

Improving Rice Productivity Under Abiotic Stress Conditions

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Abstract

Rice is the major staple food for many Asian countries including India. A considerable amount of rice biomass for which genetic potential exists in the present-day cultivars is not harvested under field conditions, primarily because of the sensitivity of this crop to various abiotic stresses. A clear cut understanding of the mechanisms of abiotic stress tolerance is essential to improve stress tolerance in this plant. Various methods are available for improving rice productivity under abiotic stressed conditions such as using the variation already present in existing genotypes or varieties, inter-specific hybridization to raise tolerance of sensitive varieties, generating variation within existing crops using recurrent selection, mutagenesis, tissue culture, breeding with stress tolerant wild relatives and genetic engineering. The availability of advanced molecular breeding tools as well as the whole genome sequence information has greatly enhanced our efforts to develop rice varieties those could have potential for productivity gains. There is a tremendous increase in the research work being carried out in this field in the recent years, possibly due to the latest innovations in the field of biotechnology and molecular breeding. With the progress being made in rice abiotic stress tolerance research, it is hoped that breakthrough in rice research would come from a combination of tools and technologies of advanced genetic research. Designer rice varieties are the need of the hour.

Keywords: Rice productivity, abiotic stress, transgenic rice

Introduction

The world population has crossed the 7 billion mark in March 2012 as per the estimate of the United States Census Bureau (USCB), and the global population growth projection is estimated to be between 7.5 and 10.5 billion by 2050. Asia harbours 60% of the world's population and has the distinction of having the world's two most populated countries, namely India and China.

Rice is the major staple food for many Asian countries including India. Asia is the biggest rice producer, accounting for 90% of the rice produced and consumed worldwide. While the population of low income countries grew by 90% between 1966 and 2000, the rice production grew 130%, thanks mainly to the green revolution technologies (Khush 2005). However the increase in agriculture output provided by the green revolution has reached a plateau, due to deteriorating irrigation infrastructure, soil degradation, stagnant technology for rain-fed farms, and the technological fatigue being reached on irrigated farms. It has been projected that by 2030, we will have to produce 40% more rice to feed the ever increasing population (Khush 2005). This goal has to be achieved within the constraints of less land, less water, less labour, and to be

sustainable and economical, with less chemical input. Precise and sustainable scientific interventions are required to achieve this goal.

A considerable amount of rice biomass for which genetic potential exists in the present-day cultivars is not harvested under field conditions, primarily because of the sensitivity of this crop to various abiotic stresses. Rice is a salt sensitive crop. In Asia, 21.5 million ha of cultivated rice lands are affected by salt stress, of which 12 million ha are saline and 9.5 million ha are alkaline or sodic (Lafitte et al 2004). It is estimated that 50 % of the world's rice production is more or less affected by drought. The crop's vulnerability to cold results from pollen sterility caused by cold in its reproductive stages (Imin et al 2004). Submergence stress adversely affects rice production in 15 million ha in the lowlands in south and south-east Asia (Septiningsih et al 2009).

A clear cut understanding of the mechanisms of abiotic stress tolerance in plants is essential for improving stress tolerance in crop plants. Since 2000, plant science has moved forward into the stage of post-genomics. A great deal of research has been carried out in the recent past in the field of plant abiotic stress tolerance

encompassing genomics, transcriptomics, proteomics and metabolomics. Researchers all over the world have been exploiting the latest technologies and bioinformatics tools and these have provided better insights into various facets of abiotic stress tolerance.

Improving rice productivity under abiotic stress conditions

Various methods are available for improving rice productivity under abiotic stress conditions such as using the variation already present in existing genotypes/varieties, inter-specific hybridization to raise tolerance of sensitive varieties, generating variation within existing crops using recurrent selection, mutagenesis, tissue culture, breeding with stress tolerant wild relatives and genetic engineering.

