Review Article

IMPROVING DROUGHT TOLERANCE IN RICE: A MINI REVIEW

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ABSTRACT
Drought is a serious environmental stress and the major constraint to rice productivity. The extent of yield losses depend on both severity and duration of the drought stress. Drought affects the morphology of rice crop, eliciting responses at physiological and molecular levels. Improving drought resistance in rice has been made through various approaches including agronomic management practices to improved soil moisture status of the target environment. Primary approach for improving drought tolerance in rice is through yield based selection. Alternatively, secondary traits have been targeted for screening plants; however, many times it shows less correlation with the yield. In addition, efforts have been made for drought mitigation using plant growth regulators and osmoprotectants. Transgenic rice expressing HVA1, LEA proteins, MAP kinase, DREB and endo-1, 3-glucanase has been generated, which has shown better tolerance to drought stress. However, none of these are tested in the target environment; therefore utility of such product still remains obscure. This review presents an overview of different drought types, crop responses at physiological level and various approaches for drought breeding integrating conventional, molecular and genetic engineering. In addition importance of drought mitigation through resource management practices for maximising yield and water productivity is highlighted.

INTRODUCTION

The importance of rice as a cereal crop is known globally with half of the global population dependant on its cultivation as a source of livelihood and income generation. Global rice productions have reached a new height with a production level of 464 million tons of rice in 2010 with an increase of 1.8% compared to previous year. Rice is the most important cereal crop in India occupying about 24% of the gross crop area in the country and contributing to about 42% of the total food grain production and 45% of the total cereal production in the country. "Green Revolution" in the country had provided a new generation of rice farming with introduction of high yielding varieties (HYV) of rice in the past. Rice production in the country has increased threefold during the last five decades with a present production level (2017-18) of 112.91 million tons (FAO, 2017) which is next only to China. The present productivity of rice has increased up to 2.6 tons/ha which is an outcome of the introduction of new varieties and technological packages in the past few years. However, the present productivity level remains below the global average of 2.7 tons/ha.

The area under rice cultivation in the country is mostly spread to the eastern region with the state of West Bengal leading in both area and production. These regions experience comparatively high rainfall during certain period of the year which favours rice cultivation. Climate change and its effect on agricultural production and productivity are looming large over the horizon. A major hurdle that hinders agricultural growth in the country relates to problems of uncertain monsoon and severe flood in many parts of the country which severely affects rice production. In the eastern states of India like Jharkhand, Orissa, and Chhattisgarh alone, rice production losses due to severe droughts average about 40% of total production (Pandey and Bhandari, 2009). In the context of current and predicted water-scarcity scenarios, irrigation has only limited potential to alleviate drought problems in rainfed rice growing systems (Bartels and Sunkar, 2005). It is therefore critical that both agronomic and genetic management strategies focus on the efficient use of available soil moisture for crop establishment, growth, and yield. Rice yields in drought prone rainfed systems remain low at 1.0 to 2.5 t ha^{-1}, and tend to be unstable because of erratic and unpredictable rainfall. Drought mitigation through improved drought resistant rice varieties and complementary practices, such as water conservation, represent an important exit pathway from poverty (Pandey and Bhandari, 2009).

At present, there is still a lack of systematical knowledge of plant drought tolerance, although many studies have been carried out on the drought tolerance mechanism and traits. Further understanding of rice drought tolerance on morphological, physiological, and molecular levels will play a very important role in breeding drought-tolerant cultivars and developing new cultivation methods. Drought damage at the late stage is the largest constraint to every rice crop. The mechanisms of maintaining continuous rooting ability, assimilation, and panicle water potential; improving assimilate translocation under stress at the late stage; and the correlation of morphological and physiological traits with yield thus urgently need investigation.

