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Research Article

Breeding for drought resistance in rice: an integrated view from physiology to genomics

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Abstract

Drought is a major constraint affecting rice production, especially in rainfed areas across Asia, Africa and South America. Development of drought resistant varieties will considerably improve rainfed rice production. Rice breeding programs focusing on drought resistance by direct selection for yield under stress have made little progress to date. Incorporation of secondary traits contributing in drought resistance will hasten development of cultivars with improved performance under water-limiting environments. Root traits such as thickness, depth and penetration ability help to avoid drought by increased water uptake from deeper soils.Greater hydraulic conductance, xylem thickness and osmotic adjustment are secondary root traits enable better extraction of available soil moisture. However, use of most root traits as selection indices in breeding programs using phenotypic measurements still entails huge investments in field nurseries or green house facilities, demanding in labour and is prone to problems of repeatability due to environmental variability. One promising approach is to map genetic loci (quantitative trait loci/QTLs) linked to root traits and use marker-assisted breeding (MAB) strategy. QTLs for many drought resistance traits consistent across environments and genetic backgrounds have been mapped in rice. Some of these QTLs co-locate with QTLs for yield and yield components under stress and are introgressed into elite lines using MAB. The introgression lines performed better under drought are released as high yielding varieties suitable for rainfed ecosystems.

Keywords:
Rice, drought resistance, QTLs, marker assisted breeding

Introduction

Rice is the staple food for more than 3 billion people in Asia, where more than 90% of the world's rice is produced and consumed (Li and Xu, 2007). It is grown worldwide in 154 million hectares (m ha) and more than 45% of the area is in rainfed ecosystems, where yields are seriously affected by drought (IRRI, 2002). Of world's rainfed lowland rice area of 41 m ha, 95% is in Asia (IRRI, 1995). The rice yields in these ecosystems remain very low at 1.0–2.0 t ha−1 and tend to be unstable due to erratic and unpredictable rainfall. Drought is the most important source of climate-related risk for rice production in rainfed areas (Pandey et al. 2007). The 2002 drought in India reduced its rice production by 17 million tons (mt), 20% of annual production. The recent drought (-23% deficit in rainfall) during kharif 2009 affecting 50% of the districts in India has been estimated to cause a loss of 11 m t in rice production. The increasing threat from water shortage and drought in many rice-growing areas of Asia, particularly the rainfed areas, has posed a great challenge to rice breeders to develop drought-tolerant and/or water-saving rice cultivars (Zhao et al. 2008).

Drought resistance

Drought mitigation, through development of drought-resistant rice varieties with higher yields suitable for water-limiting environments will be a key to improve rice production and ensure food security to 3 billion people in Asia. The progress in genetic improvement of rice for water-limiting environments, however, has been slow and limited (Evenson and Gollin 2003) due to poor understanding of the inheritance of mechanisms of tolerance and lack of efficient techniques for screening breeding materials for drought tolerance (Khush 2001). Alternatively, selection for drought-resistance traits has been suggested. The effectiveness of selection for secondary traits to improve yield under water limiting environments has been successfully demonstrated for anthesis-silking interval in maize (Liu et al. 2010), water use efficiency in wheat (Condon et al. 2004) and stay greenness in sorghum (Harris et al. 2007). However,

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few programs explicitly incorporate a drought tolerance screening step as part of their routine drought breeding activity, despite the considerable effort that has been made on the genetic and physiological analysis of traits considered to be related to genotypic differences in drought tolerance (Bernier et al. 2008). In recent years, crop physiology and genomics have led to new insights in drought tolerance providing breeders with new knowledge and tools for plant improvement (Tuberosa and Salvi, 2006). Drought resistance is improved either if the crop is able to access more water or if it can use available water more efficiently (higher transpiration efficiency) (Passioura, 2006). Several secondary traits are known to contribute in drought resistance in rice. Most of the secondary traits (e.g., root traits, leaf water potential, epicuticular wax, osmotic adjustment etc.,) have moderate to high heritabilities under stress indicating the possibility of incorporating them into breeding program (Kumar et al. 2008). Certain secondary traits such as LWP had good correlation *(r* = 0.69) with yield under stress as well in rice (Jongdee et al. 2006).