Many traditional rice varieties, which successfully resist the onslaught of natural calamities and abiotic stresses, are reported previously (Gregorio et al 2002). Traditional cultivars like Pokkali, Cheriveruppu, Nona Bokra, SR26B, Damodar and Getu are more tolerant to salinity than many elite cultivars. Wild rice *O. rufipogon* showed salinity tolerance at seedling stage comparable to Pokkali (Shylaraj et al 2006). Submergence tolerant rice varieties are important for cultivation in areas where short term “flash” flooding damages rice crops. Highly submergence tolerant varieties such as FR13A have been identified from Odisha, India. Many drought tolerant traditional rice varieties are reported in India including many from West Bengal, Kerala and Odisha. In the state of Tamil Nadu, a traditional drought tolerant rice variety named ‘kappakar’ is preferred by farmers for cultivation in the clay soils. ‘Kelas’ and Bhutmuri’ are examples of upland rice varieties that need no irrigation during cultivation (Arumugasamy et al 2007).

Traditional cultivars differ in taste, aroma, texture, shape etc and are preferred only locally and very often, they have poor agronomic traits, such as tall plant stature, photosensitivity, poor grain quality, and low yield. For a wider coverage of rice consuming population and better yield, it’s essential to transfer the stress tolerant properties of these traditional varieties to more popular varieties. Any germplasm improvement effort therefore should take into consideration the climatic or environmental conditions of the target area, for which the crop need to be developed.

Several elite stress tolerant rice varieties have been developed through conventional breeding with tolerant rice varieties (Mishra et al 1992; Gregorio et al 2002). Pokkali has been frequently used as a donor of salt-tolerance traits in breeding programs (Bonilla et al

2002; Shylaraj et al 2006). Submergence tolerant varieties such as FR13A from Odisha have been used in breeding programs (Vergara and Mazaredo 1975; HilleRisLambers and Vergara 1982). Identification of the *SUB1* gene controlling submergence tolerance enabled breeding of new, high-yielding “*Sub1* mega-varieties”, with popular characteristics such as high yield, good grain quality and local pest and disease resistance (Septiningsih et al 2009).

Idotype breeding also has been successfully exploited for increasing yield potential in cereals such as wheat, rice and sorghum (Khush 1995). Many researchers have conducted wide hybridization with stress tolerant wild species, weedy races, as well as intra-specific groups, to widen gene pools (Khush 2005).

Success in obtaining abiotic stress tolerant mutants by the application of mutation coupled with *in vitro* systems have been attained in some crop plants including rice (Lee et al 2003; Saleem et al 2005). Somaclonal variation is an important technique to generate genetic variability. Rice improvement through somaculture shows promise and is accessible to all plant breeders. Generation of salt tolerant varieties through somaclonal variation in traditional-salt tolerant *indica* cultivar Pokkali has been reported (Mandal et al 1999).

Progress in breeding and the adoption of new varieties has been slow due to the large number of mechanisms involved, the complexity of these mechanisms, and the diversity of target environments where multiple abiotic stresses often coexist (Reynolds et al 2005). Breeding for stress tolerance in rice also requires reliable screening techniques that are rapid enough to keep pace with the large amount of breeding materials generated. The introgression of multiple QTLs into elite varieties is an expensive and laborious process. In the case of stress-related QTLs, the results of marker-assisted selection (MAS) are limited (Tuberosa et al 2002; Steele et al 2006), owing to difficulties such as QTLs that have epistatic interactions and do not contribute significantly in a novel genetic background. For effective MAS programs, QTLs must be expressed and beneficial in new genetic backgrounds and need to be stable across different mapping populations and environments.

Development of a promising stress tolerant line through hybridization and selection can take about 8 to 10 years. This is aggravated by the fact that in areas where abiotic stresses are found, only one cropping season per year is possible. Therefore, conventional breeding methods need to be supplemented with recent achievements in rice biotechnology to meet the needs of the growing world population (Bajaj and Mohanty 2005).

