Breeding Rice Varieties for Abiotic Stress Tolerance: Challenges and Opportunities

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Vishnu V. Nachimuthu, Robin Sabariappan,
Raveendran Muthurajan, and Arvind Kumar

Abstract

Climate change-induced abiotic stresses are considered as notable threat to world food security affecting crop, livestock, and fisheries production which are all fundamental for sustainable development of human life. Impact of climate variability affecting water availability, nutrient levels, soil moisture, temperature, and tropical ozone in crop yield is measured in various studies. Rice, the critical crop in maintaining food security, has high vulnerability to increased frequency and intensity of extreme weather events which affects crop growth at macro- and microenvironment. Meanwhile, rising temperatures and consequent rise in sea level can make farming riskier by increasing salinity in the cultivatable lands. Decrease in productivity of rice is mainly related to extreme environmental conditions such as water deficit, high temperature, submergence, salinity, cold, and accumulation of heavy metals apart from higher incidence of pathogens and pests. Crop germplasm, wild relatives, and other species serve as main genetic sources for tolerance. These can be useful in crop breeding as they have had adaptation and acclimation responses developed through natural selection process. Hence, identification of genetic loci, mechanism, and signaling path-

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V.V. Nachimuthu • A. Kumar (✉)
South Asia Breeding Hub, International Rice Research Institute, ICRISAT Campus,
Patencheru 502342, Hyderabad, Telengana, India
e-mail: v.varthini@irri.org; a.kumar@irri.org

R. Sabariappan
Center for Plant Breeding and Genetics, Tamil Nadu Agricultural University,
Coimbatore 641003, Tamil Nadu, India
e-mail: robin.tnau@gmail.com

R. Muthurajan
Centre for Plant Molecular Biology & Biotechnology, Tamil Nadu Agricultural University,
Coimbatore 641003, Tamil Nadu, India
e-mail: raveendrantnau@gmail.com

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ways provides a paradigm to improve yield under diverse ecosystem. By using marker-assisted selection, beneficial alleles from wild relatives can be introgressed to develop climate-ready rice varieties.

15.1 Introduction

Global food production needs to be increased by at least 50% to meet out the food and fuel requirement of projected 9.1 billion people during 2050 (Yamori et al. 2013). This warrants an increase of one billion tonnes of annual cereals and around 200 million tonnes of meat. Predictions based on prevailing growth trends in major food crops, viz., rice, wheat, maize, soybean, etc., suggest that prevailing productivity growth will not be sufficient to meet the projected food demands (Ray et al. 2013). Achieving this target needs overcoming challenges, viz., yield plateau, declining land, water and labor resources, and predicted adverse effects of global climate change. Impacts of these key determinants are being witnessed all over the world, but vulnerability of agriculture in developing countries is of major concern in view of the large populations being dependent on agriculture, excessive pressure on natural resources, and poor coping mechanisms. Climate change has already started affecting yield of wheat and paddy in parts of India due to increased temperature, water stress, and reduction in number of rainy days. Its impacts are likely to aggravate yield losses in major agricultural crops thereby expected to affect food security. The projected agricultural productivity loss due to changing climate by 2100 is about 30–40% (Cline 2007; Aggarwal 2008). Predicted increase of 1–2 °C in global mean temperature along with reduced water availability may reduce cereal yields in tropical regions (Rosenzweig et al. 2013). The reduction in annual productivity may be to the tune of 22, 3, 9, and 2 million tonnes of maize, rice, wheat, and soybean, respectively (Ray et al. 2015).

Rice is the second most important cereal food crop next to wheat, and its production has to be increased by at least 30% by 2030 and 50–70% by 2050. Abiotic factors such as drought at the beginning of the cropping season, flash flooding at the reproductive stage, coastal salinity, susceptibility of fine-grained cultivars to diseases, etc. are main factors that affect the productivity of the most of the rice-growing areas. Annual rice production is susceptible to ~32% fluctuation due to climatic factors, viz., higher precipitation variation in South Asia and higher temperature variation in Southeast and East Asia rice-growing tracts (Ray et al. 2015). Enumerating the shifting pattern of abiotic and biotic stresses caused by climate change, the productivity of major calorie providers such as rice, wheat maize, and soybean has to be expanded to 87% more by 2050 to bottle up emerging global food shortage (Kromdijk and Long 2016).

Considering the magnitude of problems due to climate change, developing climate-smart rice varieties either through conventional breeding or molecular breeding or genetic engineering approaches provides for ways to tackle current predicament in rice production. Climate-smart varietal breeding aims at improving yield and its yield stability across multiple stressors induced by climate extremes. For rice production, flooding, water stress, high temperature, salinity, cold, and altered pest and disease outbreak pose major challenges for its production.

The green revolution during the 1960s was focused on higher productivity with better fertilizer responsiveness through introduction of modern semidwarf and high-yielding varieties in rice and wheat. As a consequence, two- to threefold increase in productivity has been achieved through modern plant breeding tools during the last three to four decades. However, yields are stagnating around 8 Mg ha^{-1} for the past 10–15 years even under well-managed conditions. As more than 40% of the rice-growing areas are either rainfed lowland or upland cultivation, performance of the high-yielding varieties is affected frequently due to vagaries of monsoon and other biotic/abiotic stresses. Current scenario of climate change has shifted the focus of rice breeders from just yield to combining yield with multiple stress tolerance for surviving under extreme climate events. Therefore, multidisciplinary programs have been launched for developing climate-smart rice varieties adapted to changing climatic conditions. Different innovative breeding techniques are being integrated to exploit genetic variation to develop climate-smart rice varieties exhibiting enhanced tolerance against multiple stresses coupled with high yield. An overview of the global efforts in developing rice varieties adapted to climate-induced stresses and thereby preventing yield decline by extreme weather events is discussed below.

