; Zenna *et al.*, 2010). Rice is particularly sensitive to tem-

peratures below 15°C. The extent of damage depends on the ambient air or water temperature, cropping pattern, growth stage and variety (Zenna *et al.*, 2010). Crop failure can be observed when low temperature is manifested at different growth stages, such as germination, seedling, vegetative, reproductive and grain maturity (Andaya and Mackill, 2003a,b).

When rice is exposed to air temperatures higher than 35°C, heat injuries occur. By studying weather data at the International Rice Research Institute (IRRI) farm from 1979 to 2003, Peng *et al.* (2004) show that grain yield declined by 10% for each 1°C increase in minimum temperature during the dry season, whereas the effect of maximum temperature on crop yield was insignificant. In a different study, Ziska and Manalo (1996) found that, at a constant day temperature of 29°C, increasing night temperature did not significantly alter growth or yield; however, increasing night temperature

at a day temperature of 33°C resulted in significant declines in grain-filling and grain yield.

Strategies to Improve Rice Tolerance to Abiotic Stresses for Africa

Various conventional and biotechnological approaches are being used to develop rice varieties tolerant of abiotic stresses. It is now possible to develop new tolerant rice varieties through conventional breeding in combination with marker-assisted selection or through direct transfer of tolerance genes into rice varieties via genetic engineering. At AfricaRice, two main strategies are being followed for genetic improvement of rice tolerance to abiotic stresses (Fig. 11.2): (i) the use of genetic diversity existing

in rice, with particular focus on African rice (*O. glaberrima*) and related wild species, *O. barthii*; and (ii) the use of molecular markers to transfer tolerance QTLs to elite African germplasm, in addition to conventional breeding. Efforts are also devoted to identify new QTLs for tolerance.

To ensure farmers' access to these new technologies and their rapid adoption, AfricaRice is progressively introducing participatory approaches into the various breeding programmes. In different countries, breeding lines and varieties selected for tolerance to salt stress, drought, Fe toxicity and cold were evaluated by farmers through field visits and on-farm tests against their local varieties. By 2011, some 21 promising stress-tolerant lines had been identified for potential submission to national varietal release committees. In 2010, an Africa-wide Rice

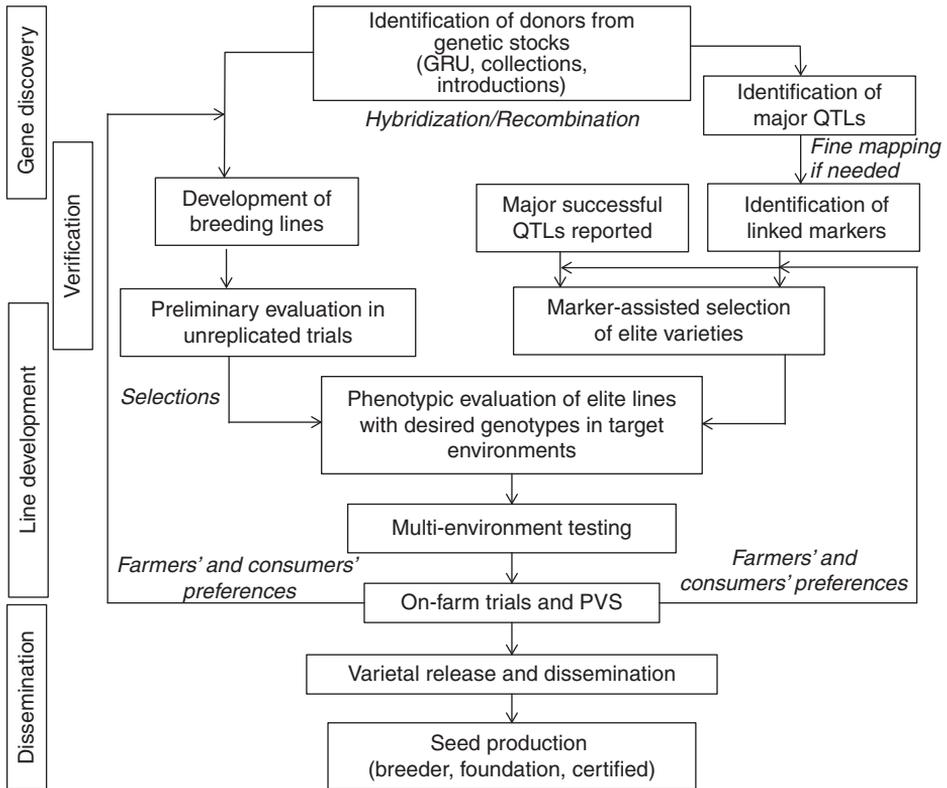


Fig. 11.2. Framework of a breeding process for genetic improvement of stress tolerance in rice. GRU, Genetic Resources Unit; PVS, participatory varietal selection; QTLs, quantitative trait loci.

