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A review on linkage mapping for drought stress tolerance in rice

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Abstract
Rice is one of the most widely grown cereal crops in the world and is the staple food of more of the world's population. Environmental degradation, including pollution, increase in night time temperature due to global warming reductions in suitable arable land, water, labour and energy dependent fertilizer provide constraints to rice productivity. Drought stress is a major abiotic threat to rice production and its yield stability which leads to production of drought tolerant rice cultivars. Linkage analysis will help us to identify the genes contributing to drought tolerance in rice and their relative contribution to the very important trait.

Keywords: drought, linkage, QTL, molecular markers, MAS

Introduction
Rice is one of the most important staple foods for more than half of the world's population (IRRI, 2006) and influences the livelihoods and economies of several billion people. Rice production systems have over recent years become increasingly threatened by the effects of climate change (Masutomi *et al.,* 2009) [59], as a large portion of the rice-growing areas are located in especially vulnerable regions. Current rice production systems rely on an ample water supply and thus are more vulnerable to drought stress.

Globally, rice is grown on 154 million hectares and approximately 45 % of this area is under rainfed conditions that have very low-yield potential (Verulkar *et al.* 2010). Rainfed rice is grown in 60 Mha of land area (Fischer *et al.* 2012). Rice has played a central role in human nutrition and culture for the past 10,000 years. It has been estimated that world rice production must increase by 30% over the next 20 years to meet projected demands from population increase and economic development (Peng *et al.*, 1999) [86]. Rice grown on the most productive irrigated land has achieved nearly maximum production with current strains (Peng *et al.*, 1999) [86]. Environmental degradation, including pollution, increase in nighttime temperature due to global warming (Peng *et al.*, 2004) [83], reductions in suitable arable land, water, labour and energy-dependent fertilizer provide additional constraints. These factors make steps to maximize rice productivity particularly important. Increasing yield potential and yield stability will come from a combination of biotechnology and improved conventional breeding. Both will be dependent on a high quality rice genome sequence.

Drought is a more complex phenomenon than most other stresses, such as salinity, submergence, pests, and diseases and a key factor affecting food security worldwide; its effects reduce 70% in crop's yield generally (Bray *et al.,* 2000). It can occur at any point during crop production and for any length of time, affecting a large array of physiological, biochemical, and molecular processes. These complexities, along with the uncertainty in drought timing, intensity, and duration, have posed a major challenge for agricultural scientists. The genetic mechanisms that condition the expression of drought tolerance in rice plants are poorly understood. Despite drought having been a focus of agricultural research for several decades, progress in delivering drought adapted rice varieties and technologies has been relatively slow. The high-resolution genetic map permits us to characterize meiotic recombination in the whole genome. In the present study, a molecular marker-based genetic analysis for drought tolerance was conducted. Whatever recent information based on the research work on the study on linkage analysis for drought tolerance in rice has been categorically reviewed in this chapter.

Rice and drought stress
Water stress at flowering is most serious and devastating to yield because it has diverse effect of pollination and causes flower abortion, grain abscission and increasing of percentage of unfilled grain (Hsiao, *et al.*, 1976).

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Worldwide, drought stress is one of the most important abiotic stress factors affecting crop productivity (Boyer, 1982) [11]. Rice's susceptibility to water stress is more pronounced at the reproductive stage and causes the greatest reduction in grain yield when stress coincides with the irreversible reproductive processes (Matsushima, 1966; Cruz and O'Toole, 1984) [61, 23]. Being a semiaquatic plant species and commonly grown in lowland having standing water during allstages of growth, rice is known to be more susceptible to shortage of irrigation waterthan most other crops (Inthapan and Fukai, 1988) [33]. Since rice is characterized by a shallow root system, it has limited water extraction capacity below 60 cm (Fukai and Inthapan, 1988) [33]. In rainfed lowland areas, one of the major abiotic constraints depressing rice production is water stress, including deficit called drought (Chang, 1979; Herdt, 1991; Lin and Shen, 1993). Drought stress is a serious limiting factor to rice production and yield stability in rainfed rice areas (Dey and Upadhyaya, 1996) [26].