Drought characterization

Characterization of drought environment, matching phenology, high potential yield and inbuilt drought resistance are vital for successful crop production in water-limiting conditions. Drought types, particularly timing and intensity, are important in determining specific plant traits required to improve drought resistance. Drought stress induces a series of complex responses beginning with stress perception, signal transduction and manifestation of responses at the cellular, physiological, and developmental levels. The set of responses observed depends upon the crop stage, severity and duration of the stress. When evaluating the usefulness of traits to increase grain yield, it is important to consider phenological development, which has an overriding effect on the grain yield under water limiting condition (Fukai and Cooper, 1995). The reproductive development in plant is highly vulnerable to water deficit (Saini and Westgate, 2000). Yambao and Ingram (1988) reported yield reduction upto 70% upon imposing drought for 15 days at panicle initiation stage, and 88% and 52% reduction when stressed at flowering and grain filling stage, respectively. Stress early during panicle initiation can delay or completely inhibit flowering, both through inhibition of floral induction and development (Saini and Westgate, 2000). Within this period two sensitive peaks have been reported, one being the period around pollen mother cell meiosis and tetrad break up and the second is anthesis to initial stage of grain development. Pollen formation in rice is highly vilnerable to drought stress (Nguyen and Sutton, 2009). Stress at meiotic stage causes pollen sterility, failure of pollination, spikelet death or zygotic abortion, but female fertility is affected only under extreme stress.

O`Toole and Namuco (1983) have reported reduced panicle exsertion when stressed at around panicle exsertion period. Panicle exsertion depends on the peduncle elongation, the uppermost internode of the stem. The spikelets in the unexserted portion of panicle remain sterile (Mackill et al. 1996). Rapid peduncle elongation occurs when the panicle attain its full length. Drought causes a reversible inhibition on peduncle elongation. Therefore under drought stress, the peduncle elongation is blocked and upon rewatering, the growth continues but the peduncle doesn’t achieve its full length (Ji et al. 2005). So a part of the panicle is trapped inside the flag leaf and these unexserted spikelets become sterile. They also found that up to 30% of this spikelet sterility was associated with poor panicle exertion resulted mainly due to the failure in peduncle elongation thereby trapping the spikelets inside flag leaf sheath .A delay in flowering is usually observed under reproductive stage drought stress (Ouk et al. 2006). Genotypes that flower early, generally escape the terminal drought. So short duration varieties can avoid the terminal drought as they mature early and thus minimize the yield loss due to drought (Kumar and Abbo, 2001). Pantuwan et al (2002) found significant delay in flowering among genotypes under drought stress, which had similar flowering time under irrigated condition. The delay was negatively associated with grain yield, harvest index, fertile panicle and filled grain percentage.

Traits associated to drought resistance in rice have been reported by many researchers and a number of authors have reviewed such traits (Fukai and Cooper 1995; Nguyen et al. 1997; Price et al. 2002; Bernier et al. 2008). These reviews indicate that increased water collection by deeper roots, restricting water loss from shoots through thicker cuticle deposition and reduced leaf area and tissue level tolerance such as osmotic adjustment are major components of drought resistance in rice. Most of these traits are related to a drought avoidance strategy, so that the drought resistant genotypes are able to maintain higher internal water status, mainly taking up more water through a better root system and/or to an extent by reducing plant water loss (Serraj et al. 2009). There is large genetic variation for most drought resistance components such as root morphology (Babu et al. 2001), osmotic adjustment and dehydration tolerance (Lilley and Ludlow, 1996) among rice germplasm thus, providing scope for improvement of drought resistance by incorporating these traits as selection criteria in breeding. However, phenotypic selection of drought resistance traits is still far from practice.