Generation of abiotic stress tolerant rice through transgenic technology

Owing to its small genome size (~389 Mb), the known genome sequence, ease of *Agrobacterium*-mediated transformation, and genetic synteny with other cereal genomes, mutant populations available for functional analysis of the important genes, and intensive QTL mapping efforts for a wide range of traits, rice is not only a model monocotyledon species for research on plant development, but also a model crop for research on cereals' genomics and evolution (George and Parida 2008).

During the last 15 years, many independent transgenic experiments have resulted in improved rice varieties with respect to a number of agronomically important traits, including quality improvement and increased nutritional value. Model organisms like *Arabidopsis*, resurrection plants, and halophytes have been used as sources for mining genes for engineering tolerance in sensitive plants (Zhu 2002; Mehta et al 2005; George et al 2007). Several candidate genes have been identified for engineering abiotic tolerance in crop plants. Over expression of genes from divergent sources functioning in various aspects of stress tolerance such as efflux of Na⁺ from the cell (Wu et al 2005), compartmentalization of Na⁺ ions inside the cell (Verma et al 2007), oxidative stress tolerance (Prashanth et al 2007), ion transport (Obata et al 2007), osmotic stress tolerance (Garg et al 2002) and transcription factors controlling the expression of genes involved in stress tolerance (Hu et al 2006) etc in transgenic rice systems have resulted in improved tolerance to various abiotic stresses without compromising on phenotypic characters as well as yield levels. Due to the similar cellular response to various stresses like drought, low temperature, and salinity, many of these experiments have achieved tolerance to multiple stresses with single gene transformations. Abiotic stress in the field conditions is complicated due to the cross talk between different stresses such as drought, salinity and cold stress. The evaluation of success of transgenic experiments should be based on proper experimentation methods under field conditions at the whole plant level including quantitative estimates of plant growth and taking the transpiration rate into account (Flowers 2004).

Understanding abiotic stress tolerant mechanisms in rice and improving productivity—recent research leads

A number of published and reported research articles in the field of rice abiotic stress tolerance and crop improvement for increased production under abiotic stress conditions are available. A search in 'pubmed' database using research terms 'rice, abiotic stress'

showed 416 articles, of which, 202 were published since 2010. Of these, 144 articles were directly connected to study of various aspects of abiotic stress tolerance in rice. Among these 144 articles, those reporting various characterization steps of individual rice genes were dominant (49), 12 of which reported over-expression of the gene in transgenic rice. 32 research articles dealt with characterization of gene families, or group of genes. Twelve research articles involved transformation of exogenous genes in rice. Among the 144 articles, roughly one-third is from various research groups in China (48), while Indian research groups have contributed roughly one fifth (32) of the total articles. A few relevant studies are reported below.

Gene characterization studies

Studies by Soltész et al (2012) reported enhanced tolerance to frost and improved germination under unfavourable conditions in transgenic barley plants over-expressing rice *Osmyb4* gene. Over-expression of *OsHsp17.0* and *OsHsp23.7* enhanced drought and salt tolerance in rice (Zou et al 2012). A R2R3-type MYB gene, *OsMYB2*, is involved in salt, cold, and dehydration tolerance in rice (Yang et al 2012). Rice Abscisic acid stress ripening (ASR1) protein was found to enhance acquired tolerance to abiotic stresses in *Saccharomyces cerevisiae* by virtue of its reactive oxygen species scavenging and chaperone-like activities (Kim et al 2012). A rice cystathionine β-synthase domain (CBS) containing protein OsCBSX4 of previously unknown function was revealed to be functioning in salinity, heavy metal and oxidative stress tolerance (Singh et al 2012a). *OsLEA5* gene, which belongs to the atypical late embryogenesis abundant (LEA) group was characterized by He et al (2012). A protein kinase gene *OsCPK12* was found to be functioning in multiple signalling pathways, positively regulating salt tolerance and negatively modulating blast resistance (Asano et al 2012). Mutant studies revealed that an inositol 1,3,4-trisphosphate 5/6-kinase gene, *OsITPK2*, was essential for drought and salt response in rice. OsBHLH148, a basic helix-loop-helix protein, interacts with OsJAZ proteins in a jasmonate signaling pathway leading to drought tolerance in rice (Seo et al 2011).