Until recently, lack of concept, direction, and protocol has remained a significant obstacle to genetic improvement of drought tolerance (Blum *et al.,* 1996). The complex quantitative genetics nature of drought tolerance was once thought to be the main constraint for breeding for improved rice varieties under drought-prone environments (Nguyen *et al.,* 1997). Drought tolerance has been considered as a valid breeding target to partially compensate for the loss in yield. Phenotypic traits associated directly with drought tolerance are unclear; however, several investigations noted that deep rooting (Ekanayake *et al.,* 1985; Lilley and Fukai, 1994; Pantuwan *et al.,* 1996; Wade *et al.,* 1996) and osmotic adjustment (Ludlow and Muchow, 1990; Jongdee and Cooper, 1998; Zhang *et al.,* 1999) are associated with drought tolerance. Conventional plant breeding attempts changed over to use physiological selection criteria since they are time consuming and rely on present genetic variability (Zhu, 2002). Worldwide, rainfed rice is over 50 per cent of the area sown and it produces only one quarter of total rice production (McLean *et al.,* 2002). In several parts of the world including India, increasing water scarcity and drought have posed as a serious threat to traditional rice cultivation practices (Tuong and Bozeman, 2003). It is estimated that 50 percent of the world's rice production is affected to a greater or lesser extent by drought (Bouman *et al.,* 2005). Studies have shown the presence of high genetic variability for many physio-morphological traits controlling drought response in rice (Manickavelu *et al.,* 2006) [57]. Drought stress is severely damaging during reproductive stages of the rice crop, especially during flowering, although drought in other stages can also lead to significant yield reductions (Liu *et al.,* 2006). Kumar *et al.* (2006) observed that the percentage of unfilled grains were significantly higher in sites that were affected by drought at reproductive stage.

According to a report, irrigation for agriculture consumes 2/3 of the world's fresh water and rice alone consumes more than 50 per cent of the water used for irrigation in Asia. Out of 70.4 per cent of the total water consumption in agriculture, about 70 per cent is used for rice production alone (Zhang, 2007). Drought stress tolerance is seen in almost all plants but its extent varies from species to species, even within the species. Water deficit and salt stresses are global issues to ensure survival of agricultural crops and sustainable food production (Jaleel *et al.,* 2007). In rainfed ecosystems, drought is considered to be the major obstacle in rice production and yield stability. Under drought, the mechanism of drought tolerance is most desirable in order to maintain

crop productivity (Passioura, 2007). Studies in MSE may limit the chances of detecting QTLs for drought resistance that are widely applicable to target populations of environments (TPEs), as the timing and intensity of stress vary over years in rainfed rice ecosystems (Pandey *et al.* 2007), which ultimately changes the plants responses and traits involved in drought-resistance mechanisms (Kamoshita *et al.,* 2008) [42].

Drought is the most serious constraint to rice production since most of the farmers' preferred rice varieties are susceptible to drought stress (Serraj *et al.,* 2009) [76]. Screening for drought resistance is being carried out mostly in the wet season in the target environments in the large rainfed drought-prone areas of eastern India and northeast Thailand (Kumar *et al.,* 2008; Verulkar *et al.,* 2010). Average yield reduction in rainfed, drought-prone areas has been found to range from 17 percent to 40 percent in severe drought years, leading to huge production losses and chronic food scarcity (Greenbio, 2011). Drought, being considered as one of the most important constraints in crop production, resulting in yield loss (Chen *et al.,* 2013) and mostly rice production in the rainfed areas, drought has posed as the most important source of climate related risk (Pandey *et al.,* 2007).

Molecular breeding for drought stress in rice

Pantuwan *et al.* (2000) [78] conducted four sets of field experiments under lowland conditions to investigate genotypic variation for grain yield and putative drought tolerant traits. Different types of drought stress were imposed in each set of experiments and they observed a larger variation existed for grain yield under both irrigated and drought stress conditions. He *et al.* (2001) investigated six agronomic traits (days to heading, plant height, number of spikelets per panicle, number of grains per panicle, 1000-grain weight, and seed set percentage) and found that five of them did not show significant differences between the two populations. Salekdeh *et al.* (2002) [101] suggested that, the identification and introgression of genomic regions with a large and consistent effect on GY (grain yield) under drought may create an opportunity to improve high-yielding but drought-susceptible varieties through MAS of large-effect QTLs.