15.2 Breeding for Enhanced Drought Tolerance

Plant drought stress is defined as “Water deficit at any plant growth stage – though with more impact during reproductive and grain filling stages” (Reynolds et al. 2016) – that results in 10% yield loss compared to an adequately-watered control. Major symptoms of drought include accelerated plant development resulting in reduced biomass, decreased seed set due to reduced panicle size or failure of pollination or reduced grain size, and reduction in harvest index (HI) due to early grain filling and premature senescence. Plant’s adaptation to soil moisture deficit is controlled by several mechanisms, viz., escape, avoidance, or tolerance strategies (O’Toole and Chang 1979). Drought escape mechanism is defined as the ability of the plant to complete its life cycle before enduring water starvation. Rapid phenological development and developmental plasticity pave way for plant’s escape from drought. Avoidance strategy makes the plant to withstand drought by maintaining higher internal water status either through increased uptake of water from soil or through reduced water loss through the canopy. Drought tolerance is the ability of the plant to survive even at low tissue water content. Translocation of assimilates capable of maintaining osmotic status is considered as an adaptive trait associated with dehydration tolerance (Arrandeau 1989). Breeding for drought tolerance still remains a challenge for breeders due to its complex genetic nature with higher environmental plasticity and involvement of multiple metabolic pathways. Rice germplasm harbors large amount of functional genetic diversity for drought tolerance-related traits/mechanism, and careful exploitation of genetic variation will allow us to integrate diverse traits for improving resilience of rice against climate change. Most of the conventional approaches in drought breeding emphasize on secondary traits such as root architecture and mass, physiological parameters such as water use efficiency, relative water content, osmotic adjustment, etc. Selection for secondary traits such as root architecture (Courtois et al. 2009; Uga et al. 2013), leaf rolling (Price et al. 1997), stomatal conductance (Price et al. 1997; Khowaja and Price 2008), relative water content, osmotic adjustment (Kamoshita et al. 2002; Nguyen et al. 2004), cell membrane stability (Tripathy et al. 2000), epicuticular wax (Srinivasan et al. 2008), stem reserve mobilization, and canopy temperature (Prince et al. 2015) has been used to develop drought-tolerant lines. Integrating all these parameters with better yield under water deficit condition was a great challenge for plant breeders. Because of low heritability and difficulty in precision phenotyping of these traits, attempts were made to use "yield under stress" as a criterion for selection in breeding programs despite the moderate heritability of yield traits (Venuprasad et al. 2007, 2008; Kumar et al. 2008, 2009). This enabled the scientists to select drought-tolerant rice genotypes directly based on yield under drought stress (Kumar et al. 2014; Lafitte et al. 2004; Lanceras et al. 2004; Bernier et al. 2007; Venuprasad et al. 2007; Kumar et al. 2008).

Completion of rice genome sequencing project and advancements in genotyping procedures have enabled us to dissect out the genetic basis of drought tolerance through linkage mapping and association mapping. QTL mapping for drought tolerance was carried out for different primary and secondary traits using various populations to dissect genetic basis of this multi-loci controlling trait (Kamoshita et al. 2008). QTLs and markers identified have been utilized via marker-assisted selection (MAS), marker-assisted backcross breeding (MABB), and marker-assisted recurrent selection (MARS) to develop drought-tolerant rice varieties.

Marker-assisted selection for better root traits (QTLs on chromosomes 2, 9, and 11) in a population derived between Kalinga III and Azucena resulted in the identification of a superior drought-tolerant rice genotype, e.g., *Birsa Vikas Dhan* 111, that was released in Jharkhand, India (Steele et al. 2006, 2007). Keeping grain yield under stress as a criterion for genetic mapping has resulted in the discovery of several mega-effect QTLs in tolerant genotypes, viz., Apo, Way Rarem, Vandana, Nagina 22, etc. Bernier et al. (2007) have reported the first large-effect QTL, namely, $qDTY_{12.1}$, associated with grain yield (explaining 33% variance under severe upland stress) under water deficit condition in a population derived between Vandana x Way Rarem. Further molecular genetics studies using the QTL-NILs revealed that this mega-effect QTL is offering enhanced drought tolerance through the production of more number of lateral roots and efficient transpiration control (Henry et al. 2014), and unexpectedly the susceptible parent Way Rarem contributed positively (Dixit et al. 2012).