Characterization of an OsPFA-DSP1, a rice protein tyrosine phosphatase, revealed that it might be involved in negative regulation of drought response (Liu et al 2012a). Another study on rice mitogen-activated protein kinase (MAPK) phosphatase, OsIBR5 revealed that its induced by abiotic stresses, but function to decrease tolerance to drought stress in transgenic tobacco plants (Li et al 2012). The rice ERF transcription factor OsERF922 negatively regulates resistance to *Magnaporthe oryzae* and salt tolerance (Liu et al

2012b). A rice bZIP transcription factor, OsbZIP52/RISBZ5 was revealed to be a potential negative regulator of cold and drought stress response in rice (Liu et al 2012c).

Rice contains orthologs of choline monooxygenase (CMO) and betaine aldehyde dehydrogenase (BADH), enzymes required for production of compatible quaternary amine, glycine betaine (GB). The studies of Luo et al (2012) revealed that rice CMO gene produces functional protein in transgenic tobacco, but not in wild type rice plants, resulting in no accumulation of glycine betaine. Of the 11 trehalose-6-phosphate synthase genes in rice (TPS) only *OsTPSI* shows TPS activity. Li et al (2011) over expressed *OsTPSI* gene in rice and observed increased tolerance of rice seedling to cold, high salinity and drought treatments without other significant phenotypic changes. Trehalose and proline concentrations were found to be higher in transgenic plants than in the wild type.

Ray et al (2012) analysed transcriptional and upstream regulatory sequence activity of two environmental stress-inducible genes, *NBS-Str1* and *BLEC-Str8*, of rice. Their studies revealed that these upstream regulatory sequences could prove useful for expressing a transgene in a stress responsive manner for development of stress tolerant transgenic systems.

In a further characterization study of *OsDREB1B*, a rice gene, initially described as highly and specifically induced by cold, Figueiredo et al (2012) reported that *OsDREB1B* is not only induced by low temperatures, but also by drought and mechanical stress. The group identified seven novel Zn-finger transcription factors that bind to the promoter of *OsDREB1B*. *OsDREB2A*, a previously reported transcription factor was found to be induced by drought and abscisic acid (ABA) treatment and improved drought stress tolerance in transgenic rice (Cui et al 2011). Another transcription factor from rice belonging to the NAC family, named ENAC1 (early NAC-domain protein induced by abiotic stress 1) was induced very quickly by various abiotic stresses including salt, drought, cold, and exogenous ABA. However, the induction of ENAC1 by abiotic stress was transient and lasted only up to 3 h. It could be possible that ENAC1 may be an early transcription activator of stress responses and function in the regulation of NACRS-mediated gene expression under abiotic stress (Sun et al 2011).

Characterization of gene families

Many studies involved identification and characterization of gene families in rice. A study of rice annexin genes revealed them to be regulated by various abiotic stresses like drought, salinity, heat and cold in

seedling stage (Jami et al 2012). Other studies exploring identification, classification and expression analysis under various abiotic stress conditions in rice includes, expression analysis of rice phospholipase A super family during abiotic stress, (Singh et al 2012b), identification of PR4 like genes involved in stress response (Wang et al 2011), genome wide expression analysis of heat shock proteins during abiotic stress (Chauhan et al 2011), identification of phosphoproteins regulated by heat stress (Chen et al 2011), expression analysis of rice acyl-CoA-binding protein gene family (Meng et al 2011), genome wide analysis of lipoxygenase gene family (Umate 2011), genome wide classification and expression studies of AP2/EREBP transcription factor family (Sharoni et al 2011), arabinogalactan protein gene family (Ma and Zhao 2010) and phytoeyanin gene family (Ma et al 2011), genome-wide survey and expression analysis of members of glutaredoxin family under various abiotic stresses (Garg et al 2010), and genome-wide analysis of NAC transcription factor family (Nuruzzaman et al 2010).