Babu *et al.* (2003) identified 5 (five) QTLs, related to drought tolerance while carrying out the genetic analysis in a rice population (CT9993×IR62266) using molecular markers. Lafitte *et al.* (2004) [47] identified a number of drought-related QTL for different growth and physiological traits involved in drought tolerance in rice. Wang *et al.* (2005) suggested that genetic improvement in drought stress tolerance for rice involves the quantitative nature of the trait, which reflects the additive effects of several genetic loci throughout the genome. Salvi and Tuberosa (2005) [102] made a first attempt to clone QTL having a substantial role to understand and manipulate the traits responsible for drought tolerance in rice.

Yue *et al.* (2005) characterized the genetic basis of drought resistance at reproductive stage in field by analyzing the QTLs for drought response index (DRI, normalized by potential yield and flowering time), relative yield, relative spikelet fertility, and four traits of plant water status and their relationships with root traits using a recombinant inbred population derived from a cross between an *indica* rice and upland rice. A total of 39 QTLs for these traits were detected with individual QTL explained 5.1–32.1% of phenotypic variation. Only two QTLs for plant water status were

commonly detected in two environments, suggesting different mechanisms might exist in two types of soil conditions.

Manickavelu *et al.* (2006) [57] studied the presence of high genetic variability for many physio-morphological traits controlling drought response in rice. Yue *et al. (*2006) analysed the genetic bases of drought tolerance (DT) and drought avoidance (DA) at reproductive stage in rice using a recombinant inbred line population from a cross between an *indica* lowland and a tropical *japonica* upland cultivar. Bernier *et al*. (2007), while screening a population of 436 F3 lines derived from a cross between two upland rice cultivars, Vandana and Way Rarem, selected some lines for drought tolerance.

qDTY 12.1 was the first reported large-effect QTL for grain yield under reproductive-stage drought (Bernier *et al.*, 2007). This QTL was identified in a population of 436 random F_3-derived lines from a cross between upland rice cultivars Vandana and Way Rarem. This QTL located between RM28048 and RM28166 and explained an R^2 of 33% under severe upland reproductive-stage drought conditions. Ninety-two rice germplasm accessions introduced from seven geographic regions of Africa, Asia, and Latin America, and eleven US cultivars, included as checks were evaluated by Agrama *et al.* (2007) [1] for yield and kernel characteristics and were genotyped with 123 SSR markers. The SSR markers were highly polymorphic across all accessions. Population structure analysis identified eight main clusters for the accessions which corresponded to the major geographic regions, indicating agreement between genetic and predefined populations. Kamoshita *et al.* (2008) [42] identified a number of QTL for several drought-related traits including deep rooting using the same rice mapping populations previously used by Babu *et al.* (2003).

To the best our knowledge, none of the studies were conducted under natural drought conditions predominant in TEs and these QTLs were identified in MSE and QTLs mapped under severe drought stress conditions (Kumar *et al*., 2008). Venuprasad *et al.* (2008) concluded moderate heritability of grain yield under drought, there by conforming the suitability of grain yield as a selection citation. In 2009, they again used an $F_{4:5}$ populations of 490 recombinant inbred lines (RILs) from the cross Apo/Swarna to detect quantitative trait loci (QTL) with large effects on grain yield under drought stress using bulk-segregant analysis (BSA). Two rice microsatellite (RM) markers RM324 and RM416, located on chromosomes 2 and 3 respectively, were shown via BSA to be strongly associated with yield under lowland drought stress. They tested effects of QTLs in a total of eight hydrological environments over a period of 3 years. The QTL linked to RM416 (*DTY 3.1*) had a large effect on grain yield under severe lowland drought stress, explaining about 31% of genetic variance for the trait ($P < 0.0001$).