Meanwhile, investigating the critical point of soil water content for root elongation and function maintenance defining the functional relationship between transpiration rate and plant physiological function expression under stress; correlations between xylem hydrological conductance with plant drought injury, and of osmotic adjustment with plant water status; and the mechanism of restorative and compensatory growth after stress at vegetative stage are also important for understanding the varietal difference of tolerance potential at different stages. In view of the present scenario of drought related problems of rice cultivation alongside available scientific research on such an issue, the present review aims at highlighting the physiological mechanism and technological advances for improving drought tolerance of rice.

Physiological adaption to drought stress

A number of adaptive strategies are encoded for resisting stress in plants. Among all the adaptive measures, the most striking one includes accumulation of water to delay or escape from such stressor. In contrast, drought tolerant plants are able to withstand stress by diminishing their metabolic functions once the water potential increases (O' Toole, 2004). Other functional strategies include regulation of stomatal closure mediated by abscisic acid. Stomata are highly specialised cells involved in gaseous exchange and accounts for high water loss through leaf transpiration process (Blum, 1996). Regarding root development, an interesting general adaptation is hydrotropism, in which the roots detect a water gradient and redirect its growth towards it (Lambers *et al.,* 2000).

Drought type and its effect on productivity

The early spring drought corresponds with field preparation, sowing, and/or seedling, transplanting of early or middle season rice, which can hinder seeding, transplanting, and/or crop establishment. The late spring and early summer drought usually correspond with the tillering stage of early or middle season rice, which can cause reduction in the tillering and rooting capacities, root function, leaf senescence or even death, and result ultimately in decrease of effective heads and yield loss (Mackill, 1996). Hot summer drought generally occurs at the critical water stages of grain filling and seed-setting of early season rice, and the reproductive stage of middle season rice, which usually causes severe damage to the rice production due to long duration of drought and high atmospheric temperatures causing strong evapo-transpiration. Its major effects on early season rice include disturbing the assimilation and the assimilate translocation, leading to reduction of grain weight and yield loss. On middle season rice, damage to panicle initiation and the meiosis of pollen mother cells occurs, desiccating spikelets and anthers, disturbing anther dehiscence and pollen shedding, inhibiting panicle exertion, and causing severe reduction of seed setting (Mackill, 1996). Autumn drought generally corresponds with the flowering and grain filling stages of late season rice, which can cause reduction of seed setting, grain weight, and grain yield. Drought for successive seasons can cause damage to rice crop at any stage and even result in crop failure. At the cellular level, the cell membranes as well as the endo-membranes as well as the change dramatically in their lipid composition and limit organelle function as well as cell integrity in response to the stress (Gigon *et al.,* 2004). Sugars accumulated under drought stress are likely to stabilize membranes and prevent membrane fusion, together with other macromolecules like LEA proteins. On the other hand, glycine betaine has been described as an osmoprotectant, maintaining water equilibrium in plant organs (Chen and Murata, 2002).

Breeding strategies for drought tolerance

Both conventional and trait-based approaches have been used in breeding programs for drought tolerance. The conventional breeding approach focus on yield based selection in a given drought environment. While such an approach has been partly successful, it requires large investments in land, labour, and capital to screen a large number of progenies besides sampling difficulty to record variability in the target environment. There is a rising need to identify more efficient tools, for genetic enhancement of drought tolerance given the low success rate of conventional breeding. Of late, specific physiological mechanisms controlling drought adaptive responses in plants has been decoded, bringing opportunities to establish efficient screening protocols, for better management of genotype × environment interactions. However, there are apprehensions regarding this approach given the low association of such traits with grain yield, besides requirement of costly equipments that could further complicate conventional and molecular breeding for drought tolerance.

Recent research and biotechnological developments have revived interest in targeted drought tolerance breeding and use of new genomics tools to enhance crop drought resistance. Marker-assisted breeding allows rapid and precise screening of specific traits, thereby serving as an important tool for drought tolerance breeding. Besides the advancement of molecular genetics, it is also important to unravel the underlying physiological mechanisms of drought response that could immensely contribute towards genetic enhancement of crop drought tolerance. Considering the complexity of drought, a holistic approach is required that integrates physiological dissection of crop drought avoidance and tolerance traits using molecular genetics tools such as marker assisted selection (MAS), microarrays and transgenic crops, with agronomic practices that lead to better conservation and utilization of soil moisture, and better matching of crop genotypes with the environment.