Studies involving transgenic rice experiments

Many studies involved generation of transgenic rice, with the majority of them involving over-expression of indigenous genes for characterization purposes (Liu et al 2012a; Cui et al 2011; Li HW et al 2011; Jiang et al 2012; Gao et al 2011b; Zou et al 2012). Studies on over-expression of exogenous genes in rice included over expression of the *Aeluropus littoralis* *ALSAP* gene (BenSaad et al 2012), the maize *ZmGF14-6* gene (Campo et al 2012), a C-repeat binding transcription factor from maize (*ZmCBF3*, Xu et al 2011), tomato ethylene response factor *TERF2* (Tian et al 2011) and were followed by analysis of transgenics for improved abiotic stress tolerance.

Other recent research leads

Cho et al (2012) investigated the effects of calcium (Ca) deficiency on cadmium (Cd) toxicity in rice seedlings, while Yadavalli et al (2012) studied the differential degradation of photosystem I subunits under iron deficiency. Another study analyzed the effects of exogenous proline and trehalose on the recovery of rice seedlings from salt-stress and the levels of antioxidant enzymes (Nounjan et al 2012). Huynh et al (2012) studied the effects of aluminium stress on membrane lipid composition and expression of lipid biosynthesis genes. Khan et al (2012) used endophytic fungi *Paecilomyces formosus* LHL10 to show that endophytic fungal association via gibberellins and indole acetic acid can improve plant growth under abiotic stress. Cyanobacteria-mediated phenylpropanoids and phytohormones in rice were found to enhance plant growth and stress tolerance (Singh et al 2011). Another

study revealed that nitrogen deficiency stress induces heritable alteration in DNA methylation and results in enhanced tolerance by progenies to the stress (Kou et al 2011). Song et al (2011) studied physiological mechanisms underlying OsNAC5-dependent tolerance of rice plants to abiotic stress.

There were only a few studies on small RNAs in connection with abiotic stress tolerance. Liu (2012d) identified novel miRNAs in the control of arsenite levels in rice. A genome-wide analysis of plant nsiRNAs revealed insights into their distribution, biogenesis and function (Zhang et al 2012). Lima et al (2011) studied changes in microRNA expression in rice roots in response to aluminium. Small RNAs from MITE-derived stem-loop precursors that regulate abscisic acid signaling and abiotic stress responses in rice was studied by Yan et al (2011). An alkaline stress-related microRNA gene, *osa-MIR393* was identified by Gao et al (2011a). Global expression profiling of 41 rice microRNAs in abiotic stress responses was carried out by Shen et al (2010). Lv et al (2010) carried out profiling of cold-stress-responsive miRNAs in rice by microarrays.

Conclusions

As discussed, it is becoming increasingly important to increase the rice production within the constraints of less land, less water, and less labour in the coming years to meet the food demand of the growing population. The availability of advanced molecular breeding tools as well as the whole genome sequence information has greatly enhanced our efforts to develop rice varieties those could have potential for productivity gains. The current efforts for developing location specific elite cultivars tolerant to the specific stress factors also need to factor in the cross talk between various abiotic stresses those often lead to the resultant varieties showing tolerance to more than one stress. Even though our analysis of the recent research leads in rice abiotic stress tolerance was limited by the search term we used, it gives a general idea of the direction the research is preceding. There is a tremendous increase in the research work being carried out in this field in the recent years, possibly due to the latest innovations in the field of biotechnology and molecular breeding. With the progress being made in rice abiotic stress tolerance research, it is hoped that breakthrough in rice research would come from a combination of tools and technologies of advanced genetic research. Designer rice varieties are the need of the hour.

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