It was also reported that, in large mapping populations, the correlation between high yield potential and good yield under drought was low but always positive (Kumar *et al.*, 2008), suggesting the possibility to combine high yield potential and good yield under drought successfully. To detect the relationship between markers and trait value, QTL cartographer 2.5.009 (Churchill and Doerge, 1994) [20], Q gene 4.3.10 (Joehanes and Nelson, 2008), and QTLNetwork 2.1 (Yang *et al.,* 2008) were used.

Bernier *et al.* (2009), from 21 experiments conducted at the IRRI and in eastern India, confirmed that *qDTY 12.1* showed an increased effect with increasing severity of drought stress. Guo *et al.* (2010) [137] detected three QTLs (*qRL-1, qRL-*

7 and*qRL-8-1*) with two software's: *Win QTL Cart 2.5* and *QTL Network 2.0*. They found a new locus *qRL-8-1*, accounting for 15.5% and 12.8% of phenotypic variations in the two environments, respectively. Swain *et al.* (2010) evaluated eighteen rice genotypes and they found the reduction in panicle number (72%) and grain yield (12%). They evaluated the six generations (P1, P2, B1, B2, F1 and F2) of six crosses of rice under drought and irrigated conditions. They observed the reduction in several characters including grain yield under drought condition. SSR technique combined with selective genotyping was used by Nguyen Thi Lang and Buu Chi Buu (2010) at Cuu Long Delta Rice Research Institute (CLRRI) and Institute of Agricultural Science for Southern Vietnam (IAS) to map quantitative trait loci (QTLs) associated with drought tolerance in rice.

Earlier, Gomez *et al.* (2010) used recombinant inbred lines (RILs) derived from locally adapted *indica* rice lines to detect QTLs for plant production traits under drought stress in TPEs, but no yield QTL was identified. Henry *et al.* (2011) [40] reported greater root length density at depth in drought tolerant genotypes such as Dular, Azucena, and Rayada compared with high yielding drought susceptible varieties such as IR64. Henry *et al.* (2011) [40] also suggested a majority of drought tolerance landraces show early flowering, tall plant height, low tillering, and low yield compared with medium to late flowering, semi dwarf plant height, high tillering, and high yield of the high yielding popular varieties. Serraj *et al.* (2011) also emphasized the importance of field experiments in TPEs to identify QTLs for rice yield under natural drought stress. Vikram *et al.* (2011) [130] started a series of experiments F_3-derived populations developed from the cross of drought-tolerant donor N22 with high-yielding mega-varieties Swarna, IR64, and MTU1010 that resulted in the identification of *qDTY 1.1*, a large-effect QTL having an effect on grain yield under severe lowland reproductive-stage drought across these three populations.

Vikram *et al.* (2011) [130] suggested that, QTL *qDTY 1.1* showed an R^2 of 13.4, 16.9, and 12.6% across two seasons of screening under severe lowland drought in N22/Swarna, N22/IR64, and N22/MTU1010 populations, respectively. Vikram *et al*. (2011) [130] also demonstrated a successful marker-assisted selection to improve yield mainly relied on the use of high-yielding lines to identify large-effect QTLs and evaluation of their consistent effects. Recently, Weber *et al.* (2012) also showed less correlation between managed and random drought stress environments for grain yield in maize. Swamy *et al.* (2011) [121], through a study on a panel of random drought tolerant donors for the identified drought yield QTLs, reported the presence of *qDTY* 12.1 in 85% of the lines, followed by *qDTY* 4.1 in 79% of the lines and *qDTY 1.1* in 64% of the lines, thus validating the high presence of these identified QTLs in drought tolerant donors.