Conventional breeding approach

A conventional breeding approach involves selecting and incorporating better characteristics or traits into the progeny based on genetic variation to obtain new individuals. To achieve this, two different plants possessing desirable traits are selected and crossed to exchange their genes, so that the new individual has a new genetic arrangement. Individuals are further tested for expression of desired characteristics and maintenance in future plant generations (Mc Couch, 2004). In a general practice, drought tolerance is selected with plant productivity where in non-commercial varieties showing drought tolerance are crossed with susceptible, high yielding rice varieties.

Utilization of drought tolerant genes

A large numbers of genes are known to be involved in plant responses under drought stress. These include mainly genes involved in signal transduction and transcriptional regulation (Xiong and Zhu, 2002; Oh *et al.,* 2005; Fujita *et al.,* 2005), biosynthesis of osmotic and other protectors. Owing to tremendous efforts over the past decade, drought tolerance in rice was dissected by using the Quantitative Trait Loci (QTL) mapping approach and novel findings have been obtained related to the genetics of drought tolerance in rice (Fu *et al.,* 2005). QTL are the genetic factors responsible for part of the phenotypic variation observed for a quantitative characteristic. Lang *et al.* (2010) identified a drought tolerant gene GU269889 which was even salt stress tolerant. Another potential gene, HRD gene which is an AP2/ERF-like transcription factor, identified by a gain of function Arabidopsis mutant hrd-D having roots with enhanced strength, branching, and cortical cells, exhibits drought resistance and salt tolerance, accompanied by an enhancement in the expression of abiotic stress associated genes was identified by Karaba *et al.* (2007). HRD over-expression in Arabidopsis produces thicker leaves with more chloroplast-bearing mesophyll cells, and in rice, there is an increase in leaf biomass and bundle sheath cells that probably contributes to the enhanced photosynthesis assimilation and efficiency for the improvement of water use efficiency coincident with drought resistance in rice. Further works should focus on the expression of the gene at different stages under drought stress.

Molecular breeding approach

Drought has been a trait which is difficult to manage through conventional phenotypic selection and it is one of the most ideal traits suitable for improvement through marker-assisted selection (MAS). Improvement in drought tolerance can be assisted using molecular markers which have made novel gene discovery and gene or allele tagging possible. Restriction Fragment Length Polymorphism (RFLP), Sequence Characteristic Amplified Regions (SCAR), Simple Sequence Repeats (SSR), Amplified Sequence Length Polymorphism (AFLP) is the various methods employed to detect linked markers. Application of marker assisted selection of new varieties has a great potential towards improvement of drought tolerance in rice. Moreover, efforts to identify major QTLs with a large and consistent effect on grain yield under drought (Bernier *et al.,* 2007; Kumar *et al.,* 2007; Venuprasad *et al.,* 2011) have marked a new strategy. However, two issues of concern to molecular biologists with drought QTLs have been large QTL x environment and QTL x genotype background effects. Most of the QTLs identified recently have shown a similar effect in diverse environments (Bernier *et al.,* 2009). The recent, identification of major QTLs governing grain yield under drought (Bernier *et al.,* 2007; Kumar *et al.,* 2007; Venuprasad *et al.,* 2011) has made possible the use of MAS for improving drought resistance. Progress in mapping QTLs for secondary traits associated with drought resistance has been extensively reviewed (Bernier *et al.,* 2008, Kamoshita *et al.,* 2008), but MAS for such QTLs has not been successfully used to improve yield under drought stress in rice. Bernier *et al.* (Bernier *et al.,* 2007) reported a QTL on chromosome 12 in a Vandana/Way Rarem population explaining about 51% of the genetic variance for yield under severe upland drought stress over two years. Kumar *et al.* (2007) reported a major QTL for grain yield under lowland drought stress in a CT9993/ IR62266 population on chromosome 1 explaining 32% of the genetic variance for the trait over two years.

