



Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Review

Root biology and genetic improvement for drought avoidance in rice

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ARTICLE INFO

Article history:

Received 24 November 2010

Received in revised form 1 March 2011

Accepted 1 March 2011

Keywords:

Drought

Rice

Roots

Breeding

QTL

Marker-assisted selection

ABSTRACT

Rice root growth encompasses a remarkable genetic diversity in terms of growth patterns, architecture, and environmental adaptations. In order to harness this valuable diversity for improving rice response to drought, an understanding of key root traits and effective drought response mechanisms is necessary. A trait-based approach with precise understanding of the target environment, including temporal and spatial heterogeneity, is a possible path toward the use of roots and dehydration avoidance traits for improved drought resistance in rice. The ability to grow deep roots is currently the most accepted target trait for improving drought resistance, but genetic variation has been reported for a number of traits that may affect drought response. Here, we review variation in rice root response to drought from a physiological perspective in terms of morphology and function with respect to the different growth environments (upland and lowland) commonly used by farmers. Recent advances in linking physiology and breeding are also presented.

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1. Introduction

Drought is a major abiotic stress, affecting 20% of the total rice-growing area in Asia (Pandey and Bhandari, 2008). Roots are the principal plant organ for nutrient and water uptake. Therefore, improving our understanding of the interactions between root function and drought in rice could have a significant impact on global food security. This review aims to synthesize previous research on rice root biology for drought and to suggest new directions of research in order to improve rice production in drought-prone regions.

Plants use different mechanisms to cope with drought stress, namely, drought escape, drought tolerance, drought recovery, and drought avoidance (Levitt, 1972; O'Toole and Chang, 1979). Among these four mechanisms, the mode of drought resistance with which roots are most likely associated is drought avoidance. Genotypes that have deep, coarse roots with a high ability of branching and penetration, higher root to shoot ratio, elasticity in leaf rolling, early stomatal closure, and high cuticular resistance are reported as component traits of drought avoidance (Blum et al., 1989; Samson et al., 2002; Wang and Yamauchi, 2006).

Achieving drought resistance in rice will be necessary for meeting the growing water shortage of the world, and it requires a deeper understanding of the mechanisms that could facilitate drought resistance (Serraj et al., 2011). Understanding the physiology of drought response can contribute to plant breeding efforts toward drought resistance (Fukai and Cooper, 1995; Serraj et al., 2009). Root traits have been claimed to be critical for increasing yield under soil-related stresses (Lynch, 2007; Serraj et al., 2004). Previously, O'Toole and Bland (1987) reviewed rice root growth at a time when genetic variation for root traits was just beginning to be explored. Given the recent advances in physiological techniques, genetics, and molecular biology, this review aims to synthesize the current knowledge of rice root systems so that it can be used to elucidate the role of roots for improvements in drought resistance.

2. Root structure and physiology

2.1. Morphological traits

Growth of the rice root, in terms of total dry matter, maximum root depth, and root length density, increases until flowering stage and then decreases sharply to maturity (Yoshida and Hasegawa, 1982). Kawata and Soejima (1974) indicated that roots produced after flowering may play an important role during the grain-filling period. The shape of the root system differs greatly with soil texture (particle size), soil water status, and soil compaction (Hoshikawa, 1989). Rice is characterized by a shallow root system compared with other cereal crops (Angus et al., 1983), having limited water extraction below 60 cm (Fukai and Inthapan, 1988). The form of the rice root system also varies with cultivation methods (Yoshida and Hasegawa, 1982; Tuong et al., 2002). In upland conditions with direct sowing, the root system generally develops deeper than in transplanted plantings in lowland conditions.

The rice root system, a fibrous root system, can be divided into different classes: seminal roots, mesocotyl roots, and nodal roots. Lateral roots emerge from each of these classes. These three classes differ in origin, anatomy, and function. When the seed germinates, the coleorrhiza emerges first and then, within a short time, the first seminal root (radical) breaks through the covering. The emergence of the root is the first sign of seed germination. The seed contains a relatively large reserve of storage carbohydrate and nutrients (Marschner, 1998), which allows the embryonic root to grow rapidly. It grows 3–5 cm long in 2–3 days after germination. Usually, the rate of elongation of the seminal root will slow down

when its length reaches 12 cm (Hoshikawa, 1989). In the case of rice, there is only one seminal or embryonic root and it is usually the longest root before the third-leaf period (Zhang et al., 2001). In general, seminal roots have a poor conducting capacity (Harada and Yamazaki, 1993) and their role in the uptake of water and nutrient is limited to the vegetative stage (around the seven-leaf stage).

Mesocotyl roots are those that grow from the mesocotyl (the axis between the node of the coleoptile and the base of the radical) and they develop only under deep seeding or when the seed is treated with certain chemicals (Yoshida and Hasegawa, 1982). Usually, they are not coarse and seldom have lateral or branch roots. Nodal roots are postembryonic roots, which arise from nodes at the base of the main stem and tillers. Functionally, nodal roots elongate deeply into soil, thus constituting a framework for the whole root system. When root length exceeds a certain size, the branching process starts by initiation, emergence, and growth of lateral roots from the root pericycle and epidermis (Morita and Yamazaki, 1993). Lateral roots, which comprise a greater proportion of the root system in total length and number (Yamauchi et al., 1987a,b; Harada and Yamazaki, 1993), are responsible for the greatest amount of water and nutrient absorption (Yoshida et al., 1982). It is still unknown how root mass or maximum root length relates to variation in lateral branching or root hairs. Three discrete types of lateral roots have been recognized in rice: the L type, which is generally long and coarse (0.2–0.3 mm), and capable of branching into higher order laterals; M types, those that were long and coarse but without a branch; and S types, those that were short, fine (0.035–0.1 mm), and non-branching but usually numerous. The different types of lateral roots vary in anatomy, developmental characteristics, carbon and nitrogen dynamics, developmental responses to various soil environments (Yamauchi et al., 1996), and genetic regulation of their development (Wang et al., 2006a). Rebouillat et al. (2009) have provided a thorough review of rice root development.