The same locus was also reported in the genetic background of a cross between IR74371-46-1-1 and Sabitri (Mishra et al. 2013). Later, a major-effect QTL $qDTY_{1.1}$ on chromosome 1 was identified in a cross involving a drought-tolerant Nagina 22 with high-yielding cultivars, i.e., Swarna, IR64, and MTU1010. This is one of the most consistent QTLs for grain yield under drought which coincide with *sd1* (semidwarf) region and QTL for plant height and flowering under water deficit condition (Vikram et al. 2011). Several other major-effect QTLs, namely, $qDTY_{2.1}$, $qDTY_{3.1}$, $qDTY_{3.2}$, $qDTY_{6.1}$, and $qDTY_{10.1}$, were reported to be associated with grain yield under water deficit conditions through the studies conducted at the International Rice Research Institute, Philippines (Kumar et al. 2013), by utilizing mapping population(s) developed between Swarna and Apo (Venuprasad et al. 2009). $qDTY_{3.2}$ was identified in the region of *HD9* that affects flowering in Vandana/Way Rarem population whereas its effect on grain yield under drought stress established from N22/Swarna population (Vikram et al. 2011). Most of the QTLs associated with grain yield under stress were found to be linked with QTLs controlling plant height and days to flowering. Co-localization of these traits is not preferred to breed varieties for various ecosystems; therefore, a suitable MAB strategy to break the linkage with these traits needs to be designed for transferring these QTLs. Pyramiding of these desirable QTLs will lead to enhanced level of tolerance. Swamy and Kumar (2013) demonstrated pyramiding of different combinations of grain yield under stress QTLs in the genetic background of IR64 and reported that BC lines harboring combination $qDTY_{2.2}$ and $qDTY_{4.1}$ yielded higher than lines with $qDTY_{2.2}$, $qDTY_{4.1}$, $qDTY_{9.1}$, and $qDTY_{10.1}$. Vikram et al. (2016) have studied the linkage and pleiotropic effects of the QTLs, i.e., $\mathrm{qDTY}_{1.1}$, $\mathrm{qDTY}_{3.2}$, and $\mathrm{qDTY}_{12.1}$, and concluded that all these three QTLs linked with QTLs for plant height and flowering. $\mathrm{qDTY}_{3.2}$ has shown positive interaction with other QTLs by reducing flowering duration, thereby helping in avoiding drought and leading to increase in grain yield. Using these QTLs, several commercial high-yielding varieties, viz., IR64, Swarna, Vandana, Sabitri, Samba Mahsuri, TDK1, and Anjali, were improved for their drought tolerance ability (Kumar et al. 2014).

To overcome the limitations in biparental linkage mapping, linkage disequilibrium mapping/association mapping strategy has been developed which takes advantage of historical recombination that provides allelic richness and better resolution to detect natural variation. Linkage disequilibrium, nonrandom associations among different genetic loci, provides a way to detect robust QTLs by using dense markers evenly distributed throughout the genome. Association analysis is done either by considering candidate gene responsible for the trait (Candidate gene association studies) or whole genome scan for detecting QTLs. In rice, association analysis is mainly done with landraces, elite cultivars, and other germplasm lines which provide abundant variations for different traits. Association mapping needs population structure and LD information for curtailing false positives. In rice, five major groups, i.e., *indica*, aus, aromatic, temperate *japonica*, and tropical *japonica*, were identified in many studies (Garris et al. 2005; Xu et al. 2012). Phung et al. (2014) has reported that LD decay was faster in *indica* subpopulation than *japonica* subpopulation. Hence *indica* subpopulation need high marker density for genomic analysis thereby provides better resolution for association analysis. Association mapping was carried out by various researchers for drought tolerance in rice with the focus on secondary traits such as root architecture. Phung et al. (2016) further identified two significant associations for root thickness on chromosome 2 and for crown root number on chromosome 11 in a panel of 200 accessions. Association analysis was performed using mixed model with population structure and kinship values for whole panel as well as for *japonica* and *indica* accessions subpanels separately. Courtois et al. (2013) has performed association analysis in *japonica* panel of 167 accessions with the identification of 51 significant associations with different root traits such as maximum root length, deep root biomass, root dry mass, shoot biomass, and root to shoot ratio. Deep rooting, an important drought avoidance trait, has been mapped to a major QTL at chromosome 2 by genome-wide association mapping as well as family-based linkage mapping (Lou et al. 2015). Genome-wide association mapping was performed by Zaniab Al-Shugeairy and Robinson (2015) for the trait drought recovery with 328 rice cultivars which reveals a locus at chromosome 2 has significant association with this trait. Therefore, various genomic regions identified for drought-related traits through association analysis provide an effective way to narrow down the wide genomic regions influencing this quantitative trait. Next-generation breeding tools, viz., nested association mapping (NAM) and multi-parent advanced generation intercrosses (MAGIC), are the renewed strategies for simultaneous tagging of genomic regions controlling drought tolerance-related traits and identification of superior recombinants.

15.3 Breeding for Heat Stress Tolerance

High temperature stress (HTS) is one of the important yield-limiting factors for most of the agriculturally important crops, and frequent occurrence of short-term heat shocks (extremely high temperatures) had been a common phenomenon during recent years (Mackay 2008). Predictions on global climate models suggest that a mean increase of 1.0–3.7 °C is expected to occur in majority of agricultural areas by the end of the twenty-first century (IPCC 2013). High temperature affects grain yield especially when it coincides with reproductive stage by affecting fertility of gametes. Reynolds et al. (2016) have reported two critical stages, viz., micro- or megasporogenesis and fertilization, which are highly sensitive to rise in temperature which can lead to loss of male and female gamete fertility, reduced pollen deposition and growth, poor fertilization, as well as early embryo abortion. The adverse effect of high temperature on crop yield can be minimized by breeding heat-tolerant genotypes utilizing functional alleles.

Even though rice is a heat-loving plant, its performance is affected when temperature is beyond threshold levels. Analysis of the temperature and rice yield during 1992–2003 at the International Rice Research Institute (IRRI) showed that rice grain yield declined by 10% for each 1 °C increase in the temperature during growing season (Peng et al. 2004). Recent studies from the Yangtze River in China showed that an estimated 3 million ha of rice were damaged and about 5.18 million t of paddy rice lost in 2003 due to a heat wave with HDT >38 °C lasting more than 20 days (Li et al. 2004; Xia and Qi 2004; Yang et al. 2004). Likewise, IR64, one of the widely grown rice varieties, which performed well over the last three decades under local hot tropical conditions in Pakistan, suffered a 30% yield decline during a heat wave in 2007 (Dr. Mari, IRRI, Dokri).