QTL mapping for drought resistance

Though several putative traits contributing to drought resistance in rice have been proposed (Bernier et al. 2008), these traits are rarely selected for in breeding programs as phenotypic selection for these traits is time- and labour-intensive and demanding in cost. Many phenotypic traits that confer resistance for abiotic stress are controlled by many genes and are known as quantitative traits. The regions within genome that contain genes associated with a particular quantitative trait are known as quantitative trait loci (QTLs) (Collard et al. 2005). Compared to conventional approaches, genomics offer unprecedented opportunities for dissecting quantitative traits into their single genetic determinants, the so called QTLs thus paving the way to marker assisted selection (MAS) and eventually, cloning of QTLs and their direct manipulation via genetic engineering (Tuberosa and Salvi, 2006). The advent of molecular markers has revolutionized the genetic analysis of complex traits such as drought resistance in crop plants. Molecular markers help to track the genetic loci controlling drought-resistance traits without having to measure the phenotype, thus reducing the need for extensive field testing over space and time (Nguyen et al. 1997). Once the tightly linked markers have been identified, the QTLs can be selected for in breeding programs using MAS.

Numerous QTLs linked to various drought resistance component traits have been mapped so far in rice using more than15 mapping populations (Kamoshita et al. 2008). These populations have been screened for different drought resistance traits grown under different stress protocols. To start with, QTLs for leaf rolling, root related traits and osmotic adjustment have been mapped in recombinant inbred (RI) lines of Co39 x Moroberekan (Champoux et al. 1995; Ray et al. 1996; Lilley et al. 1996). QTLs for root and certain physio-morphological traits were mapped using RI lines of Bala x Azucena (Price et al. 2000). QTLs for root traits and plant production traits have been mapped using doubled haploid (DH) lines of IR64 x Azucena (Yadav et al. 1997; Courtois et al. 2000; Hemamalini et al. 2000; Venuprasad et al. 2002). A DH line population derived from CT9993-5-10-1 and IR62266-42-6-2, has been extensively used by many researchers in mapping QTLs for root traits, osmotic adjustment (Kamoshita et al. 2002; Nguyen et al. 2004), cell membrane stability (Tripathy et al. 2000), epicuticular wax (Srinivasan et al. 2008). Further, some of the mapping populations were used in mapping QTLs for traits associated with reproductive stage drought resistance. A set of 187 RI lines of Zanshan97B x IRAT109 were used to map QTLs for flag leaf and panicle characteristics under reproductive stage drought stress (Liu et al. 2008; Yue et al. 2008). Most QTL mapping studies were conducted employing populations derived from *indica* × *japonica* parental lines and majority of the positive alleles for drought-resistance traits were contributed by *japonica* parents. Since *indica* and *japonica* ecotypes are grown in entirely diverse environments, *japonica* alleles may not be expressed in lowland ecosystem (Wang et al. 1994; Redona and Mackil 1996; Yano and Sasaki 1997). Hence, it is desirable to look for genetic variation among rice accessions within *indica* ecotypes (Ingram et al. 1994) and map QTLs using populations derived from *indica* rice lines adapted to the target population of environments. The *indica* × *indica* derived rice populations have been utilized in few QTL mapping studies till date (Ali et al. 2000; Kamoshita et al. *2002a* and *b*; Manickavelu et al. 2006; Biji et al. 2008). QTL mapping of drought resistance traits using locally adapted *indica* rice lines is reported recently from China and India (Yue et al. 2006; Gomez et al. 2009). However, identification of QTLs linked to yield under drought stress in target population of environment is critical.