Hormone action on the development of root architecture has been summarized by Osmont et al. (2007). Auxin and abscisic acid promote lateral root formation, cytokinin suppresses lateral root formation, ethylene has interactions with auxin and may play a role in lateral root formation through cortical cell breakdown, and gibberellic acid acts with ethylene to promote adventitious root growth in flooded rice. Studies of hormone effects on rice root growth report that ethylene mediates aerenchyma formation and adventitious root growth under flooded conditions in rice (Rzewuski and Sauter, 2008), but is not involved in the formation of barriers to radial oxygen loss (Colmer et al., 2006). Use of an antisense transgenic indicated a positive role of cytokinins for rice root development (Liu et al., 2003). ABA was observed to play a role in lateral root formation, tip swelling, root hair formation, and water permeability in roots of variety Taichung native 1 (Chen et al., 2006). Experiments with a mutant for the *OsIAA3* gene indicate an important role of auxin for gravitropism and the growth of seminal, nodal, and lateral roots (Nakamura et al., 2006). Root growth under drought is likely influenced by the interaction of plant hormones, as reported with ethylene, gibberellin, and abscisic acid for adventitious roots in deepwater rice (Steffens et al., 2006).

Many studies have restricted their analyses to a set of root parameters that includes root development with respect to tiller development, maximum root depth, total root length, root surface area, root volume, root diameter, root length density, root distribution pattern in the soil column, root to shoot ratio, root branching, root hydraulic conductance, root anatomy, root elongation rate, total plant length, and hardpan penetrability, which are of various functional significance (Table 1; Wang et al., 2006a). It has been hypothesized that coarse roots have a direct role in drought

Table 1

Root traits and their functional characteristics that are most commonly characterized in root QTL mapping studies.

Root traits	Functional characteristics
Maximum root depth	Potential for absorption of soil moisture and nutrients in deeper soil layer
Root to shoot ratio	Assimilate allocation
Root volume	The ability to permeate a large volume of soil
Root number	Physical strength, potential for root system architecture
Root diameter	Potential for penetration ability, branching, hydraulic conductivity
Deep root to shoot ratio	Vertical root growth, potential for absorption of soil moisture and nutrient in deeper soil layers
Root length/weight density	Rate of water and nutrient uptake
Root branching	Power of soil exploration (the major contribution to total root length)
Total root length/surface area	Total root system size: the size of contact with soil (major determinant for water and nutrient uptake as an entire root system)
Specific root length	Degree of branching, density of root materials, porosity due to aerenchyma development
Hardpan penetration ability	Ability to penetrate subsurface hardpans

resistance because larger diameter roots are related to penetration ability (Materechera et al., 1992; Nguyen et al., 1997; Clark et al., 2008) and branching (Fitter, 1991; Ingram et al., 1994), and they have greater xylem vessel radii and lower axial resistance to water flux (Yambao et al., 1992). The maximum depth that roots reach is genetically determined and differs substantially between cultivars grown under identical conditions, but at the same time is affected by environmental conditions in the field (Yoshida and Hasegawa, 1982). Maximum root depth of a particular genotype is achieved only when roots do not encounter a physical limit to growth. The quantity of root length (or weight) in layers within the soil profile is usually expressed in terms of root length (or weight) per unit volume of soil, referred to as root length (or weight) density. Since water is mostly absorbed passively, root length density, which reflects the development of lateral roots, can be directly related to water uptake ability of the plant. As root length density increases, water uptake usually increases, but up to a given length only, which is termed critical root length density. In rice, like other crops, the critical root length density depends on soil conditions, especially moisture (Siopongco et al., 2005), and roots are distributed in such a way that their length and mass will decrease exponentially with depth. Root density at depth determines the exploitation of water present at deeper levels.

Root to shoot ratio is a measure of the allocation of resources toward different plant components. The allocation of resources toward the root is high at early vegetative stages but decreases markedly at flowering and is almost negligible after anthesis (Gregory et al., 1996). Asch et al. (2004) reported that the proportion of total dry matter allocated to root or shoot parts depended on the rate of soil dry-down, with root–shoot ratios averaging 0.05–0.1 at flowering in soil-filled PVC pipes. Genetic variation in root–shoot ratio among *Oryza* species was also reported, and was seen among subspecies groups (Kondo et al., 2003). Japonica accessions require more resource allocation toward roots for the formation of deep root length than indica and aus accessions. Root to shoot ratio also varies with cultivation system. In upland conditions, root to shoot ratio increases (Banba and Ookubo, 1981; Kondo et al., 2000a; Price et al., 2002; Singh et al., 2000), compared with root to shoot ratio in lowland conditions (Azhiri-Sigari et al., 2000; Bañoc et al., 2000a). This response may be due to mechanical impedance in lowland conditions, which typically feature a hardpan from soil puddling. Values of deep root to shoot ratio have also been used to characterize the vertical root growth of rice.

2.2. Rice root anatomy and mechanisms for water uptake

Before water reaches transpiring leaves, it must penetrate through a series of concentric cell layers. In rice, these layers include the root epidermis, hypodermis (exodermis), sclerenchyma layer, several layers of cortex cells, endodermis, pericycle, and xylem vessels. Once water has reached the xylem vessels, it moves axi-

ally toward the aerial parts of the plant. Steudle and Peterson (1998) have summarized the “Composite Transport Model” for water uptake and transport in roots, in which apoplastic, symplastic, and transcellular pathways contribute to water uptake and transport. A combination of pathways can be used, for example, when water moves within the symplast for some distance and may then cross the plasma membrane to move within the cell wall (Steudle, 2000). Exchange between pathways possibly helps roots to adjust their water uptake ability according to transpiration demand of leaves.

Rice root anatomy characteristically exhibits cortical aerenchyma, which are associated with gas transport to roots growing in anaerobic conditions. The effects of soil moisture on aerenchyma formation have been documented, and these reports point to aerenchyma formation as prevalent in rice roots from all types of root growth media. Colmer (2003) studied 12 rice varieties, including upland, paddy, and deepwater types, and all produced aerenchyma in both drained and flooded soil conditions, as well as in aerated and stagnant solution culture. Greater aerenchyma formation was observed in the flooded/stagnant treatments, but no difference in aerenchyma formation among cultural types was reported. Aerenchyma formation has been observed under drought conditions in both aerobic and lowland genotypes, although to a lesser extent than under flooded conditions (Suralta and Yamauchi, 2008). Internal gas space may not reflect aerenchyma formation; rice roots have a root porosity of approximately 9% at 20–25 mm behind the root tips even with the absence of aerenchyma (Armstrong, 1971). Parreño-de Guzman and Zamora (2008) observed that a greater number of aerenchyma lacunae were formed under intermittent and upland water regimes than in flooded conditions. The authors reported genotypic differences when the roots were observed at tillering, but not at panicle initiation, which suggests genetic differences in the onset of aerenchyma formation. Although drought has been observed to affect aerenchyma formation, it is unknown whether aerenchyma formation affects water uptake in rice.