Multi-crop Experts' Committee Meeting conducted by the US Agency for International Development (USAID) and the Bill & Melinda Gates Foundation during 2013 has described heat stress as "Supra-optimal temperatures occurring at any plant growth stage that can result in ≥10% yield loss. This is typically characterized by accelerated plant development resulting in reduced photosynthetic area, plant biomass, and seed set. Where heat stress occurs during grain-filling, reduced grain weight (and therefore HI) will result from inhibition of starch synthesis, increased starch breakdown, and/or premature and rapid increase in senescence" (Reynolds et al. 2016).

The process of evolution has developed various adaptive mechanisms, viz., avoidance and tolerance in plants to survive under high temperature stress. Mechanism of high temperature stress avoidance includes flowering time alteration to favor flowering during the cooler period of the day, altered leaf orientation, excessive rooting, and reducing temperature by transpiration (Sailaja et al. 2015). Tolerance mechanisms against heat stress involve rapid alterations in molecular processes, i.e., production of heat shock proteins (HSP), late embryogenesis abundant (LEA) proteins, and metabolites, membrane modifications, accumulation of free radical scavengers, and altered cytoskeleton (Bita and Gerats 2013). Existence of natural genetic variation for heat-adaptive traits in crop germplasm makes the breeding a viable option for achieving yield stability in heat stress environment. Reynolds et al. (2016) has identified priority traits for high temperature stress tolerance (Table 15.1).

Table 15.1 Traits for high temperature tolerance

Trait class	Specific trait
Photosynthesis/biomass/metabolism	Canopy temperature
	Normalized difference vegetative index (NDVI)
	Final biomass
	Night respiration
	Chlorophyll fluorescence
	Starch synthesis
	Membrane thermostability
	Spectral indices for pigments (chlorophyll and carotenoid)
Fertility/source-sink partitioning	Anthesis/flowering time
	Spikelet fertility/pollen viability/pollen shedding level
	Grain filling
	Harvest index
	Phenology
	Tillering
	Assimilate remobilization
	Plant growth regulators
	Coleoptile length

Source: Reynolds et al. (2016).

Global heat stress breeding programs have successfully identified donors for different strategies to increase resilience to heat stress damage (Ishimaru et al. 2010; Jagadish et al. 2010; Ye et al. 2012). Firstly, cultivation of early maturing versions of elite genotypes suitable for summer cultivation will enable the rice plant escape from hotter months. Secondly, genetic manipulation of early-morning flowering (EMF) will shift the flowering patterns to cooler hours of the morning. Thirdly, true heat tolerance will be induced through maintained reproductive success in spite of higher temperatures coinciding with flowering. Breeding by conventional techniques for heat stress has been a challenging task due to limited information on genetic determinants, biological mechanisms, and effective screening methods. In general, genotypes are screened under multiple hot environments and selection based on its yield stability across various environments. Advancements in development of controlled climate growth chambers, phytotron facilities, etc. have enabled the scientists to devise rapid protocols for screening large number of genotypes against high temperature stress (Jagadish et al. 2010).

Intensive research efforts across the globe have resulted in the identification of few heat-tolerant rice lines, viz., Nagina 22, Dular, Kasalath, Giza178, and Todorokiwase (Tenorio et al. 2013). In general i*ndica* genotypes were found to exhibit better heat tolerance than *japonica* genotypes (Zhao et al. 2016). By using these tolerant genotypes, few major QTLs have been identified for various high temperature adaptive traits at various growth stages of rice. Through several studies using independent biparental mapping populations, around 52 main-effect QTLs and 25 epistatic QTLs explaining phenotypic variance of 2.27–50.11% have been identified (Cao et al. 2002, 2003; Zhu et al. 2005, 2006; Zhao et al. 2006; Chen et al. 2008; Kui et al. 2008; Zhang et al. 2008; Jagadish et al. 2010; Pan et al. 2011; Xiao et al. 2011). Cao et al. (2003) has identified few QTLs for seed setting under heat stress in a doubled haploid population derived between IR64 x Azucena and the most significant QTLs explaining largest phenotypic variance for seed setting was identified in IR64. Zhang et al. (2009) have identified two SSR markers, RM3735 on chromosome 4 and RM3586 on chromosome 3, to be linked to heat stress tolerance-related traits. The most significant heat-tolerant QTL explaining up to 50% of phenotype variance was found to be contributed by a heat-tolerant *indica* landrace Kasalath (Zhu et al. 2006). Wei et al. (2013) has identified a dominant locus *OsHTAS* on chromosome 9 which influences heat tolerance at seedling stage in rice. Using Giza178 as heat-tolerant donor, six QTLs were identified for spikelet fertility under HT stress in two different mapping populations derived from IR64 cross and Milyang 23 cross. One of the QTLs *qHTSF4.1* explaining phenotypic variance of 17.6% was found to increase spikelet fertility in various heat-tolerant lines (Ye et al. 2015). Zhao et al. (2016) used chromosome segment substitution lines derived from Sasanishiki (heat susceptible) and Habataki (heat tolerant) for identifying eleven QTLs for spikelet fertility, daily flowering time and pollen shedding level (Table 15.2).