QTLs - application in breeding

Numerous QTLs linked to various drought resistance and plant production traits under stress have been mapped in rice. Although these results indicate the map positions of QTLs associated with drought resistance traits, effects of those traits on plant production under drought has to be established. By comparing the coincidence of QTLs for specific traits and QTLs for plant production under drought, it is possible to test the significance of constitutive or adaptive response to improve drought resistance at field level (Lebreton et al. 1995). Fewer QTLs associated with yield under managed drought stress have been mapped in rice (Babu et al. 2003; Lafitte et al. 2004; Lanceras et al. 2004). Kumar et al. (2007) assessed the potential for improving yield under drought stress via direct selection and identified QTLs associated with yield under stress in CT9993 x IR62266 DH lines. Among the 18 QTLs identified for 11 traits, one QTL on chromosome 1 for grain yield explained a genetic variation of 32% for yield under stress. Gomez et al. (2006) mapped

QTLs linked to yield under stress using Bala x Azucena RI lines. A QTL on chromosome 3 was linked to yield under stress, days to 50% flowering and leaf drying.

A comparison of QTLs for various drought resistance and plant production traits under stress identifed in different populations of rice was made (Kanagaraj et al. 2010). The RM212-RM302-RM3825 region (135.8 to 143.7 cM) on chromosome 1 of rice has been reported to be linked with several drought resistance traits in rice such as plant height, biomass, deep root mass, leaf drying, relative water content, osmotic adjustment, basal root thickness, tiller number and deep root to shoot ratio, grain yield, plant height and panicle length and leaf drying, canopy temperature and plant height in IR20/Nootripathu rice RI lines under drought stress (Gomez et al. 2009; Kanagaraj et al. 2010). Babu et al. (2003) reported that this region was associated with RWC under stress in CT9993/IR62266 doubled haploid (DH) lines and root length, root thickness and root weight in Bala/Azucena RI lines of rice (Price et al. 2000). Kanbar *et al*. (2002) found this region to be linked to panicle length in CT9993/IR62266 DH lines and days to 50% flowering in Vandana/Way rarem RI lines (Price et al. 2000) under stress. Kamoshita et al. (2002a) reported QTLs for root depth, penetrated root thickness, deep root to shoot ratio, deep root dry weight, deep root per tiller and deep root mass to be associated with RM212 on chromosome 1 in CT9993/IR62266 DH lines and also a QTL for osmotic adjustment was reported to be close to this region in IR62266/IR60080 back cross progenies (Robin et al. 2003). This region was found to be associated with root volume (Qu et al. 2008) and basal root thickness in IRAT109/Yuefi RI lines (Li et al. 2005) and leaf drying in Zhenshen/IRAT109 RI lines in rice (Yue et al. 2006). Hittalmani et al. (2003) reported that the genomic region of 7.9 cM (135.8-143.7 cM) in chromosome 1 was associated with drought resistance traits such as leaf rolling, number of spikelets, heading date and harvest index in IR64/Azucena in rice DH lines. Xing et al. (2002) reported the QTLs for biomass and root dry weight to be associated with RM212 in Zh97/Ming63 RI lines. The major gene controlling the semi-dwarf stature, *sd-1*, was located near RZ730 (Huang et al*.* 1996*)*. This gene is known to affect many aspects of plant morphology and physiology viz, plant height (Bernier et al*.* 2007*),* stomatal conductance (Zhao et al. 2008*)* tillering, panicle length, responsiveness to fertilizer, biomass and harvest index through pleiotropic effects (Xia et al. 1991*;* Courtois et al. 1995*)* as well as root system development (Yadav et al. 1997*)*. The same region was also reported to contain QTL for cold (Lou et al. 2007) and salt (Lang et al. 2008*)* tolerance in rice. Thus, RM212 may be linked to drought-resistance traits and plant production under water stress in rice.

A meta-analysis of QTLs linked to physio-morphological traits and yield under drought stress published so far in CT9993/IR62266 DH population was done in a recent review by Kamoshita et al. (2008). The analysis was conducted with emphasis to CT9993/IR62266 DH population along with QTLs from 14 other rice populations. Four genomic regions on chromosome 1, 4, 8 and 9 were detected to have putative QTLs for drought resistance traits as well as integrative yield traits under drought stress (Kamoshita et al. 2008). The QTLs on chromosome 1 and 8 had positive impact on rice performance under drought through plant architecture, potential yield, phenology and are more adapted to intermittent drought stress scenario typical most rainfed lowland ecosysytems of Asia. On the other, QTLs on chromosome 4 and 9 influenced yield favourably through drought avoidance strategy primarily due to deeper roots. During the last 15 years, a large number of QTLs controlling rice root traits have been detected in several mapping populations. A total of 675 QTLs linked to 29 root parameters from 12 populations were subjected to meta-QTL analusis recently (Courtois et al. 2009). The meta-QTL reduced the confidence interval for maximum root length on chromosome 9 to a length of 20 kb. These QTL regions, once fine mapped will be useful in MAS and map based cloning of genes for drought resistance improvement.