With the prevalence of a few mega-varieties being cultivated on millions of hectares in major drought-prone areas in eastern India and north-eastern Thailand, the two major drought-prone areas in the world, identifying major QTLs for grain yield in the background of improved mega varieties and introgressing the identified QTLs in the same background have been suggested as an alternative approach to improve the drought resistance of current mega-varieties. Venuprasad *et al.* (2009), using this approach and bulk segregant analysis, identified two major QTLs located on chromosomes 2 and 3 for grain yield under lowland drought and one QTL on chromosome 6 for yield potential and tolerance of aerobic soil conditions. These QTLs have been identified in the background of drought-susceptible variety

Swarna, grown on millions of hectares in India, Nepal, and Bangladesh, and they are being introgressed using MAB to improve the drought resistance of Swarna. Progress has been made with the introgression in rice of the major genes for improving tolerance of bacterial leaf blight, brown spot, brown plant hopper, and several other traits. However, reports regarding the introgression of major QTLs in rice are still meagre.

Earlier, SUB1, a major QTL for submergence tolerance (Xu *et al.,* 2006), has been introgressed into Swarna, Sambha Mahsuri, IR64, and BR11 mega-varieties (Septiningsih, 2009). In the case of drought, QTLs related to grain yield under drought stress have been reported on numerous occasions in rice (Babu *et al.,* 2003; Lafitte *et al.,* 2004; Price *et al.,* 2002), but there have been no reports of the successful use of such QTLs in MAS (Bernier *et al.,* 2008). The lack of repeatability of QTL effects across different populations (QTL x genetic background interactions) and across environments (QTL x environment interactions) are the two factors limiting the use of QTLs for MAS by plant breeders (Bernier *et al.,* 2008; Courtois *et al.,* 2003; Garg *et al.,* 2002).

Genetic engineering approach

Genetic engineering which is a way of inserting a foreign drought related gene into the plant genome has opened up a wide horizon for crop improvement programme. International Rice Research Institute (IRRI) has developed high yield rice hybrids under drought stress through conventional crosses. The identification of QTLs (Lang *et al.,* 2010; Bernier *et al.,* 2008) associated with drought, established the basis for further selection based on this approach. Developing transgenic rice with improved drought resistance can be achieved through two approaches: (i) introgressing resistance gene within rice germplasm using high-throughput QTL analysis and allele mining that could be cloned and utilized for generation of drought resistant transgenic lines (ii) exploiting rice sequences demonstrated to enhance drought resistance in other species.

In rice, efforts have also been made in testing genes for drought tolerance. Expression of a fused bacteria gene TPS–TPP in rice significantly increased the level of trehalose, resulting in enhanced drought tolerance (Jang *et al.,* 2003; Xiong and Yang, 2003). Over expression of rice MAPK can significantly increase the tolerance of rice to drought, salinity, and cold (Oh *et al.,* 2005). Recently, transcription factor gene CBF3/DREB1 (Ito *et al.,* 2006) and the rice DREB1 homologue (Hu *et al.,* 2006) have been reported for their effectiveness on improving stress tolerance in transgenic rice. Hu *et al.* (2006) reported that over expression of a stress responsive transcription factor in rice resulted in significantly improved drought resistance under the field conditions, further supporting the possibility of developing drought resistance rice by transgenic approach.

Integrated management approach

Given the increasing scarcity and competition for water resources, irrigation is generally not a feasible option to alleviate drought problems in most rainfed areas. Therefore, devising any strategies would need to focus on maximum extraction of available soil moisture and improving water use efficiency of crop to further increase the biomass and seed yield. For any crop improvement programs for a given target drought environment the following steps are essential:

- Characterize the drought patterns and frequency of occurrence in the target environment
- Simulating crop responses to the major drought patterns
- Adjusting the sowing window to allow favourable period of soil moisture and climatic regimes to match with crop phenology
- Agronomic management practices to improve the soil moisture status thereby increasing available soil water to crop
- Identify plant traits that could enhance water use efficiency and crop water productivity.