Breeding Task Force was revived and this network is now responsible for multi-environment testing of new breeding lines developed for lowland, irrigated, upland, high-elevation and mangrove environments (see Kumashiro *et al.*, Chapter 5, this volume).

Tapping the gene pool of African rice

With the success of NERICA varieties, *O. glaberrima* gained renewed interest. This species is known for its good adaptation to sub-Saharan Africa environmental and soil conditions. It has tolerance to many abiotic stresses, including drought, Fe toxicity, acidity and low-input conditions (Sano *et al.*, 1984; Jones *et al.*, 1997) and has the ability to grow in a wide range of unfavourable ecosystems such as rainfed hilly areas, deepwater floating conditions and in coastal mangrove areas (Sarala and Swamy, 2005). While AfricaRice holds a collection of about 2500 *O. glaberrima* accessions, only four accessions were used to create the NERICA varieties for both upland and lowland environments. There is still a tremendous amount of unexploited genetic diversity in the primary gene pool of *O. glaberrima*. AfricaRice has embarked on the characterization of *O. glaberrima* accessions and their evaluation for different traits of interest, including tolerance to abiotic stresses.

Several *O. glaberrima* were collected in Mali (RAM series) and several donors of drought tolerance have been identified, including RAM3, RAM118 and RAM152 (Ndjiondjop *et al.*, 2007; Bimpong *et al.*, 2011a). The development of backcross interspecific lines (*O. sativa* × *O. glaberrima*) showed that drought tolerance from *O. glaberrima* is transferable to the progenies. Several introgression lines from different cross combinations were evaluated and lines tolerant of drought have been identified (Ndjiondjop *et al.*, 2007, 2010; Bimpong *et al.*, 2011b; Bocco *et al.*, 2011). Similarly, good sources of salinity tolerance have been identified within *O. glaberrima* (e.g. RAM121, TOG6224 and TOG7230), as well as some of the interspecific lowland NERICA-L varieties. These tolerant varieties do not have the tolerance allele of Pokkali at the *Saltol* locus. Further studies are assessing whether these alleles can effectively be combined with *Saltol* to breed highly

tolerant varieties. Variability also exists in the interspecific lowland NERICA and *O. glaberrima* varieties with regards to Fe-toxicity tolerance. NERICA-L 19 and NERICA-L 49 combine both tolerance to iron toxicity and good agronomic characters (Nwilene *et al.*, unpublished). The tolerance was inherited from the *O. glaberrima* parent, TOG5681. It has also been reported that CG14, the *O. glaberrima* parent of upland NERICA varieties, has remarkable tolerance to Fe-toxicity stress (Sahrawat and Sika, 2002), while TOG7235, TOG6216, TOG7442 and TOG7291 show moderate tolerance (Mendoza *et al.*, 2000). About 500 accessions from the AfricaRice *O. glaberrima* collection are being evaluated at Vallée du Kou (Burkina Faso) to identify new sources of tolerance to Fe toxicity in this species. New research directions are also being considered in view of the current and anticipated rise in temperature resulting from climate change. New projects are in the pipeline to incorporate heat tolerance into local African varieties. For this trait, too, *O. glaberrima* could be exploited to confer early morning flowering in interspecific crosses to avoid spikelet sterility due to heat stress (Yoshida *et al.*, 1981; Manneh *et al.*, 2007).