In recent years, several researchers developed mapping populations between high-yielding lines (IR64, Swarna and MTU1010) and drought-tolerant local landraces and wild cultivars to map grain yield QTLs (Srividhya *et al.,*2011; Vikram *et al.,*2011; Ghimire *et al.,*2012; Yadaw *et al*., 2013) [130, 67] for reproductive stage-specific drought stress. One of the most consistent QTLs, *qDTY 1.1*, contributed by donor N22 was identified in the background of mega-varieties MTU1010, IR64, and Swarna (Vikram *et al.*, 2011) [130]. This QTL was also contributed by another donor *Dhagaddeshi* to IR64 and *Swarna* (Ghimire *et al.,* 2012). Dixit *et al.* (2012) [29] suggested that despite being one of the largest QTLs reported for grain yield under reproductive-stage drought, explaining

51% of the genetic variation, a study of epistatic interaction in a Vandana/WayRarem population showed two loci (*qDTY 2.3* and *qDTY 3.2*) to be interacting with *qDTY 12.1* and significantly enhancing the yield of *qDTY 12.1*-positive lines. Later on, *qDTY 12.1* was also identified to show a similar high effect in lowland reproductive-stage drought in an IR74371-46-1-1/Sabitri population (Mishra *et al.* 2013) [67].

Similarly, *qDTY 3.2* was identified to show a large effect in an IR77298-14-1-2-10/Sabitri population (Yadaw *et al.,* 2013) [67]. *qDTY 12.1* showed an effect against Vandana from donor WayRarem (Bernier *et al.* 2007) in lowland and against recipient variety Sabitri in lowland from donor IR74371-46-1-1 (Mishra *et al.,* 2013) [67]. Sandhu *et al.* (2013) [105] conducted experiments for mapping QTL for yield, root-related traits, and agronomic traits under aerobic conditions using HKR47 × MAS26 and MASARB25 × Pusa Basmati 1460 $F_{2:3}$ mapping populations. A total of 35 QTL associated with 14 traits were mapped on chromosomes 1, 2, 5, 6, 8, 9, and 11 in MASARB25 x Pusa Basmati 1460 and 14 QTL associated with 9 traits were mapped on chromosomes 1, 2, 8, 9, 10, 11, and 12 in HKR47 × MAS26. Sandhu *et al.* (2013) [105] suggested two large-effect QTLs (*qDTY 12.1* and *qDTY 3.2*) which were identified in two different populations. These were validated for their effect in Nepal by phenotyping the full mapping population in Nepal in the second season (Mishra *et al.,* 2013; Yadaw *et al.,* 2013) [67]. *qDTY 6.1* showed an effect against *Swarna* in upland from donor Apo (Venuprasad *et al.* 2012) [129] and in lowland against recipient variety TDK1 from donor IR55419-04 9 (Dixit *et al.,* 2014). Recombinant inbred lines of IR20 × Nootripathu, two *indica* cultivars adapted to rainfed target populations of environments (TPEs), were evaluated by Prince *et al.* (2015) [90] in one and two seasons under managed stress and in a rainfed target drought stress environment, respectively. Prince *et al.* (2015) [90] also identified 9 QTLs for physio-morphological and 24 QTLs for plant production traits in managed and natural drought stress conditions in the TPEs, respectively. Yield QTLs that were consistent in the target environment over seasons were identified on chromosomes 1, 4, and 6, which could stabilize the productivity in high-yielding rice lines in a water-limited rainfed ecosystem.

Genetic linkage map analysis for drought tolerance in rice
A linkage map using DNA markers was made for rice (McCouch *et al.,* 1998; Saito *et al.,* 1991; Kurata *et al.,* 1994) [45]. A molecular map was also constructed by Price *et al.* (1994) for the rice genome comprised of 726 markers (mainly restriction fragment length polymorphisms; RFLPs). The mapping population was derived from a backcross between cultivated rice, *Oryza sativa*, and its wild African relative, *Oryza longistaminata*. The initial skeleton linkage map was constructed using MAPMAKER/EXP3.0 (Lincoln *et al.,* 1993) [50], based on a RIL population derived from the same parents.
A 2275-marker genetic map of rice (*Oryza sativa* L.) covering 1521.6 cM in the Kosambi function was constructed by Harushima *et al.* (1998) [39] using 186 F_2 plants from a single cross between the *japonica* variety Nipponbare and the *indica* variety Kasalath. The map provided the most detailed and informative genetic map of any plant. Centromere locations on 12 linkage groups were determined by dosage analysis of secondary and telotrisomics using >130 DNA markers located on respective chromosome arms.