Adopting the new generation rice varieties

Farmers require a variety that includes a combination of drought resistance with high yield potential in favourable seasons, high quality, and resistance to diseases and pests will be adopted by farmers. Highly stress-tolerant lines that are deficient in many other aspects will be rejected by farmers and these lines are not usable as donors in national breeding programs. Any products resulting from drought resistance breeding must perform in the target environment and well adopted by the farmers to have an impact, however, the whole exercise has its own limitation in achieving the desired success.

Germplasm selection is usually conducted on-station under standardized conditions, including much higher input use and crop management intensity, often not representative of the conditions in farmers' fields. Critical factors for the adoption of new varieties may be varietal traits difficult to capture in the selection process, such as weed competitiveness, performance on poor soils and under widespread crop management constraints, and a range of post-harvest characteristics such as straw quantity, harvest ability, storability, and cooking/eating quality. Therefore, the most promising drought-resistant breeding lines are evaluated with farmers in farmers' fields through participatory varietal selection, using the "mother and baby trial" methodology (Snapp, 2002). The promising breeding lines also needs to be tested in conventional agronomic trials under the most common crop management constraints occurring in the target environments, for example, late transplanting, beushening, and low nutrient availability.

Improved cultivation systems

Improving cultivation systems has long been recognized as a practical approach to enhance crop drought tolerance. Raising seedlings on dry beds can stimulate rooting, producing healthy seedlings and improved transplanting survival, helping seedlings evade drought. Drying fields moderately, known as hardening, at tillering stage can stimulate nodal rooting from early tiller and forming deep rooting (Kondo *et al.,* 2002) and improve water-use efficiency (Mugo *et al.,* 1999). The plastic-sheet-covered cultivation developed recently in some parts of China has also proved practical for enhancing rice drought tolerance and water conservation. Some plant growth regulators have been shown to be involved in the expression of plant drought tolerance. Examples are regulation of stomatal closure, induction of gene expression for drought adaptation (Blum *et al.,* 1999), and increase in drought tolerance and restoration after stress (IRGSP, 2005) by abscisic acid (ABA); and paclobutrazol promoting tillering and rooting. Mineral nutrients are also involved in expression of plant drought tolerance – phosphorus can increase rooting number and depth, while potassium can improve metabolism under stress.

Limitations and constraints in breeding programmes

Drought has long been considered as the most severe factor affecting rice production. At the same time, the complex nature of this trait has long been discussed. However, matching efforts to tackle this situation have not been put forth by either breeders or research managers. The complex research problems can be resolved only by making concentrated efforts at scientific and management levels. There is a lack of trained drought breeders and physiologists dedicated to work on this problem and a link of breeders and physiologists with molecular biologists is missing. Very few breeding programs situated in the rainfed drought-prone ecosystem have a systematic drought breeding program and screening. Even at institutes that have a drought breeding program, there is little activity to systematically screen drought tolerant donors, study their combining abilities, and develop pre-breeding lines for use in a drought breeding program. In the national system, in most of the countries, yield testing in rainfed environments is still done under irrigated conditions, providing favourable conditions for a drought-susceptible variety to excel.

Opportunities in breeding programmes

With the predicted increased severity and frequency of drought occurrence in days to come, it is necessary to commit resources to develop a trained mass of drought breeders and physiologists and link them with molecular biologists to practically use published research. Realization has to be generated among breeders to screen breeding lines under severe stress with mean yield of less than 1.5 t ha-1. For rainfed drought-prone ecosystems, the most appropriate strategy would be to test yield under two situations, irrigated and severe drought, in order to select lines combining high yield under both situations. This would require additional resources to be added to the present system of testing. Proof of concept that conventional breeding based on direct selection for yield under artificially imposed drought stress can result in actual gains in drought resistance (Kumar *et al.,* 2007; Venuprasad *et al.,* 2009) needs to be introduced in breeding programs. The development of near-isogenic genetic stocks that differ in drought resistance (Bernier *et al.,* 2008) will lead to better understanding of molecular and physiological mechanisms of drought.