QTLs for yield under drought

Yield being the ultimate aim, recent studies focus mapping QTLs for yield under drought stress directly without analysing the mechanisms conferring drought resistance. Bernier et al. (2007) reported a large effect QTL for grain yield under reproductive stage stress in upland rice. It was detected on chromosome 12, located between the SSR markers RM28048 (42.5 cM) and RM511 (55.5 cM), in a population of 436 random F_3 derived lines from a cross between Vandana and Way Rarem from experiments conducted for 2 years.. In this study, QTLs for biomass, harvest index, days to flower, plant height, flowering delay, drought response index and panicle number under stress were mapped in the same region. The qtl12.1 explained 51% of genetic variance for grain yield and also a large proportion of genetic variance for other related traits. The effect of this QTL has been tested in 10 field trials in Philippines and eastern India (Bernier et al.

2009a). It was reported that the qtl12.1 improved yield in most of the upland trials where the drought stress was severe or moderate except for one trial which was severely stressed, thus proving the large and consistent effect of this locus on grain yield under upland drought conditions, in a range of environment. Further the physiological mechanisms by which qtl12.1 affects grain yield have been studied (Bernier et al. 2009b). The study reveals that the qtl12.1 influences water uptake under upland stress and increases harvest index. Three QTL regions viz., RM6703, RM520 and RM511, respectively on chromosomes 1, 3 and 12 were found have significant effect on yield under drought stress in different genetic backgrounds. These loci need to be fine mapped and their effects further characterized in other populations in order to determine their potential deployment via MAS for improving drought resistance (Venuprasad et al. 2009). Four QTLs for spikelets per panicle co-locating with those of number of grains per panicle have been mapped and validated in near isogenic background in rice leading to the possibility of map based cloning of genes for these two yield components in rice (Zhang et al. 2009).

Marker Assisted Selection

Selection for most secondary traits in a breeding program using phenotypic measurements still entails extensive investments in field nurseries or green house facilities, labour intensive and is prone to problems of repeatability due to environmental variability (Nguyen et al. 1997). One promising approach is to map QTL influencing drought resistance traits and crop productivity in stressful environments. Once the tightly linked markers have been identified, they can be used to develop MAS strategy for breeding applications. QTLs for many putative drought resistance traits have been mapped in several rice lines. Several of these QTLs are consistent across environments and genetic backgrounds indicating that they are evolutionarily conserved in rice germplasm as an adaptive response to drought stress. Interestingly, certain QTLs associated with drought resistance traits co-locate with QTLs linked to yield and yield components under stress. For instance, QTL regions RZ19-RZ909, RG938–RG620, RG978–RG598 and R41–RM242 respectively, on chromosomes 1, 4, 8 and 9 were consistently identified by several research groups using different mapping populations that influence a range of drought resistance traits and yield and its components under drought stress in rice (Kamoshita et al. 2008; Courtois et al. 2009; Kanagaraj et al. 2010). Genomic regions mapped for several drought resistance traits such as root traits, phenology and yield and its components under water stress in the same locus would be important QTLs since they not only govern drought tolerance but also are responsible for grain yield under stress (O'Toole, 2004). These alleles with effects across different drought situations and genetic backgrounds are valuable and might be possible candidates for MAS. However, many research steps are required from QTL discovery to the practical application of markers in a breeding program. The three main research areas include: QTL confirmation, broad-range QTL testing and marker validation which are collectively referred to as QTL application research. Precision phenotyping is critical to the success of QTL but unfortunately, the importance of refining and development of new methods for precise phenotypic measurements is often neglected in the genomics era (Collard et al. 2008).