He *et al.* (2001) reported the comparison of molecular maps and mapped agronomic trait loci between DH and RIL populations derived from the same rice cross, ZYQ8 (*indica*) × JXI7 (*japonica*). *Oryza glaberriima* is an endemic African cultivated rice species. To provide a tool for evaluation and utilisation of the potential of *O. glaberrinia* in rice breeding, Lorieux *et al.* (2002) developed an interspecific *O. glaberriima* x *Oryza sativa* genetic linkage map. It was based on PCR markers, essentially microsatellites and STSs. Segregation of markers was examined in a backcross population.
A genetic linkage map consisting of 245 SSR markers was constructed for mapping QTL for these traits by Yue *et al.* (2006). A total of 27 QTL were resolved for 7 traits of relative performance of fitness and yield, 36 QTL for 5 root traits under control, and 38 for 7 root traits under drought stress conditions, suggesting the complexity of the genetic bases of both DT and DA. Yue *et al.* (2006) constructed a genetic linkage map consisting of 245 SSR markers for mapping QTL for these traits. A total of 27 QTLs were identified for 7 traits of relative performance of fitness and yield, 36 QTL for 5 root traits under control and 38 for 7 root traits under drought stress conditions. Only a small portion of QTLs for fitness- and yield-related traits overlapped with QTLs for root traits, indicating that DT and DA had distinct genetic mechanisms.
Two high density genetic linkage maps were constructed by Song *et al.* (2010) based on 21,478 single nucleotide polymorphism loci mapped in the Williams 82 x *G. soja* (Sieb. & Zucc.) PI479752 population with 1083 RILs and 11,922 loci mapped in the Essex x Williams 82 population with 922 RILs. SSR marker genotypes and phenotypes of flag leaf rolling index (LRI) were investigated by Guo *et al.* (2010) [137] in *Xiushui 79* (P_1, a japonica rice variety), *C Bao* (P_2, a japonica restorer line) and 254 recombinant inbred lines derived from the cross between P_1 and P_2, and in two environments. A genetic map of this cross was constructed, QTLs for LRI were detected and their interactions with environments were analyzed. Among 818 pairs of SSR primers, 90 primers showed polymorphism between P_1 and P_2, and 12 markers showed highly significant correlation with LRI in both environments based on single marker regression analysis. The genetic map containing 74 information loci has a total distance of 744.6 cM, with an average of 10.1 cM between two adjacent loci.
Xie *et al.* (2014) proposed a new approach to correct the recombination fraction between epistatic distorted markers in backcross and F_2 populations under the framework of fitness and liability models. The information for three or four markers flanking with an epistatic segregation distortion locus was used to estimate the recombination fraction by the maximum likelihood method, implemented via an expectation–maximisation algorithm. Using 202 F_2 individuals derived from a hybrid between the variety 578 and the landrace Sanfensan, Song *et al.* (2015) constructed a genetic linkage map consisting of 22 linkage groups covering 2070.50 cM and including 208 simple sequence repeat (SSR) markers. The minimum distance between adjacent markers was 0.01 cM and the average was 9.95 cM. Each linkage group contained 2–22 markers.
Badoni *et al.* (2016) developed genome-wide 84634 ISM (intron-spanning marker) and 16510 InDel-fragment length polymorphism-based ILP (intron-length polymorphism) markers from genes physically mapped on 12 rice chromosomes. These genic markers revealed much higher

amplification-efficiency (80%) and polymorphic-potential (66%) among rice accessions even by a cost-effective agarose gel-based assay. A wider level of functional molecular diversity (17–79%) and well-defined precise admixed genetic structure was assayed by 3052 genome-wide markers in a structured population of *indica, japonica*, aromatic and wild rice.

Conclusion

The identification of genes affecting abiotic stress tolerance is a major step in understanding the genetic basis of plant response to drought for the development of drought tolerant cultivars. The development of genetic maps based on markers that are simple to generate, highly reproducible, codominant, and specific for known linkage groups are highly desirable for their application in breeding. It is hoped that this genetic map will prove useful in locating and manipulating genes of interest and in selection of yield-determining traits found linked with molecular markers in segregating populations.

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