At the molecular level, sequencing of the rice genome and the development of new genomics and post-genomics tools for detecting genetic polymorphism, gene discovery, and functional analysis of stress-related genes and mechanisms (McNally *et al.,* 2009), and the localization of QTLs with large effects on yield under drought stress that may be useful in marker-aided backcrossing (Bernier *et al.,* 2007; Venuprasad *et al.,* 2009) have opened a new era. Pyramiding three or more QTLs to enhance yield under drought could be a possible strategy for the near future.

REFERENCES

Babu, R.C., B.D. Nguyen, V. Chamarerk, P. Shanmugasundaram, P. Chezhian. 2003. Genetic analysis of drought resistance in rice by molecular markers: association between secondary traits and field performance. *Crop Sci.,* **43**: 1457–1469.

Bartels, D. and R. Sunkar 2005. Drought and salt tolerance in plants. *Crit. Rev. Plant Sci*. **24**: 23-58.

Bernier, J., A. Kumar, R. Venuprasad, D. Spaner and G. Atlin. 2007. A large-effect QTL for grain yield under reproductive-stage drought stress in upland rice. *Crop Sci.,* **47**: 507-516.

Bernier, J., G.N. Atlin, R. Serraj, A. Kumar and D. Spaner, D. 2008. Breeding upland rice for drought resistance. J. *Sci. Food Agric*., **88**: 927-939.

Bernier, J., R. Serraj, A. Kumar, R. Venuprasad, S. Impa, V. Gowda, R. Owane, D. Spaner and G. Atlin. 2009 Increased water uptake explains the effect of *qtl12.1*, a large-effect drought-resistance QTL in upland rice. *Field Crops Res*., **110**: 139-146.

Fu, B.Y., J.H. Xiong, L.H. Zhu, X.Q. Zhao, H.X. Xu, Y.M. Gao, Y.S. Li, J.L. Xu, Z. Li and K. 2007. Identification of functional candidate genes for drought tolerance in rice. *Mol. Gen. Genom.,* **278(6)**: 599-609.

Blum, A., J.X. Zhang, H.T. Nguyen. 1999. Consistent differences among wheat cultivars in osmotic adjustment and their relationship to plant production. *Field Crops Res.,* **64**: 287–291.

Blum, A. 1996. Crop responses to drought and the interpretation of adaptation. *Plant Growth Regul*., **20:** 135-148.

Cabuslay, G.S., O. Ito and A.A. Alejar 2002. Physiological evaluation of responses of rice (*Oryza sativa* L.) to water deficit. *Plant Sci.*, **163**: 815-827.

Chen, T.H.H. and N. Murata. 2002. Enhancement of tolerance of abiotic stress by metabolic engineering betaines and other compatible solutes. *Curr. Opinion Plant Biol*., **5**: 250-257.

Courtois B., L. Shen, Petalcorin, S. Carandang, R. Mauleon, Z.K. Li. 2003. Locating QTLs controlling constitutive root traits in the rice population IAC 165 × Co39. *Euphytica*, **134**:335–345.

FAO. Rice Market Monitor Trade and Markets Division Food and Agriculture Organization of the United Nations 2017. XX (3).

Fujita, Y., M. Fujita, R. Satoh, K. Maruyama, M.M. Parvez, M. Seki, K. Hiratsu, M. Ohme-Takagi, K. Shinozaki and K. Yamaguchi-Shinozaki. 2005. AREB1 is a transcription activator of novel ABRE dependent ABA signaling that enhances drought stress tolerance in Arabidopsis. *Plant Cell*, **17**: 3470–3488.

Garg, A.K., J.K. Kim, T.G. Owens, A.P. Ranwala, Y.D. Choi, L.V. Kochian and R.J. Wu. 2002. Trehalose accumulation in rice plants confers high tolerance levels to different abiotic stresses. *Proc. Nat. Acad. Sci. USA*, **99**: 15898–15903.

