



Mapping quantitative trait loci and marker assisted selection for the improvement of drought tolerance in rice

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Abstract: Drought stress is a major constraint to rice production especially in rainfed ecosystems. The development of drought tolerant rice cultivars through conventional breeding has met with little success. The complexity of drought tolerance mechanism(s) and the difficulty in incorporation of physiological selection criteria in breeding programmes are important reasons for this lack of progress. Deep and thick roots enable rice plants to access deep soil moisture and help to avoid drought. Capacity for osmotic adjustment (OA) helps to maintain turgor under water stress and sustains growth under declining soil moisture. Both root traits and OA are difficult to phenotype in large segregating progenies. Quantitative trait loci (QTL) mapping combined with marker-assisted selection (MAS) approach offers a tool for indirect selection of complex traits such as drought tolerance. Molecular markers linked to various root traits and OA have been mapped in rice. Consistent QTL linked to root traits and OA have been identified thus enabling MAS of these traits. However, the value of these QTL have to be tested under field conditions in the target ecosystems using near isogenic lines. QTL linked to field drought tolerance in terms of grain yield under stress have been mapped recently. QTL for root traits overlapped with QTL for drought tolerance in the field. Identification and introgression of such QTL into high yielding elite cultivars will lead to increase in rice production in drought-prone rainfed ecosystems.

Key words: Rice, Drought tolerance, QTL mapping, Marker-assisted selection, Root traits, Osmotic adjustment.

Introduction

Impact of drought on rice production

Rice (*Oryza sativa* L.) is the principal food crop for more than a third of the world's population. Rice is cultivated in 148 million hectares globally over a wide range of agro-ecological conditions with varying temperatures, water regimes and soil texture. About 27 per cent of world's rice area is under rainfed lowland without assured water supply during critical periods of crop growth (Khush, 1997). Another 12 per cent is under rainfed uplands without any surface water accumulation. Of world's rainfed lowland rice area of 41 million hectares, 95 per cent is in Asia. In south and south east Asia, future increase in rice production would largely come from the rainfed lowland ecosystem (Garrity *et al.* 1986). Nearly 50 per cent of this area is classified as drought-prone and may experience frequent and severe water deficits at any time during the rice growth. Rice environments in India are extremely

diverse. India has the largest area under rice in the world. Of the 44 million hectares of total rice area in India, 45 per cent is irrigated, 33 per cent is rainfed lowland, 15 per cent is rainfed upland and 7 per cent is flood-prone (<http://www.fao.org>). Rice is the staple food for nearly 65 per cent of the population in India. Presently, India's annual rice production is around 90 million tonnes. By 2025, India must increase its rice production by at least 70 per cent to feed the growing population. This increase has to be achieved with less water and less labour from ever shrinking arable land available for rice cultivation. Since much of the area under rice is rainfed, yields are drastically reduced by the occurrence of drought stress due to insufficient and uneven rainfall during the crop growth period. Drought stress has been identified as the major constraint to rice production and yield stability by farmers in the rainfed lowlands of eastern India (Widawsky and O'Toole, 1990). Development of high yielding drought tolerant rice cultivars

will considerably improve rainfed rice production. However, little progress has been made in breeding for drought tolerance, since the fundamental mechanisms of drought tolerance in rice are poorly understood.

Components of drought tolerance - Root traits

Progress in conventional breeding for drought tolerance has been slow due to the complexity of drought tolerance and low genetic variance of yield under water stress conditions. Alternatively, yield improvements in water-limited environments could be achieved by identifying drought tolerance component traits and selecting for those traits in a breeding programme (Nguyen *et al.* 1997). Plants have evolved many strategies to deal with periods of water deficits. Several putative traits contributing to drought tolerance in rice have been identified. Root characteristics such as thickness, depth of rooting and root length density have been associated with drought tolerance in rice (Yoshida and Hasegawa, 1982; Ekanayake *et al.* 1985). A rice variety with extensive and deep root system will be able to reach the soil water at depth to meet its evaporative demand under water deficit situations (Ludlow and Muchow, 1990). The compact soil layers at relatively shallow depths may have adverse effects on rice under prolonged dry spells (O'Toole and De Datta, 1986). Increased root thickness helps the plant to improve the water uptake and also allows to penetrate the soil hardpans, characteristic of lowland rice fields. Drought tolerance in rice can be improved through a deep and thick root system. However, incorporation of root traits in breeding programme is difficult, because measuring root traits is time consuming and labour intensive (Ingram *et al.* 1994). Further, measurement of root system traits requires uprooting of plants resulting in loss of plant material (Shen *et al.* 1999).