In their adaptation to growth in flooded conditions, rice roots display a unique formation of apoplastic barriers compared with other crop plants. The role of suberin and the Casparian band in limiting water uptake has received mixed reports. In drought-stressed lowland rice, the implications of apoplastic root barrier formation are complex since the soil at the start of the season is flooded, then fluctuates or steadily decreases based on rainfall patterns. Hose et al. (2001) concluded that the extent and rate of Casparian band and suberin lamella formation depend on environmental conditions (drought, hypoxia, salt, heavy metal, and nutrient availability). Typically, a greater degree of Casparian band and suberin lamella development resulted in less water permeability of the root. Formation of an exodermis in rice was induced by growth in stagnant solution, and resulted in an effective barrier to radial

oxygen loss in rice (Colmer et al., 1998). Components of root barriers include a lignified sclerenchyma layer, a suberized exodermis (hypodermis), and a rhizodermis (a cell layer outside of the exodermis).

The effects of apoplastic barriers on water uptake and transport in rice are unclear since genotypes of rice can be adapted to flooded or non-flooded conditions. Kondo et al. (2000a) reported that maize reduced soil water potential to lower levels than rice under drought conditions, and that, in addition to having a smaller root length than maize, rice had a lower ability to take up water per unit root length. Water uptake in rice declined markedly under severe drought stress compared with mild stress, whereas water uptake in maize was similar at the two stress levels, possibly due to the deeper root growth that was observed in maize. Consistent with these results, Miyamoto et al. (2001) reported a much lower hydraulic conductivity of rice roots compared with those of other species, but with no visible differences in endodermis, exodermis, or aerenchyma formation between lowland (IR64) and upland (Azucena) varieties grown in solution culture. However, the root hydraulic conductivity of IR64 was significantly lower than that of Azucena in aeroponically grown roots, which is an expected trend given the environment to which these varieties are adapted. This points to the importance of root growth environment for studying hydraulic conductivity.

Root hydraulic conductivity has been further characterized in IR64 (lowland) and Azucena (upland) rice, with emphasis on separating the individual root components affecting water movement. In both studies described below, no differences between varieties were reported. Ranathunge et al. (2003) observed hydraulic conductivity of the outer part of the rice root (cortex and exodermis) to be 30 times that of the endodermis and stele. Subsequently, Ranathunge et al. (2004) used ink to block the apoplast and HgCl_2 to close aquaporins, and concluded that water movement is predominantly through the apoplast since the ink had a bigger effect on root hydraulic conductivity. The authors noted a low resistance of the exodermis, but did not notice any patchiness of Casparian bands, which may have increased their permeability. These studies were later questioned for using aerated solution as a growth medium, which likely did not induce the formation of a tight barrier in the outer part of the root (Garthwaite et al., 2006).

Hydraulic conductance of whole root systems in rice has been recently reported in rice roots from both solution and soil culture (Matsuo et al., 2008). In solution culture, root hydraulic conductance was greater in a lowland japonica variety (Koshihikari; previously classified as drought-susceptible) than in an upland variety (Sensho; mildly drought-resistant). In soil, the root hydraulic conductance of an upland indica variety (Beodien; drought-tolerant) was greater than that of Koshihikari. The authors concluded that root hydraulic conductivity may be more affected by water channels than by root anatomy. Root water uptake ability and hydraulic conductance have been evaluated according to root pressure, determined by root system xylem sap flux through cut stems (or "bleeding rate"). Xylem sap flux of lowland variety Koshihikari decreased with decreasing water availability in a water-saving trial, but did not change in two upland varieties (Beodin and Sensho; Matsuo and Mochizuki, 2009b). Root pressure has also been attributed to recovery from xylem cavitation in response to drought (Stiller et al., 2003). Before breeders can be recommended to breed cultivars with high water uptake ability, it is necessary to confirm the role of high root hydraulic conductivity in maximizing plant growth and yield under drought.

Aquaporin expression has been reported to correlate directly with root hydraulic conductance (e.g., Javot et al., 2003 in *Arabidopsis* and Sakurai et al., 2005 in rice). Thirty-three aquaporin genes have been identified in rice from all four major subfamilies (plasma membrane intrinsic proteins (PIPs), tonoplast intrinsic

proteins (TIPs), Nod26-like intrinsic proteins (NIPs), and small and basic intrinsic proteins (SIPs); Sakurai et al., 2005). In rice, expression of each aquaporin gene in roots varies with root tissue, but is generally more abundant at the root tip than in other parts of the root (Sakurai et al., 2008). This is due to the prevalence of aerenchyma along the length of rice roots, as the reduced expression away from the tip differs from that of other crops (e.g., maize; Hachez et al., 2006).

Most research in rice on aquaporins and drought focuses on PIPs. Studies comparing drought-stressed upland and lowland rice generally report a greater response in aquaporin gene expression from upland rice. To date, all aquaporin studies in rice that included a drought treatment did so using polyethylene glycol (PEG) in solution culture. Lian et al. (2004) observed an up-regulation of the PIP *RCW3* in upland rice under drought, but not in lowland rice. When the *RCW3* was inserted into the same lowland rice background, however, greater osmotic root hydraulic conductance, leaf water potential, and transpiration were observed. Lian et al. (2006) examined the expression of all rice PIPs, and reported differential expression between upland and lowland rice, roots and shoots, well-watered and drought conditions, and notably between drought and ABA treatments. Interestingly, some PIPs were down-regulated under drought. In a whole-genome comparison of gene expression under drought and well-watered conditions, all genes showing increased expression in upland rice also existed in lowland rice (Wang et al., 2007). Since upland rice is typically understood to be more drought-resistant than lowland rice, this led the authors to suggest that over-expression of some of these genes may improve the drought resistance of lowland varieties.