One of the major limitations in the use of *O. glaberrima* for the improvement of *O. sativa* was the interspecific hybrid sterility (Ghesquiere *et al.*, 1997). Even though AfricaRice succeeded in the development of interspecific varieties – NERICA – the introgression of useful traits from *O. glaberrima* into *O. sativa* is still tedious and time-consuming. AfricaRice and Institut de recherche pour le développement (IRD) have developed interspecific bridges between the two cultivated species. These interspecific bridges comprise *O. sativa* lines carrying large introgressions of the *O. glaberrima* genome that are compatible with *O. sativa* in subsequent crosses. Marker-assisted selection was carried out on backcross progenies to select the homozygous lines bearing the *O. glaberrima* allele at the *S1* locus. The *S1* gene encodes a gamete eliminator which induces both male and female gamete abortion through allelic interaction in interspecific *O. sativa* × *O. glaberrima* crosses (Sano, 1986; Garavito *et al.*, 2010). The fertility restoration is monitored for three generations to derive fertile backcross inbred lines (BILs – BC₁F₃) with improved crossability with *O. sativa*. For more details see Lorieux *et al.* (Chapter 10, this volume).

In addition to *O. glaberrima*, genetic variability for tolerance to abiotic stresses is also present in *O. sativa*, especially in the traditional varieties, and this is being exploited. Through germplasm exchange, tolerant varieties identified elsewhere are included in breeding programmes to enhance tolerance to abiotic stresses in the local varieties. Meanwhile, agronomic and quality traits preferred by consumers are incorporated in the new tolerant lines to meet the market demand.

Speeding up the development of tolerant varieties through molecular breeding

With a better understanding of the mechanisms and genetics of stress tolerance, breeders are now using more precise breeding approaches – notably marker-assisted backcrossing (MABC) – to develop varieties with higher levels of tolerance and acceptable grain quality. For many abiotic stresses, major QTLs/genes have been identified in rice (Jena and Mackill, 2008; Ismail and Thomson, 2011). Some of these QTLs have been fine-mapped and a MABC system developed to incorporate them into high-yielding varieties. Incorporation of these QTLs into popular varieties demonstrates substantial impacts on rice productivity in farmers' fields (Singh *et al.*, 2009; Thomson *et al.*, 2010a,b; Ismail and Thomson, 2011; Mackill *et al.*, 2012). Likewise at AfricaRice, MABC has been initiated for all abiotic stresses for which major QTLs have been identified and successfully used. A certain set of QTLs is targeted for each rice production environment and research conducted at different AfricaRice stations.

Improving drought tolerance of rice has been hindered by the low level of genetic variability and the complex inheritance of the trait, as well as the difficulty of accurately measuring the level of tolerance. Molecular approaches to improve drought tolerance have been widely applied to rice, and numerous QTLs identified for secondary traits associated with drought response, including rooting traits (depth, volume, thinness, penetration ability), leaf rolling and death, membrane stability, and osmotic adjustment (Laffite *et al.*, 2006). However, very few studies have mapped QTLs related to better yield under drought. A few major QTLs for yield

under drought have been identified that can result in substantial yield improvement under drought (Bernier *et al.*, 2007; Venuprasad *et al.*, 2009; Vikram *et al.*, 2011). These QTLs offer considerable opportunities for enhancing drought tolerance of rice varieties for Africa for both uplands and lowlands. Drought tolerance QTLs *qt12.1* and *DTY3.1*, respectively associated with yield under upland stress and lowland stress (Bernier *et al.*, 2007; Venuprasad *et al.*, 2009), are targeted for marker-assisted selection (MAS) at AfricaRice. Near-isogenic lines (NILs) contrasting for grain yield under drought, developed at IRRI, are being tested under upland and lowland conditions in Benin and Nigeria. The *qt12.1* co-localizes with the *Pup1* (P uptake-1) QTL that confers tolerance to P deficiency (Chin *et al.*, 2010). AfricaRice is aiming to transfer the *Pup1* QTL into the background of popular upland varieties. A preliminary survey using *Pup1* gene-specific markers showed that almost all upland varieties tested (including upland NERICA varieties) have Kasalath (*Pup1* donor) allele at all or part of the loci tested, but very few have the gene *OsPupK46-2*, which seems to be the major determinant of *Pup1* effect (Gamuyao *et al.*, 2012). This gives room for improvement of both drought and P deficiency.