Osmotic adjustment and dehydration tolerance

Osmotic adjustment (OA), defined as active accumulation of solutes under water stress, is a shoot-related drought tolerance mechanism and has received greater attention as an effective component of drought tolerance in crop plants

(Ludlow and Muchow, 1990). OA allows maintenance of turgor potential in plants experiencing water stress. OA delays leaf rolling, tissue death and leaf senescence in rice under water stress (Hsiao *et al.* 1984) and has been shown to enhance grain yield under water-limited environments in several other crops (Zhang *et al.* 1999). There is significant genetic variation for OA among rice lines (Lilley and Ludlow, 1996; Babu *et al.* 2001). However, adoption of this trait in breeding programmes has been slow due to inability to rapidly screen large breeding populations for OA. The measurement of OA currently requires complex and time consuming procedures.

Dehydration tolerance (the ability of leaves to tolerate desiccation level water stress, assists the plant organs to survive short-term water deficits. The lowest leaf water potential that leaves reach just prior to death (lethal leaf water potential) has been used to determine dehydration tolerance (Flower and Ludlow 1986). During terminal stress, dehydration tolerance may allow plants to maintain metabolic activity for longer time and to translocate more stored assimilates to the grain (Fukai and Cooper 1995). So, if dehydration tolerance of rice increased by breeding approaches then it could be possible to increase or at least stabilize the yield of rainfed rice. Genotypic variation for dehydration tolerance capacity of rice is large (Lilley and Ludlow, 1996; Babu *et al.* 2001). However, incorporation of this trait in breeding program is hampered by complex experimental protocols requiring heavy investment in creating controlled environment facilities.

Molecular markers and drought resistance improvement

With the advent of molecular markers it is easier to dissect the complex traits such as drought tolerance. Polygenic characters which were previously very difficult to analyze using traditional plant breeding methods, would now be easily mapped using molecular markers (Mohan *et al.* 1997). Molecular markers offer scope for improving the efficiency of conventional plant breeding by carrying out selection not directly on the trait but on the

molecular markers linked to the trait of interest, thus reducing the need for extensive field testing over time and space (Babu *et al.* 1996). Recent advances in DNA marker technology together with the concept of marker-assisted selection (MAS) strategy offer solutions for difficulties encountered in breeding for improved drought tolerance. Molecular markers linked to complex root and shoot traits would provide a new tool for selecting cultivars with drought tolerance capacity and thereby improving rice productivity under rainfed conditions.

QTL mapping for drought tolerance component traits

This review focuses on quantitative trait loci (QTL) analyses in rice, a strategy that has the potential to identify and manipulate genes involved in the complex phenomenon of drought tolerance. The basis of QTL detection, regardless of the crop to which it is applied, is the identification of association between genetically determined phenotypes and specific genetic markers (McCouch and Doerge, 1995). A summary of various drought tolerance traits for which QTL have been mapped in rice has been given in Tables 1 and 2. Champoux *et al.* (1995) mapped QTL associated with five parameters of root morphology namely root thickness, root:shoot ratio, root dry weight per tiller, deep root dry weight per tiller and maximum root length and QTL linked to the drought avoidance in the field using a recombinant inbred (RI) line population of Co39/ Moroberekan (Table 1). Moroberekan is a drought tolerant upland *japonica* variety with deep and thick root system that allows to avoid drought stress by accessing water from the deep soil layers. Co39 is a lowland *indica* variety with a shallow root system and is drought sensitive. More than 50 per cent of the QTL associated with field drought avoidance overlapped with QTL for root morphology and all the alleles that have positive effect in either case were derived from Moroberekan (McCouch and Doerge, 1995). Ray *et al.* (1996) mapped QTL associated with total number of roots and root penetration index using these RI lines. A subset of this population (52 RI lines) was used by Lilley *et al.* (1996) to map QTL linked to OA and dehydration tolerance and one putative QTL for OA and five QTL for the dehydration tolerance were mapped (Table 2).