3. Genetic variation of rice root traits in response to drought

3.1. Genetic variation for morphological traits

Significant genetic variation exists among different rice cultivars for root morphological traits (O'Toole and Bland, 1987) such as root diameter (Armenta-Soto et al., 1983), root depth (Nicou et al., 1970; Reyniers and Binh, 1978; Yadav et al., 1997; Mambani and Lal, 1983a; Nemoto et al., 1998; Kato et al., 2006), root pulling force (O'Toole and Bland, 1987; Ekanayake et al., 1985a), deep root to shoot ratio (Yoshida and Hasegawa, 1982), root number (Armenta-Soto et al., 1983), root growth plasticity (O'Toole, 1982; Ingram et al., 1994; Price et al., 2002), and root penetration ability (Babu et al., 2001; Clark et al., 2008, 2000; Ali et al., 2000).

Studies on genetic variation for root traits in rice have been ongoing for decades. In 1970, Nicou et al. reported significant genetic variation for root traits among both upland and lowland cultivars of Asia, Africa, and South America. Asian lowland varieties had finer and more highly branched roots, whereas African and South American cultivars had larger diameter and less branched roots. Chang et al. (1972) compared root traits of several upland and lowland varieties and found that drought resistance was associated with coarse, long roots, a dense root system, and a high root to shoot ratio. Yoshida and Hasegawa (1982) also reported genetic variation in root depth, with a tendency for upland rice cultivars to have deeper roots than lowland rice cultivars. Ingram et al. (1994) used cultivars belonging to different types of rice for root studies and found tropical japonica types to have larger root systems than indica types. In another study, Lafitte et al. (2001) investigated the genotypic variation for root traits in different types of rice and reported that indica rice types had fine, highly branched superficial roots with narrow xylem vessels and low root to shoot ratio, whereas japonica types had coarse roots with wider vessels, less branched long roots, and a large root to shoot ratio. Aus

types were reported to have intermediate root diameter, with a root distribution profile similar to that of japonica types but with finer roots. Other comparisons among rice varieties (Thanh et al., 1999; Azhiri-Sigari et al., 2000; Kondo et al., 2003; Matsuo and Mochizuki, 2009a; Uga et al., 2009; Henry et al., 2011) further reflect the genetic diversity for root traits in rice. Yu et al. (1995) reported genotypic variation for root penetration ability of rice cultivars by using the wax layer method, in which different paraffin waxes were mixed to achieve a known mechanical impedance and included in the root-growth medium. Using the same method, Babu et al. (2001) found that japonica accessions have a higher root penetration index (number of roots penetrating the wax layer/total number of nodal and seminal roots) than indica types in lines used to develop doubled haploid mapping populations (CT9993/IR62266 and IR58821/IR52561) for mapping and tagging root traits.

Many wild species in the genus *Oryza* may offer genetic resources for drought resistance research since they have more novel alleles than cultivated rice (Zhang et al., 2006). In an experiment under greenhouse conditions, wild species of *Oryza* (mostly belonging to the primary gene pool) were compared for root and other drought-adaptive traits (Liu et al., 2004). That study revealed that some wild species have superior root growth under drought stress. *Oryza longistaminata* accessions and some japonica cultivars showed either an increase in total root mass or an increase in the proportion of root mass in the deeper soil layers under drought, whereas indica cultivars and *Oryza rufipogon* accessions did not show any difference.

Evaluation of mutants for root traits can provide important insights into root growth and development. In rice, some mutants without seminal roots or without lateral roots have been identified. So far, ten genes have been identified in rice relating to root growth, out of which mutants of six genes, *rm1* and *rm2* (Ichii and Ishikawa, 1997), *rrl1* and *rrl2* (Inukai et al., 2001a), *srt5* (Yao et al., 2002), and *srt6* (Yao et al., 2003), are involved in a reduction in seminal root elongation. Mutants of two genes, *cr11* and *cr12* (Inukai et al., 2001b), are involved in a reduction in number of nodal roots, one (*rm109*; Hao and Ichii, 1999) is involved in blocking lateral root initiation, and one (*rh2*; Ichii et al., 2000) is involved in reducing root hairs. Other mutants include *cr14* (Kitomi et al., 2008), *lrt1* (lateral rootless phenotype; Chhun et al., 2003a), *arm1* and *arm2* (lateral root number decreases; Chhun et al., 2003b), and *lrt2* (lateral rootless phenotype; Wang et al., 2006b). Most of these genes have not been identified except for *cr11* (Inukai et al., 2008).

Root hairs are extensions of epidermis cells of roots that are considered to be an important structure for nutrient uptake as they cover almost 77% of the surface area of the root in any crop (Jills et al., 2000). Experiments with the root hairless mutant *rh2* indicated that root hairs do not have a primary role in water uptake at the seedling stage under drought and even their contribution to nutrient uptake differs by element and culture method (Suzuki et al., 2003). More research at different stages and different drought levels is necessary to assess the potential role for root hairs in water uptake under drought. In addition, lateral roots generally have a large effect on overall plant architecture (Yamauchi et al., 1987a,b) and play key roles in water uptake (Varney et al., 1993), particularly under drought conditions (Bañoc et al., 2000b; Wang et al., 2009). Continued research with root trait mutants could open the way to more thorough genetic and molecular analysis and could support molecular breeders in breeding crops with improved root architecture once the phenotypes of these traits are better understood.

3.2. Genetic variation for root anatomy

In addition to root morphological features, considerable variation is also documented for root anatomical traits among rice varieties (Terashima et al., 1987; Kondo et al., 2000b) and in some

instances this variation has been linked with ability to extract soil water. Additive gene effects were important in the expression of root xylem vessel area so that such traits could be studied efficiently in an early-segregating generation (Bashar, 1987). Root resistance to water flow can be considered in terms of two components: radial resistance and axial resistance (Landsberg and Fowkes, 1978). It is currently thought that radial water flow is more limiting than axial water flow (Steudle and Peterson, 1998), but several studies have promoted the idea of selecting larger xylem vessels for breeding drought resistance. Harajima (1936) reported that there were fewer primary xylem elements in seminal roots of upland japonica varieties than in those of lowland japonica varieties. In experiments with both solution culture and lowland field conditions, Kondo et al. (2000b) studied root anatomical traits, including stele diameter, metaxylem number, and metaxylem diameter in both upland and lowland rice cultivars, and found that traditional upland japonica cultivars had the largest stele and metaxylem diameter.