A mutant NH219 of Nagina 22 was found to exhibit enhanced level of tolerance against HT stress, and single-marker analysis among F_2 segregates of IR64 × NH219 revealed significant association of RM1089 with number of tillers and yield per

Table 15.2 QTLs identified for heat tolerance in rice, particular quantities trait loci (QTL) on chromosome (Chr) number

QTL	Chr.	Marker	Position (Mb)	Population	Donor	References
qSFht2	2	RM1234-RM3850	11.3–35.4	SasanishikiXHabataki CSSL	Habataki	Zhao et al. (2016)
qtl2.2		C601	30.3	Bala × Azucena RIL	Azucena	Jagadish et al. (2010)
qHt2		RM183-RM106	25.1	T219 × T226 RIL	T226	Chen et al. (2008)
qhts-2		RM406-525	28.3–35.2	Zhongyouzao 8 × Toyonishiki RIL	Toyonishiki	Zhang et al. (2008)
qSFht4.2	4	RM3916-RM2431	28.6–34.9	SasanishikiXHabataki CSSL	Habataki	Zhao et al. (2016)
qhr4–3		RG214-RG143	31.7–33.7	IR64 × Azucena DH	IR64	Cao et al. (2003)
qPSLht5	5	RM1248-RM4915	0–4.3	SasanishikiXHabataki CSSL	Habataki	Zhao et al. (2016)
qhts-5		RM405-274	3.1–26.9	Zhongyouzao 8 × Toyonishiki RIL	ZYZ8	Zhang et al. (2008)
qDFT3	3	RM3766-RM3513	6.9–25.1	SasanishikiXHabataki CSSL	Sasanishiki	Zhao et al. (2016)
qhr3–1		RZ892-RG100	5.2–12.9	IR64 × Azucena DH	Azucena	Cao et al. 2003)
qhts-3		RM157b-282	12.41	Zhongyouzao 8 × Toyonishiki RIL	Toyonishiki	Zhang et al. (2008)
qDFT8	8	RM5891-RM4997	26.6–28.2	SasanishikiXHabataki CSSL	Sasanishiki	Zhao et al. (2016)
qtl8.3		RG598	27.6	Bala × Azucena RIL	Bala	Jagadish et al. (2010)
qDFT10.1	10	RM6737-RM6673	18.7–23.0	SasanishikiXHabataki CSSL	Sasanishiki	
qtl10.1		C16	20.8	Bala × Azucena RIL	Bala	Jagadish et al. (2010)
SSPF10, SSPc10,	11	RM6132-RM6100	18.8–18.9	996 × 4628 RIL	996	Xiao et al. (2011)
qDFT11		RM1355-RM2191	17.2–24.7	SasanishikiXHabataki CSSL	Sasanishiki	Zhao et al. (2016)
qtl11.1		G1465	24.2	Bala × Azucena RIL	Azucena	Jagadish et al. (2010)
qPSLht1	1	RM1196-RM6581	21.9–31.5	SasanishikiXHabataki CSSL	Sasanishiki	Zhao et al. (2016)
qhr1		RG381-RZ19	30.9	IR64 × Azucena DH	Azucena	Cao et al. (2003)

plant, RM423 with leaf senescence, RM584 with leaf width, and RM229 with yield per plant (Poli et al. 2013). In an African rice cultivar, a major QTL TT1 involved in the degradation of ubiquitinated proteins during heat stress influencing thermotolerance was identified (Li et al. 2015). Many putative QTLs identified in various studies were overlapped or adjacent with each other suggesting the existence of heat-tolerant alleles widely across the chromosomes. Fine mapping of these QTLs will provide extensive information on underlying candidate genes and metabolism involved in high temperature tolerance stress. Fine mapping of these QTLs will provide extensive information on underlying candidate genes and metabolism involved in high temperature stress. These QTLs can be introgressed into commercial varieties for developing heat-tolerant lines.

15.4 Breeding for Submergence Tolerance

Submergence is becoming a second major abiotic stress affecting rice production under rainfed lowlands of Asia. During recent years, extent of damage caused by submergence stress has increased due to extreme weather events such as unexpected heavy rains that inundate rice areas. Consequences of submergence range from low light intensity, limited oxygen availability (hypoxia), soil nutrient effusion, physical injury, and increasing pest and disease access. Rice is extremely susceptible to anaerobic conditions during all its growth stages starting from germination (anaerobic germination), early vegetative growth, and post-flowering (Angaji et al. 2010). Flooding during germination and early seedling growth affects seedling establishment in direct seeded rice, both in rainfed and irrigated areas, because of their high sensitivity to hypoxia at this stage (Ismail et al. 2009). Hence, developing submergence-tolerant rice varieties is inevitable to sustain rice production in South and Southeast Asia. Limited genetic variation has been reported for submergence tolerance, and landraces or traditional genotypes, viz., FR13A, Goda Heenathi, Thavalu, Kurkaruppan, etc., were found to exhibit high level of tolerance to submergence (Miro and Ismail 2013). As these genotypes are poor yielders and inferior in their grain quality, developing high-yielding varieties that are submergence tolerant and readily accepted by farmers will help in sustaining increased rice productivity in target regions.

Understanding of the physiological and biochemical bases of submergence tolerance has progressed well in recent years, making it possible to design efficient phenotyping protocols, and has paved way for further genetic and molecular studies, to discover genes underlying component traits associated with tolerance. High-yielding rice cultivars with enhanced tolerance to repeated flooding, better regeneration capacity, and faster growth after flooding to produce sufficient biomass in a shorter period and to minimize delay in flowering when submerged are needed for flood-prone areas. Thorough biochemical studies involving susceptible and tolerant rice genotypes revealed that maintenance of high levels of stored carbohydrates in the seedlings prior to submergence coupled with minimum shoot elongation and retention of chlorophyll were contributing for enhanced tolerance.