The utility of the QTL depend on the magnitude of phenotypic variation explained and on their consistency over environments and mapping populations. Thus a double haploid (DH) line population of IR64/Azucena developed through anther culture was used to identify QTL linked to total root weight, deep root: shoot ratio, deep root weight per tiller, maximum root length and root thickness (Yadav *et al.* 1997). Most of the detected QTL were common across the various root traits. Comparison of QTL detected in IR64/Azucena DH lines with those of Co39/Moroberekan RI lines showed many common QTL for several root traits. Price and Tomos (1997) used an F_2 population derived from Bala/Azucena and mapped QTL for root thickness and root cell length using phenotypic data obtained from a hydroponic screening system. Some of the QTL identified for maximum rooting depth, root thickness and root dry weight in this population were also found in Co39/Moroberekan RI lines (Champoux *et al.* 1995). Ray *et al.* (1996) found that chromosome 6 contained major QTL for root penetration index. This was co-located with QTL for root length at all stages of development in Bala/Azucena F_2 population. QTL mapping of two other drought tolerance indices *viz.*, leaf rolling and stomatal behaviour was also done by Price *et al.* (1997) in this population. The F_2 progenies were forwarded to F_6 by single seed descent and was used to locate QTL linked to both field performances under drought and root penetration ability using a wax-layer system (Price *et al.* 2000). A total of 17 QTLs associated with drought avoidance was mapped in this population in tests conducted in the uplands of Philippines and West Africa (Price *et al.* 2002). The authors also illustrated the degree of QTL by year and QTL by site interaction and demonstrated the value of calculating averages for identification of the more stable but small effect QTL. This information is potentially valuable to the breeders in crop improvement programme for water limiting environments. A greenhouse experiment with this population was conducted to investigate the effect of rooting environment on root growth QTL (Price *et al.* 2002a). The results gave different patterns of QTL indicating the phenomenon of QTL by environment interaction. The results showed that

Table 1. QTL identified for various root traits in rice using different mapping populations

Trait	No. of QTL detected	Population	Reference
Basal root thickness	18	Co39/Moroberekan RI lines	Champoux <i>et al.</i> 1995
	8	IR64/Azucena DH lines	Yadav <i>et al.</i> 1997
	5	IR64/Azucena DH lines	Hemamalini <i>et al.</i> 2000
	6	CT9993/IR62266 DH lines	Zhang <i>et al.</i> 2001
	6	CT9993/IR62266 DH lines	Kamoshita <i>et al.</i> 2002
	6	IR58821/IR52561 RI lines	Kamoshita <i>et al.</i> 2002a
	7	Bala/Azucena RI lines	Price <i>et al.</i> 2002a
Penetrated root thickness	8	IR58821/IR52561 RI lines	Ali <i>et al.</i> 2000
	11	CT9993/IR62266 DH lines	Zhang <i>et al.</i> 2001
	4	IR64/Azucena DH lines	Zheng <i>et al.</i> 2000
Adventitious root thickness	2	Bala/Azucena F ₂ progenies	Price and Tomos, 1997
	25	IR64/Azucena DH lines	Yadav <i>et al.</i> 1997
	10	Bala/Azucena F ₂ progenies	Price and Tomos, 1997
	5	IR64/Azucena DH lines	Hemamalini <i>et al.</i> 2000
	6	Bala/Azucena RI lines	Price <i>et al.</i> 2002a
	9	CT9993/IR6226 DH lines	Kamoshita <i>et al.</i> 2002
	5	IR58821/IR52561 RI lines	Kamoshita <i>et al.</i> 2002a
Number of penetrating roots	4	Co39/Moroberekan RI lines	Ray <i>et al.</i> 1996
	7	IR58821/IR52561 RI lines	Ali <i>et al.</i> 2000
	2	IR64/Azucena DH lines	Zheng <i>et al.</i> 2000
	7	Bala/Azucena RI lines	Price <i>et al.</i> 2000
Total root number	19	Co39/Moroberekan RI lines	Ray <i>et al.</i> 1996
	2	IR58821/IR52561 RI lines	Ali <i>et al.</i> 2000
	2	IR64/Azucena DH lines	Zheng <i>et al.</i> 2000
	3	Bala/Azucena RI lines	Price <i>et al.</i> 2000
	10	IR64/Azucena DH lines	Hemamalini <i>et al.</i> 2000
	12	Bala/Azucena RI lines	Price <i>et al.</i> 2002a
Deep root per tiller	6	CT9993/IR62266 DH lines	Kamoshita <i>et al.</i> 2002
	6	IR58821/IR52561 RI lines	Kamoshita <i>et al.</i> 2002b
Root penetration index	6	Co39/Moroberekan RI lines	Ray <i>et al.</i> 1996
	6	IR58821/IR52561 RI lines	Ali <i>et al.</i> 2000
	4	CT9993/IR62266 DH lines	Zhang <i>et al.</i> 2001
	4	IR64/Azucena DH lines	Zheng <i>et al.</i> 2000
	7	Bala/Azucena RI lines	Price <i>et al.</i> 2000
Total root weight	23	IR64/Azucena DH lines	Yadav <i>et al.</i> 1997
	5	CT9993/IR6226 DH lines	Zhang <i>et al.</i> 2001
Penetrated root dry weight	3	CT9993/IR62266 DH lines	Zhang <i>et al.</i> 2001
Maximum root depth	5	IR58821/IR52561 RI lines	Ali <i>et al.</i> 2000
	1	CT9993/IR6226 DH lines	Zhang <i>et al.</i> 2001