If MAS-based approaches to improvement of rice cultivars for drought tolerance are to be practical, it is likely that they will be based on the introgression of alleles with large, additive effects on yield under stress. QTLs with these characteristics have been recently reported by several groups (Bernier et al. 2008). The QTL on chromosome 9 between markers RM316 and RM219 was consistent and stress-specific, explaining 14–25% of the total phenotypic variation (Yue et al. 2006). A yield-enhancing drought resistance QTL with the largest effect was identified recently in rice (Bernier et al. 2007). This QTL located on chromosome 12 between markers RM28048 and RM511 explained 51% of the genetic variance for grain yield under drought stress in flowering and grain-filling stages under field conditions.

In rice, despite the small number of consistent QTLs for use in MAS, a few attempts to introgress QTLs linked to drought resistance into elite varieties have been made (Price, 2002; Courtois et al. 2003). Most efforts to improve drought tolerance of rice through MAS has been devoted to the use of root-related QTLs. Large chromosomal segments corresponding to QTLs associated with root length from a upland variety, Azucena were introgressed into the IR64 background. Most of the lines carrying the desired introgressions failed to have deeper roots than IR64 (Shen et al. 2001). The lack of effect of the QTLs on root length may be because those QTLs were responsible for a small proportion of the total phenotypic variation (6–18%) and had not been fine-mapped. These results indicate that only fine-mapped alleles with large confirmed effects on performance under stress are appropriate targets for MAS (Bernier et al. 2008).

MAS to introgress QTLs controlling root traits into an Indian upland rice variety was successfully demonstrated by Steele et al. (2006). They introgressed five QTL regions associated with root traits from Azucena into Kalinga III. The target QTL on chromosome 9 (RM242-RM201) significantly increased root length under drought stress and non-stress conditions confirming that this QTL from Azucena finctions in a novel genetic background. This QTL was found to improve root penetration ability as well (Clarke et al. 2008). The study showed that a single backcross will result in higher frequency of segregants with desirable alleles when adapted line is used as a recurrent parent (Steele et al. 2004). Such marker evaluated selection in target ecosystem with farmers participation resulted in development and release of improved rice variety viz., Birsa Vikas Dhan 111 in Jharkhand (Steele et al. 2007).

QTL associated with root traits from a DH line of CT9993 xI R62266 are being introgressed into RD6, a popular rice variety in Thailand through MAS. QTLs linked to root traits from chromosome 4, 8 and 9 are being introgressed into IR20 and IR64 using MAS in TNAU, Coimbatore. Near isogenic lines of IR62266 introgressed with QTL for root penetration ability and basal root thickness from chromosome 4 of CT9993 through MAS were field tested recently and results showed improved performance of the NILs as compared to recurrent parent (Chandra Babu, unpublished).

Looking into the future

Presently, a large number of markers are available and populations of more agronomically important varieties can be employed as parents (Courtois et al. 2003). A more extensive survey of drought-resistant rice germplasm will hopefully lead to the identification of lines carrying major genes conferring drought resistance. Such a survey is currently being performed at IRRI and is yielding encouraging results (Bernier et al. 2007). The improvement of drought tolerance should not be achieved with a parallel limitation of yield potential (Cattivelli *et al.,* 2008). QTLs for drought-related traits coincident with QTLs for yield potential should be considered as priority targets for MAS (O' Toole, 2004). A number of QTLs are identified for several drought resistance traits. Key genomic regions have been identified that co-locate with QTLs for traits that directly or indirectly impact grain yield under stress. These regions, once fine mapped, appear promising for the eventual use in MAS and/or map based cloning of genes for development of drought resistant rice varieties. In addition to selection for specific traits or specific genomic regions, direct selection for yield under drought itself appears useful. General adaptability and acceptability of genotypes hastens development and further adoption of high yielding rice lines suitable for rainfed environments.

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