Several QTLs controlling submergence tolerance have been reported by many authors including a single major quantitative trait locus (QTL) on chromosome 9 (Xu and Mackill 1996; Nandi et al. 1997; Toojinda et al. 2003). Most of these reports were based on the exploitation of the landrace FR13A, one of the most submergence-tolerant cultivar originated in eastern India. A major QTL named Sub1 with a LOD score of 36 and an R^2 value of 69% (Xu and Mackill 1996) was found to confer tolerance against complete submergence for up to 2 weeks. Further fine-mapping of Sub1 using back cross inbred lines has resulted in the identification of a genomic region of approx. 0.06 cM (Xu et al. 2000). Sequencing the Sub1 region in an FR13A-derived line revealed the presence of three genes encoding putative ethylene responsive factors (ERF), Sub1A, Sub1B, and Sub1C. Out of these three putative candidates, Sub1A was subsequently identified as the major determinant of submergence tolerance (Xu et al. 2006). Cloning and characterization of a major QTL *Sub1* and subsequent identification of candidate genes underlying the effect of this QTL not only generated knowledge on the molecular mechanisms controlling submergence tolerance but also helped to design tightly linked gene-based markers for molecular breeding programs aimed at developing submergence-tolerant rice cultivars (Siangliw et al. 2003; Toojinda et al. 2005; Neeraja et al. 2007).

Considerable genetic variation exists in rice germplasm for anaerobic germination under flooding, and genotypes, viz., Khao Hlan On, Ma-Zhan Red, Khaiyan, Kalonji, Kharsu, and Nanhi, exhibited better germination under anaerobic conditions leading to better crop stand (Miro and Ismail 2013). Several genomic regions influencing anaerobic germination under flooding were identified by exploiting tolerant landraces. Two major QTLs, viz., qAG9-2 on chromosome 9 (Angaji et al. 2010) and qAG7-1 on chromosome 7 (Septiningsih et al. 2013), were reported using Khao Hlan On and Ma-Zhan Red, respectively. Recently, *qAG-9-2* was fine-mapped, and a candidate gene *OsTPP7* encoding a trehalose-6-phosphate phosphatase was identified to control anaerobic germination. Functional characterization of *OsTPP7* suggested its involvement in enhancing starch mobilization to drive embryo germination and coleoptile elongation (Kretzschmar et al. 2015). Both Sub1 and qAG9-2 are being extensively deployed in rice breeding programs to enhance submergence tolerance at both germination and vegetative stages. In 2003, IRRI initiated a program to introduce the *Sub1* QTL into six mega-varieties, like Swarna, Samba Mahsuri, BR11, IR64, CR1009, and TDK1, using marker-assisted breeding which has been extended to other popular high-yielding varieties that are grown in flood-prone regions of Asia and Africa (Septiningsih et al. 2009). The productivity and quality of these Sub1 varieties are indistinguishable from that of the parental cultivars under non-submerged conditions based on field trials and farmers' experience. *Sub1* introgressed lines showed a yield advantage of 1–3.5 Mg ha^{-1} based on the duration and flood conditions.

15.5 Breeding for Salinity Tolerance

Rice production is often constrained due to problems associated with soil and irrigation water. Among the soil factors, salinity remains at the top by affecting rice productivity significantly. It has been estimated that about 100 million ha of agricultural area suitable for rice cultivation in South and Southeast Asia is not under rice cultivation due to soil-associated problems (Senadhira et al. 1994). Sustained increase in rice production to meet the emerging demand in rice consumption warrants bringing in these areas under rice cultivation. Salinity is due to accumulation of soluble salts in the soil affecting crop growth and productivity. Salinity affects plant growth by reduced water uptake, cellular toxicity, and imbalance among nutrients inside cells (Munns et al. 2006). Rice productivity in both coastal area or salinity prone inlands is affected significantly thereby hindering harvest of potential yield of popular varieties.

Rice is sensitive to salinity throughout its life cycle starting from germination to reproductive phase. Limited genetic variation was found to exist in rice germplasm, and several studies have been conducted to identify intricate networks of salt tolerance mechanisms. Research across several salinity-acclimatized crops has revealed existence of salt tolerance mechanisms, viz., salt exclusion, control of net Na+ uptake across the plasma membrane (intracellular influx), and tonoplast (vacuolar and prevacuolar compartmentalization) of both root and shoot cells to minimize cytosolic and organellar ion toxicity, K^+/Na^+ ion homeostasis, vacuolar osmotic adjustment through biosynthesis of osmo-protectants, and compatible solutes for turgor maintenance and hormonal modifications (Munns and Tester 2008).

Survey of genetic variability in rice germplasm for salinity tolerance-related traits has led to the identification of tolerant cultivars such as Pokkali and Nona Bokra. Still, breeding for salinity tolerance has been slow in progress due to complex nature of genetic and physiological mechanisms underlying salinity tolerance. Key objectives in breeding for salt tolerance in rice include earliness, exclusion of sodium at root and shoot level, enhancing tissue tolerance, improved potassium uptake, upregulation of antioxidants, stomatal responsiveness, enhanced source partitioning, and high yield, most of which are quantitative traits. With a view to determine genetic basis of salinity tolerance in rice, an RIL population was developed from a cross between the salt-susceptible variety "IR29" and salt-tolerant "Pokkali." An important QTL *Saltol* associated with the sodium and potassium ratio in shoots and salinity tolerance at the seedling stage was identified in chromosome 1 (Gregorio 1997; Bonilla et al. 2002). Similarly, several QTLs controlling salt tolerance traits were identified after mapping analysis of an $F_{2:3}$ populations as developed from a cross between the susceptible *japonica* cultivar Koshihikari and salt-tolerant *indica* cultivar Nona Bokra. It includes major QTLs for Shoot K^+ concentration (*qSKC-1*) in chromosome 1 as it is associated with shoot K^+ ion concentration and Shoot Na+ concentration (*qSNC-7*) in chromosome 7 (Lin et al. 2004). Subsequent cloning reveals OsHKT1;5 (previously *SKC1*) gene that encodes sodium transporter that helps to control K^+ homeostasis under salinity by unloading Na+ from xylem. Existence of allelic variation in this region is said to confer salinity tolerance in rice seedlings by maintaining Na^+ and K^+ in shoots and leaf blades. Some *OsHKT1;5* alleles effectively maintain shoot K^+/Na^+ homeostasis owing to specific amino acid variations that enhance K^+ over Na^+ transport into root xylem sap and that alter either protein transmembrane stability or phosphorylation that affects function (Ren et al. 2005). Besides *Saltol* locus, many studies have identified various QTLs for different tolerant traits (Mangrauthia et al. 2014). Numerous genes have also been identified through functional genomics studies of salt stress responses which have shown improved tolerance either by over- or underexpression. Availability of NGS techniques allowed us to clone major genes for developing SNP and InDel markers which can be utilized to transfer these QTLs through marker-assisted backcross approach for developing improved rice varieties for salt stress environments.