Deep root weight	8	Co39/Moroberekan RI lines	Champoux <i>et al.</i> 1995
	17	IR64/Azucena DH lines	Yadav <i>et al.</i> 1997
	7	CT9993/IR62266 DH lines	Kamoshita <i>et al.</i> 2002
	5	IR58821/IR52561 RI lines	Kamoshita <i>et al.</i> 2002a
	6	Bala/Azucena RI lines	Price <i>et al.</i> 2002a.
Root dry weight per tiller	14	Co39/Moroberekan RI lines	Champoux <i>et al.</i> 1995
	2	IR64/Azucena DH lines	Hemamalini <i>et al.</i> 2000
	20	IR64/Azucena DH lines	Yadav <i>et al.</i> 1997
Shoot biomass	7	CT9993/IR62266 DH lines	Kamoshita <i>et al.</i> 2002
	2	IR58821/IR52561 RI lines	Kamoshita <i>et al.</i> 2002a
	8	Bala/Azucena RI lines	Price <i>et al.</i> 2002a
Root/shoot ratio	16	Co39/Moroberekan RI lines	Champoux <i>et al.</i> 1995
	1	IR64/Azucena DH lines	Hemamalini <i>et al.</i> 2000
Deep root/shoot ratio	26	IR64/Azucena DH lines	Yadav <i>et al.</i> 1997
	11	Bala/Azucena RI lines	Price <i>et al.</i> 2002a
	6	CT9993/IR62266 DH lines	Kamoshita <i>et al.</i> 2002
	5	IR58821/IR52561 RI lines	Kamoshita <i>et al.</i> 2002a
Root volume	1	Bala/Azucena F ₂ progenies	Price and Tomos, 1997
	5	IR64/Azucena DH lines	Hemamalini <i>et al.</i> 2000
Root pulling force	6	CT9993/IR62266 DH lines	Zhang <i>et al.</i> 2001

Table 2. QTL identified for osmotic adjustment, dehydration tolerance and certain other shoot-related drought resistance component traits in rice