Gigon, A., A. Matos, D. Laffray, Y. Zuily-Fodil, and A. Pham-Thi. 2004. Effect of drought stress on lipid metabolism in the leaves of Arabidopsis thaliana (Ecotype Columbia). *Ann. Bot.* (London) **94**: 345–351.

Hu, H., M. Dai, J. Yao, B. Xiao, X. Li, Q. Zhang and L. Xiong. 2006. Overexpressing a NAM, ATAF, and CUC (NAC) transcription factor enhances drought resistance and salt tolerance in rice. *Proc. Nat. Acad. Sci*. USA **35**: 12987– 12992.

IRGSP (International Rice Genome Sequencing Project) 2005. The map-based sequence of the rice genome. *Nature*, **436**: 793-800.

Ito, Y., K. Katsura, K. Maruyama, T. Taji, M. Kobayashi and M. Seki. 2006. Functional analysis of rice DREB1/CBF-type transcription factors involved in cold-responsive gene expression in transgenic rice. *Plant Cell Physiol*. **47**: 141–153.

Jang I.C., S.J. Oh, J.S. Seo, W.B. Choi, S.I. Song, C.H. Kim, Y.S. Kim, H.S. Seo, Y.D. Choi and B.H. Nahm. 2003. Expression of a bifunctional fusion of the Escherichia coli genes for trehalose-6-phosphate synthase and trehalose- 6-phosphate phosphatase in transgenic rice plants increases trehalose accumulation and abiotic stress-tolerance without stunting growth. *Plant Physiol*., **131**: 516–524.

Kamoshita, A., R.C. Babu, N.M. Boopathi and S. Fukai. 2008. Phenotypic and genotypic analysis of drought resistance traits for development of rice cultivars adapted to rainfed environments. *Field Crops Res*., **109**: 1-23.

Karaba, A., S. Dixit, R. Greco, A. Aharoni, K.R. Trijatmiko, N. Marsch Martinez N., A. Krishnan, K.N. Nataraja, M. Udayakumar and A. Pereira. 2007. Improvement of water use efficiency in rice by expression of *HARDY*, an *Arabidopsis* drought and salt tolerance gene. *Proc. Nat. Acad. Sci*., **104**:15270–15275.

Kondo, M., M.V.R. Murty and D.V. Aragones. 2000. Characteristics of root growth and water uptake from soil in upland rice and maize under water stress. *Soil Sci. Plant Nutr.*, **46**: 721-732.

Kumar, R., R. Venuprasad and G.N. Atlin. 2007. Genetic analysis of rainfed lowland rice drought tolerance under naturally-occurring stress in eastern India: heritability and QTL effects. *Field Crops Res.*, **103**: 42-52.

Lafitte, H.R., A.H. Price and B. Courtois. 2004. Yield response to water deficit in an upland rice mapping population: associations among traits and genetic markers. *Theor. Appl. Gen*., **109**: 1237-1246.

Lambers H.F., Stuart-Chappin III, and T.L. Pons 2000. Plant Physiological Ecology. Springer-Verlag, New York, USA, pp. **540**.

Lang-Mladek, C., O. Popova, K. Kiok, M. Berlinger, B. Rakic and W. Aufsatz, W. 2010. Transgenerational inheritance and resetting of stress-induced loss of epigenetic gene silencing in Arabidopsis. *Mol. Plant.*, **3**: 594–602.

Mackill, D., W. Coffman and D. Garrity. 1996. Rainfed Lowland Rice Improvement. International Rice Research Institute, Manila, Philippines.

McCouch, S. 2004. Diversifying selection in plant breeding. *PLoS Biol.*, **2**: e347-e347.

McNally K.L., K.L. Child, R. Bohnert, R.M. Davidson, K. Zha, V.J. Ulat, G. Zeller, R.M. Clark, D.R. Hoen, Bureau, Stokowski, D.G. Ballinger, K.A. Frazer, D.R. Cox, B. Padhukasahasram, C.D. Bustamante,D. Weigel, D.J. Mackill, R.M. Bruskiewich, G.R. Tsch, C.R. Buell, H. Leung and J.E. Leach. 2009. Genomewide SNP variation reveals relationships among landraces and modern varieties of rice. *Proc. Nat. Acad.Sci.* USA, 106: 12273–12278.