15.6 Breeding for Cold Tolerance

Climate variability with increased occurrence of extreme temperatures is destructive to crop growth and productivity. One of the extreme temperature stresses is cold stress caused by suboptimal temperature to cause significant yield reduction in rice. Generally, rice growth is affected at all stages of development when temperature reaches below 15 °C (Howarth and Ougham 1993; Fujino et al. 2004). Cold stress comes under two categories, namely, chilling and freezing based on temperature of 0–15 °C and below 0 °C, respectively. Cold temperature impairs various physiological and metabolic processes that affect crop development based on developmental stage and intensity of low temperature stress. It affects seedling stage by inhibiting seed germination, reducing seedling vigor, and inducing leaf discoloration that weakens photosynthesis by decreasing total chlorophyll content. Besides, it reduces plant height and causes leaf necrosis, chlorosis, and mottled chlorosis. During panicle development and booting stage, spikelet sterility along with irregular grain maturity and poor grain quality caused by cold stress has the highest impact on rice productivity.

Few rice cultivars mostly belonging to *japonica* subspecies have possessed tolerance to low temperature stress (Mackill and Lei 1997). *Javanica* cultivars, an ecotype of *japonica* such as Silewah, Lambayeque 1, and Padi Labou Alumbis, have contributed cold tolerance genes for *japonica* breeding lines (Saito et al. 2001). Several genetic analyses have revealed the complex nature of cold tolerance because of its interaction nature with environment. Genetic analysis by Nishimura and Hamamura (1993) revealed the dominant digenic control tolerance of low temperature at the reproductive stage. Later, Nagasawa et al. (1994) have identified cold tolerance as a complex quantitative trait controlled by four or more genes. In order to breed cold-tolerant cultivars by understanding its genetic mechanism, many QTL analyses were carried out in various biparental mapping populations as well as germplasm panel in different developmental stages, i.e. germination, seedling, and reproductive stages (Table 15.3). The *japonica* cultivars have better cold tolerance than *indica* cultivars at both germination and booting stage. QTL analysis carried out in different populations suggests that QTL hotspot for cold tolerance existed in

Table 15.3 QTLs identified for cold tolerance in rice

Genetic loci	Traits	Chromosome no.	References
Ctb1, Ctb2	Spikelet fertility/undeveloped spikelet	4	Saito et al. (2001)
qCT-7	Spikelet sterility/culm length	7	Takeuchi et al. (2001)
qCTB2a, qCTB3	Spikelet fertility/undeveloped spikelet	2, 3	Andaya and Mackill (2003b)
qCTS12a	Seedling growth	12	Andaya and Mackill (2003a)
Ctb1	Spikelet fertility	4	Saito et al. (2004)
Dth, cl, fer, pe, dc	Days to heading/culm length/ spikelet fertility/ panicle neck exertion/discoloration	1, 3, 5, 6, 7, 8, 9, 11	Oh et al. (2004)
qCTB-1-1, qCTB-10-2	Booting stage	1, 10	Dai et al. (2004)
qSV-3-1/2, -5, -8-1/2	Seedling growth	3, 5, 8	Zhang et al. (2005)
qLVG2, qLVG7-2, qCIVG7-2	Vigor of germination	2, 7	Han et al. (2006)
qCTS12	Seedling growth	12	Andaya and Tai (2006)
qCTS4	Seedling growth	4	Andaya and Tai (2007)
qCTS-2	Seedling growth	2	Lou et al. (2007)
qLTG3-1	Vigor of germination	3	Fujino et al. (2008)
qCTB-1-1, -4-1/2, -5-1/2, -10-1/2, -11-1	Spikelet fertility	1, 4, 5, 10, 11	Xu et al. (2008)
qSCT-1, qSCT-5, qSCT-6	Seedling growth	1, 5, 6	Jiang et al. (2008)
qCTP11, qCTP12	Vigor of germination	11, 12	Baruah et al. (2009)
qPSST-3, -7, -9	Spikelet fertility/reproductive stage	3, 7, 8, 9, 11	Suh et al. (2010)
Ctb1	Spikelet fertility/undeveloped spikelet	4	Saito et al. (2010)
qCtss11	Seedling growth	11	Koseki et al. (2010)
qCTB-5-1/2/3, -7	Vigor of germination	5, 7	Lin et al. (2010)
qCTS4a, qCTS4b	Seedling growth	4	Suh et al. (2012)
qLTB3	Seed fertility	3	Shirasawa et al. (2012)

(continued)

Table 15.3 (continued)