Trait	No. of QTL detected	Population	Reference
Osmotic adjustment	1	Co39/Moroberekan RI lines	Lilley <i>et al.</i> 1996
	5	CT9993/IR62266 DH lines	Zhang <i>et al.</i> 2001
Dehydration tolerance	5	Co39/Moroberekan RI lines	Lilley <i>et al.</i> 1996
Leaf relative water content	2	Co39/Moroberekan RI lines	Lilley <i>et al.</i> 1996
	11	IR64/Azucena DH lines	Courtois <i>et al.</i> 2000
	8	Bala/Azucena RI lines	Price <i>et al.</i> 2002
Leaf rolling	18	Co39/Moroberekan RI lines	Champoux <i>et al.</i> 1995
	1	Azucena/Bala F ₂ progenies	Price <i>et al.</i> 1997
	11	IR64/Azucena DH lines	Courtois <i>et al.</i> 2000
	1	IR64/Azucena DH lines	Hemamalini <i>et al.</i> 2000
	5	Bala/Azucena RI lines	Price <i>et al.</i> 2002
Leaf drying	2	IR64/Azucena DH lines	Hemamalini <i>et al.</i> 2000
	10	IR64/Azucena DH lines	Courtois <i>et al.</i> 2000
	11	Bala/Azucena RI lines	Price <i>et al.</i> 2002
Stomatal conductance	2	Azucena/Bala F ₂ progenies	Price <i>et al.</i> 1997
Relative growth rate	10	IR64/Azucena DH lines	Courtois <i>et al.</i> 2000
Cell membrane stability	9	CT9993/IR62266 DH lines	Tripathy <i>et al.</i> 2000.

the genetic control of the root growth is complex. This study also suggested that both constitutive and drought-specific gene action may contribute to rooting depth under drought stress and that there is a considerable amount of QTL x environment interaction.

Hemamalini *et al.* (2000) used a subset of the DH line population derived from IR64/Azucena and mapped putative QTL for plant height, root length, total root number, root volume, root thickness, root dry weight, root:shoot ratio and leaf rolling under mild moisture stress imposed during the vegetative stage. Three QTL for root length, one QTL for root to shoot dry weight ratio and two QTL for root thickness identified by Yadav *et al.* (1997) were also identified in this study and the common QTL exhibited allelic effects in the same direction. Zheng *et al.* (2000) used IR64/Azucena DH population to map QTL for root penetration ability. Several putative QTL for penetrated root number, total root number, root penetration index, penetrated root thickness and maximum penetrated root length were identified in this population. Almost all the identified QTL for root-penetration index were derived from the Azucena alleles. In general, traditional upland adapted *japonica* rice cultivars have a well-developed root system with inherent higher root penetration ability (Yu *et al.* 1995). Courtois *et al.* (2000) located QTL for drought avoidance indices such as leaf rolling, leaf drying, leaf relative water content and relative growth rate under water stress using the DH line population of IR64/Azucena in three different field trials. QTL consistent across the trials and QTL common across certain traits were located.

Tripathy *et al.* (2000) used a CT9993-5-10-1-M/IR62266-42-6-2 derived DH population to map QTL for cell-membrane stability, which is one of the major selection indices for drought tolerance. One of the QTL for cell-membrane stability was mapped on chromosome 8, where a QTL for OA was mapped in this DH population (Zhang *et al.* 2001). OA is known to maintain turgor in cells during water deficit. Turgor maintenance in turn protects cell membrane stability. Zhang *et al.* (2001) used this DH population to better

understand the genetic basis for drought resistance in rice. Among the putative QTL identified for OA and root traits, QTL for OA did not overlap with any of the QTL for root traits. This reveals that molecular mechanisms of drought tolerance via OA and drought avoidance via a better root system are different and not negatively linked to each other. This was also indicated by lack of negative phenotypic correlations between OA and root traits in these DH lines (Zhang *et al.* 1999a). Thus the two divergent drought resistance strategies, drought avoidance through a deep and thick root system and drought tolerance via shoot-related OA can be selectively combined into one cultivar. Such a strategy would be of immense benefit in drought-prone rainfed lowlands where intermittent drought and compacted soils are of major concerns. Kamoshita *et al.* (2002) demonstrated the importance of phenotyping environment and suggest prospects for selection of QTL for deep root morphology, root thickness and vigorous seedling growth under anaerobic conditions to improve the constitutive root system of rainfed lowland rice. They emphasized the importance of defining conditions for phenotyping which relate closely to the target environment where the traits are to be expressed and in reproducing those conditions consistently in repeated screening. There was some consistency in QTL regions identified in CT9993/IR62266 DH population, despite the presence of QTL x environment interactions. QTL for deep root thickness near RG 476 in chromosome 4 was identified across populations. These consistent QTL could be used for introgression into elite rainfed lowland rice using MAS program.