Mugo, S.N., M. Banziger and G.O. Edmeades. 1999. Prospects of using ABA in selection for drought tolerance in cereal crops. In: Ribaut, J.-M., and D. Poland, editors, Molecular approaches for the genetic improvement of cereals for stable production in water-limited environments. June 1999. CIMMYT, Mexico. 73- 78.

O'Toole, J.C. 2004. Rice and water: The Final Frontier. First International Conference on Rice for the Future. 31 August- 2 Sept 2004, Bangkok, Thailand.

Oh, S.J., S.I. Song, Y.S. Kim, H.J. Jang, S.Y. Kim and M. Kim. 2005. Arabidopsis CBF3/DREB1A and ABF3 in transgenic rice increased tolerance to abiotic stress without stunting growth. *Plant Physiol*., **138**: 341–351.

Pandey, S. and H. Bhandari. 2009. Drought: economic costs and research implications. *In* J. Serraj, J. Bennet and B. Hardy, eds., Drought frontiers in rice: crop improvement for increased rainfed production. World Scientific Publishing, Singapore, 3-17.

Price, A.H., K.A. Steele, B.J. Moore and R.G.W. Jones 2002. Upland rice grown in soil-filled chambers and exposed to contrasting water deficit regimes. II. Mapping quantitative trait loci for root morphology and distribution. *Field Crops Res*., **76**: 25–43.

Septiningsih, E.M., A.M. Pamplona, D.L. Sanchez, C.N. Neeraja, G.V. Vergara, S. Heuer, A.M. Ismail and D.J. Mackill. 2009. Development of submergence-tolerant rice cultivars: the *Sub1* locus and beyond. *Annals Bot*., **103**: 151-160.

Snapp, S. 2002. Quantifying farmer evaluation of technologies: the mother and baby trial design. *In* M.R. Bellon and J. Reeves eds., Quantitative analysis of data from participatory methods in plant breeding. DF: CIMMYT. Mexico, 9-17.

Venuprasad, R., C. Dalid, M. Del Valle, M.E. Bool, D. Zhao, M. Espiritu, T. Sta. Cruz, M. Amante, G. Atlin and A. Kumar. 2009. Identification and characterization of large-effect quantitative trait loci (QTL) for grain yield under lowland drought stress in rice using bulk-segregant analysis (BSA). *Theor. Appl. Gen*., **120**: 177-190.

Vikram, P., B.P.M. Swamy, S. Dixit, M.T. Sta Cruz, H.U. Ahmed, A.K. Singh, A. Kumar. 2011. qDTY1.1, a major QTL for rice grain yield under reproductive-stage drought stress with a consistent effect in multiple elite genetic backgrounds. *BMC Genetics*, **12**: 89.

Xiong L. and Y. Yang. 2003. Disease resistance and abiotic stress tolerance in rice are inversely modulated by an abscisic acid-inducible mitogen-activated protein kinase. *Plant Cell***, 15**, 745–759.

Xiong, L. and J.K. Zhu. 2002. Molecular and genetic aspects of plant responses to osmotic stress. *Plant Cell Env*., **25**: 131–139.

Xu, K., X. Xia, T. Fukao, P. Canlas, R. Maghirang-Rodriguez, S. Heuer, A.M. Ismail, J. Bailey-Serres, P.C. Ronald and D.J. Mackill. 2006. *Sub1A* is an ethylene response factor-like gene that confers submergence tolerance to rice. *Nature*, **442**: 705-708.

Yue, B., L. Xiong, W. Xue, Y. Xing, L. Luo and C. Xu. 2005. Genetic analysis for drought resistance of rice at reproductive stage in field with different types of soil. *Theor. Appl. Gen*., **111**: 1127–1136.

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