For irrigated areas affected by salinity, the tolerance QTL *Saltol*, derived from the salt-tolerant cultivar Pokkali (Bonilla *et al.*, 2002; Thomson *et al.*, 2010a), is being incorporated into elite irrigated rice varieties, such as Sahel 108, Sahel 201 and ITA 212, to improve their tolerance to salinity. Advanced backcross breeding lines (BC₂–BC₃) have been obtained with *Saltol* introgression using FL478 and Pokkali as donor parents. In the Sahel, where rice is also affected by cold stress at the vegetative stage, AfricaRice scientists are targeting the cold tolerance QTLs (*Ctb-1*, *Ctb-2*) identified in Silewah (Saito *et al.*, 2004) and *qCTS12a* identified in M202 (Andaya and Mackill, 2003b). For submergence-prone areas, African *Sub1* lines were developed using WITA 4, a popular variety in Nigeria, as recipient (Gregorio *et al.*, unpublished) and new versions using NERICA-L 19, TOX4004, Kogoni, FARO44 and BW348-1 as recipients are in the pipeline. The major QTL *Sub1*, identified from FR13A (Xu and Mackill, 1996), provides tolerance to complete submergence for up to 2 weeks. Asian *Sub1* varieties

have been extensively evaluated in South and South-east Asia and in Africa. In all cases, similar results were obtained (Table 11.2), with consistent yield advantages of 1 t/ha to over 3 t/ha compared with the original varieties following submergence for durations of about 4 to over 18 days (Mackill *et al.*, 2012). However, this QTL is not effective in areas that are likely to experience prolonged waterlogging or partial stagnant flooding of over 20 cm (Singh *et al.*, 2011). Therefore for these areas and for deep-water conditions, new materials should be developed targeting elongation ability.

Another powerful marker-assisted approach, marker-assisted recurrent selection (MARS), is being implemented for the improvement of drought tolerance in the lowlands. Allele diversity within bi-parental populations is exploited by MABC to increase the frequency of beneficial alleles for quantitative traits. Cyclical recombination of lines bearing interesting chromosomal segments will then be conducted and favourable alleles accumulated. Six populations have been developed and more than 200 lines are under evaluation for drought tolerance in Nigeria, Mali and Burkina Faso (M.-N. Ndjiondjop, Cotonou, Benin, 2012, personal communication).

With the use of molecular markers, AfricaRice expects to increase the efficiency and effectiveness of its breeding programmes compared to conventional breeding methods.

Challenges and Outlook

Anticipating the effects of climate change on rice production

Climate change is emerging as one of the most important challenges of the 21st century. Africa is particularly vulnerable to climate change, because of its high proportion of low-input, rainfed agriculture compared with other regions of the developing world (IPCC, 2001). The changes in key climatic variables (i.e. rainfall and temperature) will likely modify the distribution, frequency and severity of abiotic stresses. Prediction models in some cases provide contradictory conclusions, but what is clear is that increased flooding in low-lying areas, greater frequency and severity of droughts in arid and semiarid areas, rising of sea water level (which will increase salinity intrusion in

Table 11.2. Performances of rice lines bearing the resistance allele at *Sub1* locus after 21 days of submergence at AfricaRice station, Ibadan (Nigeria), in the 2009 dry season. Survival is expressed as the number of surviving hills under submergence as a percentage of survival without submergence. (From Gregorio, unpublished.)

Variety	Survival (%)	Yield under submerged conditions (t/ha) ^a	Yield under normal conditions (t/ha)	Yield reduction (%)
TDK1-Sub1(BC ₃ F ₃)	95.45	3.62a	4.46	18.99
Swarna-Sub1(BC ₃ F ₃)	90.95	3.56a	4.45	19.92
BR11-Sub1	95.34	2.60b	4.11	36.49
Samba	94.42	2.59b	3.94	34.16
Mahsuri-Sub1(BC ₃ F ₃)				
Samba	96.45	2.37b	3.62	34.47
Mahsuri-Sub1(BC ₂ F ₃)				
CR1009-Sub1	96.95	2.21b	3.61	29.78
IR64-Sub1(BC ₃ F ₃)	96.92	2.21b	3.02	26.89
IR64	21.43	1.32c	3.19	58.46
Samba Mahsuri	17.44	0.81cd	3.83	78.73
Swarna	19.49	0.64de	4.29	85.16
FARO 35 (ITA 212)	20.41	0.41de	3.61	88.61
WITA 4	4.08	0.08e	3.77	97.99