In another study by Yambao et al. (1992), root diameter was demonstrated to be an effective selection index for xylem size in roots with diameters up to about 1.2 mm. The authors hypothesized that coarse roots would confer drought resistance because they have greater xylem vessel radii and lower axial resistance to water flux, but it was concluded that this would not effectively contribute to improving drought resistance.

3.3. Heritability

Information on heritability and gene action of a plant trait is a prerequisite for a successful breeding program. Such studies rely heavily upon a relatively large number of plants to arrive at statistically significant results, thus making root traits difficult to incorporate. As such, information on heritability and gene action of rice root traits is still very limited. Earlier studies (Chang et al., 1982; Armenta-Soto et al., 1983; Chang et al., 1986) using aeroponic systems found that dominant genes control root number, root depth, and root mass, whereas root diameter is controlled by both dominant and recessive genes. Armenta-Soto et al. (1983) reported higher narrow-sense heritability estimates for root diameter (62%), root length (60%), and root number (44%).

Ekanayake et al. (1985a), using F₁, F₂, and F₃ populations from a cross between IR20 (shallow, fine root system) and MGL-2 (deep, coarse root system), reported that root diameter, root dry weight, and root length are polygenic traits with substantial proportions of additive variation and with narrow-sense heritabilities greater than 50%. They suggested that selection for these root traits based on individual plant performance could be successful in early-segregating generations. In another study, Ekanayake et al. (1985b) observed low inheritance in lowland rice for root pulling force, which is the vertical force required to remove one plant from the soil. Low heritability for some root traits is a common breeding concern, but the issue can be resolved by developing suitable selection methods that take full advantage of genetic variability and also make possible rapid selection, by increasing both heritability and selection response (Richards and Passioura, 1981).

4. Roots for improvement of drought resistance in rice

The relationships between root growth and grain yield under drought are complex. Positive associations between root length and grain yield have been documented in rice (Mambani and Lal, 1983a; Lilley and Fukai, 1994). In contrast, Ingram et al. (1994) found no significant association between the two traits. It may be that a simple correlation between root growth and yield could be expected only in well-defined target environments (Mambani and Lal, 1983a; Ekanayake et al., 1985a). Venuprasad et al. (2002), in

a study involving simultaneous evaluation of root character and grain yield, concluded that genotypes with a deep rooting habit had an advantage in stress conditions and that those genotypes that had produced deep roots prior to the onset of stress showed improved productivity compared with a genotype that did not have the capacity to produce roots prior to the onset of stress. The study also suggested, based on QTL mapping, that the loci for productivity traits were not congruent with those related to root morphology, except at one locus. Subsequently, [Toorchi et al. \(2006\)](#) and [Kanbar et al. \(2009\)](#), based on canonical correlation studies conducted under contrasting moisture regimes, suggested that maximum root depth, root–shoot ratio, and root dry weight conferred an advantage to grain yield under stress.

Rice cultivation has two major land management systems, commonly referred to as upland and lowland. These two systems differ greatly in their yield potentials because of soil characteristics that affect root growth and plant response to drought, and are therefore considered in separate sections in this review.

4.1. Upland rice

Rice cultivars adapted exclusively to upland conditions are typically characterized by a deep and coarse root system, tall stature, thicker stems, and fewer tillers ([Ge, 1992](#); [Ling et al., 2002](#)), whereas lowland rice cultivars have shallow and finer roots, a large number of roots, and many tillers ([Lang et al., 2003](#)). In upland fields during stress, the major sources of water for growth and development are rain that is retained by the soil and groundwater. A coarse and deep root system, for soil penetration and access to water reserves deep in the soil, is considered valuable for improved drought resistance under upland conditions ([O'Toole and Chang, 1979](#); [Ling et al., 2002](#)). Rice root systems and their relationship to drought resistance were previously reviewed by [Yoshida and Hasegawa \(1982\)](#). The authors noticed large variation among upland rice cultivars for root length density below 30 cm and suggested that the effect of drought stress depends on the ability of plants to develop a deep root system. [Chang et al. \(1986\)](#) also found that rice with a deep root system avoided drought better than a shallow root system.

Advantages conferred by a deep root system depend on three major factors: duration of the drought period, availability of water at depth, and rate of water uptake. If water is not limited in upper layers of the soil, the plant may not benefit from the formation of deep roots. In upland conditions, [Puckridge and O'Toole \(1981\)](#) found that deep-rooted cultivar Kinandang Patong extracted more water at a depth of 40–70 cm than shallow-rooted cultivars (IR20 and IR36). Similar results were also obtained by [Mambani and Lal \(1983b\)](#), [Lilley and Fukai \(1994\)](#), and [Kato et al. \(2007\)](#). Such comparisons of water uptake are difficult to estimate in lowland conditions due to the complex interactions of deep drainage and lateral water movement in the subsoil.

A range of trends have been reported regarding root growth response to drought stress in upland rice, including both root growth inhibition and root growth promotion in drought stress treatments. [Kato et al. \(2006\)](#) have reviewed the effects of various water regimes on deep root growth and biomass partitioning to roots in upland rice. The authors concluded that while many studies report an increase in root: shoot ratio and deep root growth in response to drought, conditions as timing of the drought at seedling stage, very severe drought stress, and presence of hardpans have reduced resource partitioning to roots. Conclusions about drought effects on root growth may also differ because root mass and root length can show opposite trends, especially when root diameter decreases because of drought, resulting in greater length but less mass.

4.2. Rainfed lowland rice

Drought resistance mechanisms that are appropriate for upland systems may not be suitable for rainfed lowland conditions and vice versa ([Mackill et al., 1996](#)), mainly because of the unique hydrology of rainfed lowlands in which soil transitions from flooded and anaerobic to drought and aerobic ([Wade et al., 1999](#)). In addition to the differences in water status between upland and lowland conditions, the effect of cultivation on soil properties is a major factor determining differences in root growth and drought adaptability between upland and lowland rice.