Genetic loci	Traits	Chromosome no.	References
24 loci	Booting stage (association analysis)	3, 4, 6, 8, 9, 10, 11	Cui et al. (2013)
qCTG6, qCTG7-1, qCTG7-2, qCTG-8, qCTG-11, qCTS5(1), qCTS6(1), qCTS11(1)-1, qCTS11(1)-2, qCTS11(2)-1, qCTS11(2)-2, qCTS2(2), qCTS7(2), qCTS8(2)	Germination/seedling stage	1, 2, 6, 7, 8, 11	Ranawake et al. (2014)
51 QTLs, qCTSSR6-3 (both *indica* and *japonica*)	Germination/booting stage (assoc. analysis)	All chromosomes	Pan et al. (2015)

Modified from Zhang et al. (2014)

chromosome 11 which harbors several QTLs affecting all developmental stages, and it has synteny with chromosome 5A of wheat and 5H of barley that has the cluster of *FR2* (Frost Resistance 2) and *CBF* genes (also known as *DREB*) (Ranawake et al. 2014). Nonetheless, complete understanding of genetics and molecular basis of cold tolerance is lacking due to unreliable phenotyping methods and complex environmental interaction of this stress. Therefore, it is crucial to explore on phenomics to increase the reliability of QTL studies for breeding cold tolerance in rice. After careful validations, identified QTLs may be useful to hasten the development of improved cold-tolerant genotypes through marker-assisted breeding approach.

15.7 Transgenic Breeding

In rice, transgenic breeding, one of the genetic engineering tools, has proven its effect as a viable option for developing stress-tolerant lines. It is mainly carried out either by quantitative expression alteration or site specificity in expression of desirable genes. Transgenic breeding are mainly aimed at developing plants with genes encoding transcription factors such as DREB, NAC proteins, MYB, and MYC and genes involving the production and accumulation of osmolytes, late embryogenesis abundant protein genes, heat shock proteins, reactive oxygen scavengers, aquaporins, and transporter proteins (Wang et al. 2016). For abiotic stress tolerance, DREB (dehydration-responsive element-binding protein) transcription factor is widely utilized for improving stress tolerance for drought, heat, salinity, and cold (Reddy et al. 2016). With the availability of genetic information on signal transduction and pathways of various complex traits, transgenic breeding has tremendous potential for creating climate-smart rice varieties by transferring multiple genes for different stress tolerance.

15.8 Multi-stress Tolerance Breeding

Anthropogenic climate change can potentially enhance different biotic and abiotic stresses in agriculture. But global warming, the main threat of this century, causes climate change effects with extreme weather events of heavy downpour, low temperature, and high temperature associated with water deficit. The rapid weather phenomenon can expose crops at any growth stage to multiple kinds of stresses in a crop season. This necessitates development of new crop cultivars possessing multiple stress tolerance, more yield, and yield stability across different environments. Genomic advances favor deciphering genetic information for different complex traits, which can pave way for pyramiding multiple QTLs/genes for developing multi-stress-tolerant lines. In rice, attempts have been made by various groups to pyramid QTLs/genes for developing climate-smart rice cultivars. Shamsudin et al. (2016) has introgressed three QTLs for drought tolerance, i.e. $qDTY_{2.2}$, $qDTY_{3.1}$, and $qDTY_{12.1}$, in the background of an elite Malaysian rice cultivar MR219. Basmati rice cultivars were constantly improved by multiple genes/QTLs for bacterial leaf blight, brown plant hopper, and blast and gall midge diseases. The International Rice Research Institute is involved in developing climate-smart rice varieties by pyramiding multiple genes/QTLs conferring biotic and abiotic stress tolerance in different varietal backgrounds suitable for different rice-growing parts of the world (Arvind Kumar, Personal communication). Renu-Singh et al. (2016) reported about a project involving successful pyramiding of various QTLs for drought, namely, qDTY1.1, $\mathrm{qDTY}_{2.1}$, $\mathrm{qDTY}_{2.2}$, $\mathrm{qDTY}_{3.1}$, $\mathrm{qDTY}_{3.2}$, $\mathrm{qDTY}_{9.1}$, and $\mathrm{qDTY}_{12.1}$, into submergence-tolerant lines, i.e. Swarna-Sub1, Samba Mahsuri-Sub1, and IR64-Sub1. In India, there is a multi-institutional network project funded by the Department of Biotechnology, Government of India, for introgressing QTLs for drought, submergence, cold tolerance, blast, bacterial blight, and gall midge into various high-yielding mega-varieties for developing climate-resilient rice varieties using marker-assisted breeding approach (Agarwal et al. 2016).

15.9 Conclusion

Climate change impact on food security is one of the major challenges in present-day life. Various crop modeling studies coupling weather parameters and crop response conducted in rice, wheat, maize, soybean, oilseeds, cassava, sugarcane, banana, common bean, and millets show its negative impact on crop yield. This information emphasizes the need to include climate change factors in breeding objectives to increase food production. Rice, being the staple food for more than half of world population, has to maintain its production and productivity in order to promote food security. But rising levels of biotic and abiotic stresses due to varying weather pattern possess great challenge to maintain rice production. Several multi-stress-tolerant rice cultivars are being developed by various research groups utilizing various omics tools for understanding its genetic and physiological mechanism in order to cope up with the constraints possessed by climate change. Dissecting genetic basis of different traits through QTL analysis and gene identification can accelerate the breeding process of climate-ready rice. Marker-assisted selection serves as an effective tool to introgress positive alleles in desirable genetic background. Thus, to reduce food security risks from global climate variation, multi-stress-tolerant cultivar breeding with various genomics tools would spur the efforts for stress resilience in rice.

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