^aNumbers followed by the same letters are not significantly different from each other.

coastal areas) and excessive heat stress, will more likely be observed. An increase in CO₂ concentration in the absence of increases in temperature is expected to increase productivity of rice. However, if the temperature rises by about 1°C or more, the situation reverses, particularly in tropical climates (Ahmed *et al.*, 2010). Globally, climate-change effects will adversely affect rice production. Breeding programmes should, therefore, be adjusted in anticipation of these changes, to develop rice varieties adapted to future environments. Breeding for abiotic-stress tolerance is one important option, but other alternatives should also be considered. Research is being coordinated by IRRI to introduce the C₄ metabolic pathway into rice. This is expected to enhance yield potential of the current rice varieties by 30–50%. Besides, the new varieties are expected to require less nitrogen and water and also possess better adaptation to unfavourable climates, particularly to areas with higher temperatures and insufficient water resources (Sheehy *et al.*, 2007).

Changes in the climatic patterns will result in several other modifications in agricultural practices. As described by Satya and Maiti (2011), changes in the management practices for increasing crop productivity (such as water-saving and water-harvesting technologies), shift in cultivation patterns (rice to be replaced by wheat in drier and cooler areas and *vice versa* for wetter and hotter areas), changes in sowing and harvesting times to avoid stressful windows of time, reduction of crop growth duration, etc., are expected to be important determinants for shaping future agriculture to cope with worsening climate adversities. Additionally, a clear understanding of target environments and their evolution in terms of climate change will be an important objective to better set priorities and match new rice varieties to future climates in particular regions. The use of prediction models, such as RIDEV (Rice Development) developed by AfricaRice in the 1990s, will help in this exercise. This risk-assessment and planning model was developed to estimate the cycle duration and yield losses due to temperature-induced sterility for any combination of rice genotype, site, planting date and planting method in the Sahel (Dingkuhn, 1995). Additionally, it gives crop management recommendations based on the crop phenology. There are studies ongoing at

AfricaRice, in collaboration with CIRAD scientists to improve RIDEV, thus allowing for predictions of crop responses to climate change.

Precise and high-throughput screening for tolerance of abiotic stresses

While high-throughput genome-wide genotyping is becoming increasingly accessible and is cost reducing, phenotyping of large germplasm collections and populations for stress tolerance in field trials is still laborious, imprecise and costly. The immediate difficulty of working with abiotic stresses still lies in reliably measuring the stress and quantifying the tolerance of the stress in large populations.

Field trials targeting climatic factors such as drought and temperature extremes are often unpredictable, while uniform stress conditions are difficult to achieve in trials for problem soils. This means that selection pressure is generally inconsistent and sometimes even contradictory across years and seasons (Lafitte *et al.*, 2006). Moreover, different stresses are often found together. For example, salinity problems are rarely due only to the common salt, NaCl; severity of Fe toxicity is dependent on other mineral deficiencies such as P and K; and during some periods both drought and heat stress can be concomitant. Most soil problems, such as Al and Fe toxicities and Zn deficiency, considerably hinder root growth and regeneration, increasing the crop's sensitivity to drought and nutrient deficiency. In general, abiotic stress conditions in the field are rarely due to a single factor and these are the typical farm conditions that are very difficult to reproduce in the laboratory or greenhouse. The complexity of the tolerance traits involved and the strong effect of the environment, and in most cases, the insufficient knowledge of the mechanisms involved in tolerance, add to these difficulties. There is therefore a need for high-throughput screening protocols to allow the evaluation of a large number of lines under the same conditions. For these reasons, phenotyping remains the current bottleneck for crop improvement and proper molecular mapping (Xu and Crouch, 2008; Serraj *et al.*, 2009).