Puddling, the mechanical breakdown of surface soil aggregates, is the most common land preparation method for lowland rice in South and Southeast Asia. Hardpans that develop from puddling improve soil water retention capacity ([Sharma and De Datta, 1985](#)) but hinder root penetration to reach moisture in deeper zones of soil after drying occurs ([Ghildyal, 1978](#); [Hasegawa et al., 1985](#); [Yu et al., 1995](#); [Clark et al., 2000, 2002](#); [Babu et al., 2001](#); [Samson et al., 2002](#)). In a survey conducted in 35 rice-growing locations of South and Southeast Asia by [Sharma et al. \(1994\)](#), resistance to penetration in the surface 10 cm averaged 0.64 MPa under flooded conditions and 1.7 MPa in puddled fields without standing water. Elsewhere, root penetration declined (>50%) at soil strengths of 0.5–2 MPa ([O'Toole, 1982](#)) and declined even more at 3 MPa and above ([Bengough and Mullins, 1990](#)). Across species, morphological and physiological changes in plant growth due to effects of hardpans on roots include a reduction in transpiration rate and leaf area expansion, and ultimately a decrease in dry matter accumulation ([Masle and Passioura, 1987](#); [Ludlow et al., 1989](#); [Assaeed et al., 1990](#); [Masle, 1992](#)). These effects may be due to direct consequences of reduced root access to water and nutrients. The presence of a hardpan in shallow soil layers may further promote uneven moisture distribution in the soil profile, so that a root system tends to be partially exposed to dry soil, causing stomates to close while the rest of the root system can access water ([Siopongco et al., 2008, 2009](#)). In addition to the presence of a hardpan and greater stratification of soil characteristics due to puddling, rainfed lowland soils differ from upland soils in that severe soil cracking occurs upon soil drying. Soil cracking, which can penetrate hardpans, strongly influences rainfall infiltration and water evaporation processes ([Tuong et al., 1996](#)). [Sanchez \(1973\)](#) reported that soil cracking impeded root development based on visual observations; otherwise very little is known of the effects of soil cracking on growth of rice root systems.

Results of several lowland experiments ([Hasegawa et al., 1985](#); [Sharma et al., 1987](#); [Mambani et al., 1989](#); [Nabheerong, 1993](#); [Pantuwan et al., 1996](#); [Samson et al., 1995](#)) indicate that 69–94% of roots are located in the top 10 cm of the soil and very few roots are found below 30 cm. Vertical deep root penetration would help rice to avoid drought stress; however, root penetration is often restricted by the presence of a hardpan. Genotypic variation in the ability of rice to penetrate compacted soil layers and simulated compact layers has been shown to exist ([O'Toole, 1982](#); [Yu et al., 1995](#); [Ray et al., 1996](#); [Ali et al., 2000](#); [Price et al., 2000](#); [Zheng et al., 2000](#); [Babu et al., 2001](#); [Clark et al., 2002](#); [Samson et al., 2002](#)). Rice shows less soil penetration ability than other species. [Iijima et al. \(1991\)](#) indicated that maize roots were better able to penetrate hard soil than rice roots. In general, roots of dicotyledonous plants have a higher penetration rate than monocot roots ([Materechera et al., 1992](#)), and upland rice cultivars have greater penetration ability than lowland cultivars ([Yu et al., 1995](#)). Changes in soil conditions can greatly alter root distribution patterns. However, the mechanism by which roots penetrate compacted soil layers is not well understood. It remains to be demonstrated whether the penetrated root mass has any role in the uptake of moisture and increasing grain yield in lowland conditions.

Some studies claim that root plasticity might be an important physiological trait in genotypic adaptation for drought stress under lowland conditions (Ingram et al., 1994; Yamauchi et al., 1996). Root plasticity can be defined as the ability of a genotype to adjust its root growth phenotype according to environmental constraints (O'Toole and Bland, 1987). The timing of root growth in response to the resupply of water following a period of drought stress is a vital feature of root growth plasticity (e.g., Bañoc et al., 2000a). Genetic variation has been observed in rice for plasticity in several root traits, including the ability of lateral roots to develop in response to rewatering after soil drying (Bañoc et al., 2000b), and also in response to soil drying after flooding (Suralta et al., 2010). Genetic differences have also been observed in the ability of seminal roots to continue elongation and form aerenchyma under flooded conditions after drought (Suralta and Yamauchi, 2008; Suralta et al., 2008a,b, 2010). Another definition of root plasticity is the ability to adjust root architecture, such as the ratio of fine to coarse roots or the angle of root growth. Under progressive drought (not intermittent drought; Kato et al., 2006), this type of plasticity may be valuable for improved rice growth under drought by allocating resources to increased root growth only when needed. These abilities are quite important for rainfed lowland rice due to the unique soil environment as mentioned earlier, and thus the desirable roots traits are not as simple as those for upland rice such as deep or coarse roots. Different genotypes have exhibited different responses in plasticity depending on type of drought stress (Kano et al., 2011); this points to the importance of understanding the target environment for exploiting various drought resistance donor germplasm.

4.3. Phenotyping and QTLs

Many studies across crops have indicated considerable genotype \times environment ($G \times E$) interactions for root traits, which is expected given the number of environmental factors (i.e., soil physical, chemical, and biological) that affect root growth. In rice, Kondo et al. (2003) investigated $G \times E$ interactions by using both upland and lowland varieties at three upland sites in the Philippines, where both site and nitrogen treatments contributed to environmental variation. In that study, genotype accounted for the largest proportion of variation for specific root weight, nodal root number,

and root to shoot ratio, whereas the environmental effect of nitrogen treatment was relatively high for total dry weight and deep root length ratio (length of roots at depth/total root length measured). These results emphasize the importance of characterizing experimental conditions for root studies.

Root traits are generally controlled by many genes through quantitative trait loci (QTL). Since the first study by Champoux et al. (1995) to locate genes controlling rice root traits with molecular markers, many QTLs related to root traits have been identified in rice using 12 different mapping populations (Table 2), with QTLs, identified and analyzed in rice for more than 30 root morphological parameters. The most studied root traits in all QTL mapping studies are maximum root depth, root diameter, and root to shoot ratio.

The most notable contrast among rice root QTL studies is the vast array of growth media and observation methods used. Since the $G \times E$ effect on root growth is particularly important for rice under drought conditions, with lowland soils being a complex layering of de-aggregated soil over a hardpan and ranging from flooded paddies to dry cracked soils over the same season, understanding how growth and observation methods affect root QTL studies is key for using our knowledge of QTLs to improve drought resistance in rice. Most of the above QTL studies have measured root traits in containers under controlled conditions, although it has yet to be proven whether these results reflect true genetic differences (Steele et al., 2007). Although there are many comprehensive reviews of methods for root study that describe methods commonly used (e.g., soil cores, monolith, minirhizotrons, pots, and solution culture; Gregory, 2006; Smit et al., 2000; Böhm, 1979), some methods have been particularly used for rice and are outlined here.