In all these studies, QTL for root traits and OA have been studied using population derived from *indica/japonica* inter-subspecific crosses and majority of the alleles for desirable root traits are contributed by *japonica* ecotypes. However, the *indica* and *japonica* types are grown in diverse ecosystems and the trait that confers drought resistance in one environment may not be useful in another ecosystem (Ingram *et al.* 1994). Further, *japonica* alleles are not usually expressed under lowland conditions (Wang *et al.* 1994). Hence, it is desirable to look for genetic variation among rice accessions

within *indica* ecotypes and map QTL using populations derived from *indica* parents adapted to the target environment. Thus Ali *et al.* (2000) used IR58821-23-B-1-2-1/IR52561-UBN-1-1-2 (*indica/indica*) derived RI lines to map QTL for total root number, penetrated root number, root penetration index, penetrated root thickness and penetrated root length. Kamoshita *et al.* (2002a) evaluated this lowland adapted population for phenotypic variation and QTL for gross root morphology under anaerobic conditions in contrasting solar radiation regimes. Several QTL for root traits identified in this population were found to be common across different rice populations. For example, one marker interval, RG256-PC32M10 in chromosome 2, contained QTL for deep root morphology in both experiments in this study and also had QTL for root penetration ability in the study of Ali *et al.* (2000). Another example is, the interval on chromosome 4 (PC150M11-PC11M4), which not only contained QTL for deep root morphology in both experiments, but also had QTL for root thickness and shoot biomass. More detailed physiological analysis of this region in the future may provide a greater understanding of the relationship between these root traits and shoot biomass and possibly grain yield.

Marker assisted selection and future research strategies

Consistent QTL identified across genetic backgrounds and environments are most valuable since they could be transferred into desirable genetic backgrounds with the aid of markers and selected in early generations. The results of comparative mapping studies within and across species suggested that there are several conserved genomic regions (for eg., the genomic regions RG939-RG214 on chromosome 4 and R1394A-G2132 on chromosome 8) which contain a gene or cluster of genes that may confer drought adaptation in rice (Zhang *et al.* 2001). However, research is needed to determine whether the QTL identified for various root and shoot-related drought resistance components also influence yield and/or yield stability under water stress in the field environment. Further, QTL linked to rice plant performance under drought stress in the field

condition need to be identified with relevance to improve overall productivity of rice through MAS (Courtois *et al.* 2000). Research in this direction is in progress at this laboratory and initial results indicated positive genetic linkage/pleiotropy between root traits and grain yield under water stress in the field in rice. There was co-location of QTL for root traits and QTL for yield under stress (Babu *et al.* 2002).

In rice, several authors have demonstrated the efficiency of MAS for the successful transfer of major genes for blast resistance (Inukai *et al.* 1996; Hittalmani *et al.* 2000) and bacterial blight resistance (Huang *et al.* 1997). MAS has been applied for the genetic improvement of quantitative traits in several crops such as tomato (Lawson *et al.* 1997; Bernacchi *et al.* 1998), maize (Graham *et al.* 1997) and barley (Han *et al.* 1997; Toojinda *et al.* 1998). Shen *et al.* (2001) reported improvement of rice root system by MAS of several root QTL. They have also studied the possible effects of these introgressed segments on other agronomic traits through pleiotropy or linkage drag. In the same way, work is currently underway to transfer the QTL for root morphological traits from Azucena into a popular Indian drought susceptible variety, Kalinga III by MAS (Price *et al.* 2002). Near isogenic lines are being developed for OA with *japonica* background. Near isogenic lines will serve as valuable material to test the utility of the introgressed QTL. This will also lead to understand the mechanisms underlying physiological and molecular nature of the QTL and to evaluate the contribution of the QTL to yield in the target environment (Price *et al.* 2002b).

Conclusions

Considerable progress has been made in mapping QTL linked to various drought resistance components such as root traits and OA in rice. Consistent QTL for root traits and OA have been identified across testing environments and genetic backgrounds thus leading to MAS of these complex traits. QTL linked to field drought tolerance have also been located. Results revealed genomic regions with pleiotropic effect on root traits and drought avoidance in the field. Drought avoidance via

deep and thick roots and drought tolerance via capacity for OA can be selectively combined into high yielding background using MAS and near isogenic lines will serve as valuable material to test the utility of the introgressed QTL. Work progressing in different laboratories will lead to the development of high yielding cultivars which will help to increase rainfed rice production.

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