Well-characterized environments and well-established selection criteria are prerequisites for developing a reliable and precise phenotyping system (Xu and Crouch, 2008). Developments in thermal, spectral reflectance, fluorescence and multi-sensor imaging may provide rapid, economic and non-invasive selection criteria (Chaerle and Van Der Straeten, 2000; Jones and Schofield, 2008). Once such reliable phenotyping methodologies are developed they can be transferred to national (NARS) partners to conduct multi-location/multi-environment trials using the same protocols to assess the responses of new breeding lines under a wider range of, or site-specific, stresses. This should be accompanied by effective data-acquisition systems to acquire and analyse the data in the shortest possible time. One major constraint for progress in Africa is the limited resources devoted to research on abiotic stresses, including lack of trained scientists and efficient phenotyping facilities. Greater investments in these areas would help build stronger breeding programmes to tackle existing challenges and ensure the capacity to develop adaptive and mitigation measures to cope with future adversities.

Breeding rice varieties with multiple stress tolerance

The desired features of new climate-ready rice varieties should include tolerance to various abiotic stresses that prevail in areas where these varieties are targeted for commercial use. This will entail combining tolerance of two or more stresses like drought and heat, salinity and excess water, cold and excess water, P deficiency and drought or Fe toxicity and excess water, into one genetic background. In most cases, breeders select for multiple stress tolerance by performing most of their selection process at actual field sites, as in participatory varietal selection (PVS) approaches. For example, studies of the distribution of the *Pup1* QTL in diverse germplasm have shown that most of the drought-tolerant lines and varieties developed for upland conditions also have the *Pup1* QTL (Chin *et al.*, 2010). With the progress made in the development of molecular tools, identification of QTLs and the use of DNA markers in breeding, it is now possible to

make the precise desired combinations. For example, varieties combining submergence tolerance and salt tolerance are being developed by pyramiding *Sub1* and *Saltol* QTLs through MABC (Mackill *et al.*, 2012). These lines are needed in the coastal and mangrove areas of sub-Saharan Africa which can experience both salinity and submergence. The availability of high-throughput single-nucleotide polymorphism (SNP) genotyping platforms will also enable more efficient MABC by reducing the cost per marker and speeding up the process through 'multiplexing' (Thomson *et al.*, 2010b). AfricaRice, IRRI and Cornell University are developing SNP chips specific to African rice, *O. glaberrima* (M. Semon and M.-N. Ndjiondjop, Cotonou, Benin, 2012, personal communication).

Studies of the interactive effects of different stress combinations should be emphasized (Ismail *et al.*, 2007), since they will give greater insight into the positive and negative effects of combining genes for higher tolerance of the same or different abiotic stresses. The remaining challenge will be to incorporate these complex adaptive traits into high-yielding varieties through QTL pyramiding, while simultaneously retaining the adaptive features, high yield potential and grain quality of the recurrent varieties (Ismail *et al.*, 2008). Meanwhile, tolerance to pests and diseases should not be neglected. Climate-ready varieties should also possess sufficient resistance to major diseases that occur in the targeted rice-production zones of Africa.

Conclusions

Rice production in sub-Saharan Africa is constrained by various environmental stresses. Climate change adds more uncertainties, particularly for smallholder subsistence farmers. Stabilizing crop yields and limiting yield losses will undoubtedly reduce resource-poor African farmers' vulnerability to poverty and food insecurity. Several options exist with the most cost-effective one being crop improvement using different strategies and technologies as discussed in this chapter. The genetic variation observed in rice for tolerance to various abiotic stresses could be effectively exploited for crop improvement by using tolerant varieties and landraces as donors

in breeding programmes using modern tools. Major QTLs have been identified for almost all abiotic stresses, including drought, providing considerable opportunity for enhancing rice tolerance of these stresses. These major QTLs are being used to improve varieties that are widely popular among farmers in the target regions.

More effort is, however, needed to collect and preserve local African germplasm, including wild species, in order to identify better donors for use in breeding and for tagging novel QTLs/genes. Precise high-throughput phenotyping protocols also need to be in place for effective screening of breeding lines, as is a good knowledge of the target environments. The new tolerant

varieties should perform well under both stress and non-stress conditions and also retain acceptable grain quality to ensure their adoption and acceptance by both farmers and consumers. Furthermore, the availability of rice cultivars tolerant to abiotic stresses will provide an incentive for farmers to invest in the costly processes of high input use and efficient postharvest technologies, and in land reclamation and preservation, besides other efficient agricultural practices. Overall, this will result in greater and more sustainable productivity in vulnerable regions of sub-Saharan Africa even with the anticipated climate change and its adverse effects on rice production.

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