Other than the minirhizotron method, in which transparent tubes are inserted into the soil at an angle and a portable micro-camera is inserted to visualize the roots, roots are typically assessed in the field using destructive methods, including soil cores and monoliths. In lowland rice fields where flooding can impede the collection of known soil volumes, root pulling force, the force that is required to uproot rice plants, has been used as a means of evaluating the relative size and depth of root systems (O'Toole and Soemartono, 1981). In this method, plants are lifted from the soil using a device that clamps to the base of the plant and is attached to a force meter. Root pulling force is dependent on root length density of the portion of the root system that remains in

Table 2
QTLs related to root characteristics in rice.

Genetic background	Parent type	Number of QTLs (range of phenotypic variation (R^2))	Screening methods and treatments	Reference
CO39 \times Moroberekan (RILs)	I \times TJ	56 (6.0–33.0%) 29 (6.0–19.0%)	PVC cylinders; well watered and drought stress Wax-petrolatum layer system; well watered	Champoux et al. (1995) Ray et al. (1996)
IR64 \times Azucena (DH)	I \times TJ	39 (4.0–22.3%) 12 (4.0–35.0%) 3 (12.9–30.7%)	PVC cylinders; aerobic Wax-petrolatum layer system; well watered PVC cylinders; well watered and drought stress	Yadav et al. (1997) Zheng et al. (2000) Venuprasad et al. (2002)
CT9993 \times IR62266 (DH)	TJ \times I	29 (11.9–26.7%) 36 (8.0–37.0%) 38 (3.6–51.8%)	PVC cylinders; drought stress Wax-petrolatum layer system and field; aerobic PVC cylinders; drought stress	Hemamalini et al. (2000) Zhang et al. (2001) Kamoshita et al. (2002b)
Bala \times Azucena (F_2)	I \times J	21 (5.0–38.0%)	Solution culture	Price and Tomos (1997)
Bala \times Azucena (RILs)	I \times TJ	17 (5.0–18.0%) 25 (5.4–28.0%) 28 (5.4–13.5%)	Wax layer system; well watered Glass-sided chambers; drought stress Soil box method; well-watered and drought stress	Price et al. (2000) Price et al. (2002) MacMillan et al. (2006)
IR1552 \times Azucena (RILs)	I \times TJ	23 (11.4–20.0%)	Pot culture, well-watered and drought stress	Zheng et al. (2003)
IR58821 \times IR52561 (RILs)	I \times I	28 (6.0–27.0%) 20 (5.7–29.9%)	Wax petroleum layer system; well watered PVC cylinders; drought stress	Ali et al. (2000) Kamoshita et al. (2002a)
IAC165 \times Co39 (RILs)	TJ \times I	29 (6.3–24.4%)	PVC cylinders; aerobic	Courtois et al. (2003)
Akihikari \times IRAT109 (BIL)	TJ \times TJ	5 (8–24%)	Solution culture	Horii et al. (2006)
IRAT 109 \times Yuefu (DH)	TJ \times TJ	51 (1.1–25.6%)	PVC cylinders, lowland field; well watered and drought	Li et al. (2005)
Zhenshan 97 \times IRAT 109 (RILs)	I \times TJ	53 (2.6–29.8%)	Lowland field and PVC cylinders; well-watered and drought stress	Yue et al. (2008)
Otomemochi \times Yumenohatamochi	J \times J	20 (7.0–31.2%)	Lowland field; well-watered and drought stress	Ikeda et al. (2007)
IR64 \times Kinandang Patong (RILs)	I \times TJ	10 (8.7–23.9%)	Upland field; well watered	Uga et al. (2008)

the soil (Ekanayake et al., 1986). It was reported that a high pulling force is associated with the plant's ability to develop deeper and larger diameter roots with great penetration ability. However, heritability of root pulling force was relatively low (Ekanayake et al., 1985b) since many other soil factors in addition to root depth affect root pulling force. In controlled environments, containers including large PVC cylinders, rhizotrons, and pots have been used for QTL studies. The PVC cylinder system (typically > 15 cm diameter and 1 m height) is considered an improvement over pot culture since root depth is less restricted, and soil moisture with depth and soil drying are more representative of field conditions (Upchurch and Taylor, 1990). Some container studies include a wax layer for the assessment of root penetration ability. The wax layer system was first applied for screening root penetration ability by Taylor and Gardner (1960). Wax layers consisted of 60% wax and 40% petrolatum white with a resistance of 1.4 MPa at 27 °C. Later, this system was used to simulate the hardpan present in lowland fields (Yu et al., 1995; Ray et al., 1996; Ali et al., 2000; Babu et al., 2001; Clark et al., 2002, 2008). However, Clark et al. (2002) found that cultivars with good penetration under the wax layer screen did not consistently show superior performance in the field. Growth of root systems in baskets has been used to predict rooting depth indirectly according to growth angle (Oyanagi et al., 1993). Using the basket method, Kato et al. (2006) demonstrated the relationship between high root growth angle and root depth in rice, and Uga et al. (2009) observed variation in root growth angle in rice accessions under upland field conditions. Container studies have included the injection of herbicide at depth to screen for deep root growth (Robertson et al., 1985). Aeroponic and solution culture with PEG studies have also been conducted to assess root growth over time. Although this wide range of phenotyping environments/systems used for QTL studies may contribute to inconsistency in the loci identified, relatively large differences in root production among genotypes can be consistently observed regardless of root-zone container size (Shashidhar, personal communication).

The type of progeny used for rice root QTL studies has included F₂ (Price and Tomos, 1997; Price et al., 1997), backcross inbred lines (Kato et al., 2008), doubled haploid lines (Yadav et al., 1997; Zheng et al., 2000; Hemamalini et al., 2000; Venuprasad et al., 2002; Toorchi et al., 2002; Babu et al., 2003; Kamoshita et al., 2002a; Zhang et al., 2001), and mostly recombinant inbred lines (Champoux et al., 1995; Ray et al., 1996; Price et al., 2000, 2002; Ali et al., 2000; Kamoshita et al., 2002b; Courtois et al., 2003; Zheng et al., 2003). The number of progeny has ranged from 56 (Hemamalini et al., 2000) to 220 (Kamoshita et al., 2002a). The number of QTLs identified for root traits has ranged from 1 to 19 and the amount of phenotypic variability explained among the progeny examined by any one QTL ranged from about 4% to as much as 66.6% (Uga et al., 2011). It is also important to note that the number of QTLs identified depends on the threshold value specified. In most of the studies, all QTLs showing a positive effect on root traits were derived from a drought-resistant parent.

Most of the QTL mapping studies for rice root traits conferring drought tolerance have been conducted using progenies derived by crossing varieties belonging to a different subspecies group (japonica × indica; as reviewed in Kamoshita et al., 2008) rather than by using progenies derived by crossing varieties belonging to the same subspecies group, that is, indica × indica or japonica × japonica. Often, these parental lines exhibit slight morphological differences, but their progeny exhibit considerable genetic variability for many root traits (transgressive segregation). Obtaining valuable QTLs or genes for breeding basically depends on trait diversity between the donor and the recurrent parents. All the segregating populations of the above QTL studies have one modern (improved) and one traditional variety. Under such circumstances, mostly positive alleles are derived from the modern cultivar and they are already present

in improved varieties (Cattivelli et al., 2008). This explains the need for inter-specific crosses to explore novel alleles, and reflects the background dependency of QTLs.

4.4. Genetic improvement for drought avoidance

Traditional accessions can be resistant to drought because of a long history of natural selection in the target environments. Transfer of primary or secondary traits, such as those associated with root growth, to desirable backgrounds to enhance grain yield is complicated by a lack of clear understanding of the genetics of component traits and their interactions, and a lack of tightly linked markers. Recently, Uga et al. (2011) and Obara et al. (2010) reported a major QTL for rooting depth (*Dro1*) and root length (*qRL6.1*) using basket and solution culture (hydroponic) methods, respectively. Despite the large number of minor and major QTLs identified, only two attempts have been made in rice to introgress a root QTL into another background. Based on the QTL investigation of Yadav et al. (1997), Shen et al. (2001) conducted a study for introgressing a root depth QTL from a deep-rooted variety, Azucena, into IR64 in three cycles of marker-assisted backcrosses. However, few lines with a significantly improved phenotype (deeper roots) resulted from that effort. In another study, Steele et al. (2006) introgressed four QTLs related to root length and diameter and one QTL related to aroma into an Indian upland variety, Kalinga III, in a 6-year marker-aided backcross program. One target segment (RM242–RM201) on chromosome 9 significantly increased root length under both irrigated and drought stress treatments, confirming that this root length QTL from Azucena functions in a novel genetic background.

Tightly linked markers for each root QTL are necessary for improving root traits through marker-assisted selection. Sharma et al. (2002) identified tightly linked markers for root traits adopting bulked segregant analysis and found two markers (OPBH14 and RM201) to be cosegregating with maximum root depth in the IR64/Azucena mapping population and these were validated across different germplasm (Chaitra et al., 2006). Vinod et al. (2006) identified candidate genes for root traits related to morphology and physiology. These were validated in the CT9993/IR62266 mapping population, which was evaluated for root traits under contrasting moisture regimes. Prabuddha et al. (2008) identified near-isogenic lines for several root traits, and candidate genes that were found to be associated with a particular root trait were also validated with the near-isogenic lines.

Problems associated with these studies were: (1) QTLs introgressed were not fine-mapped with appropriate selectable markers, so the desired gene might have been lost in the selection process; and (2) the QTLs identified had a small effect on the phenotype itself. Thus, the challenge for molecular breeders is to discover heritably stable major QTLs that function independently of genetic background, and to develop an effective breeding method for the application of such QTLs. Once a major QTL is identified and validated, positional cloning is the approach most commonly used to close the genotype-phenotype gap (Salvi and Tuberosa, 2005). In spite of such great effort, no QTL cloning has been achieved so far in rice for root traits. In QTL mapping, the main factor limiting the precision of QTL localization is the number of progenies used in the study, more so than other factors such as using more molecular markers or using better statistical techniques (Kearsey and Farquhar, 1998). Association mapping is a promising method for complex trait dissection and it focuses on association within populations of unrelated individuals. Using association mapping, it is possible to locate QTLs with better precision than using a mapping population (Courtois et al., 2009). Linking our knowledge of QTL mapping with precision phenotyping that is representative of the target drought environment is critical for future progress in drought resistance for rice.

Another necessary approach for progress in drought resistance through rice root traits is an integration of the knowledge generated thus far. Kamoshita et al. (2008) have summarized the large number of studies in rice for drought resistance in QTL mapping studies of at least 15 different populations. Rice root QTLs for drought have been compiled using QTL meta-analysis in multiple populations (Norton et al., 2008; Courtois et al., 2009). Multiple QTL studies from a single population (Bala × Azucena: Khowaja et al., 2009) have also been conducted that identified several dense clusters of root QTLs. This integrative approach across a large number of studies conducted in multiple environments/phenotyping systems is more likely to identify important areas of the genome for rice root response to drought than any single QTL study alone.

As a breeding strategy, incorporating drought resistance for a particular stage of development (i.e., vegetative or flowering stage) would be counter-productive should stress occur at a non-targeted stage. When the stage of occurrence, duration, and intensity of stress is unpredictable, breeding for drought resistance irrespective of growth stage is likely to be most effective. Root traits that result in improved plant water status through a stress-prone growing season could confer non-stage-specific drought resistance. For example, conventional breeding for root-related drought resistance in rice was conducted using farmer-participatory plant breeding approaches (Shashidhar, 2008). By crossing a traditional drought-tolerant accession (Budda) with IR64 and forwarding the filial generations simultaneously under severe stress and well-watered conditions, several advanced lines were obtained. Water received by each segregating line was budgeted. Screening for root morphology using large container studies was adopted in advanced generations. The advanced lines (ARB series) were nominated for trials along with the accession from other breeders in India and material from IRRI. Trials were conducted across India under three hydrologies at each site and repeated over three years, and selected lines performed well across three years in severe stress (Verulkar et al., 2010). The lines have been released for cultivation in the drought-prone districts of Karnataka in India.

4.5. Genomics and proteomics

Some genes and signaling pathways involved in the anatomical and morphological development of rice roots have been identified (see reviews by Coudert et al., 2010; Rebouillat et al., 2009), particularly for crown root initiation. Although advancements in understanding the genetic basis of rice root attributes have been made, it is still unclear exactly how these attributes affect water uptake under drought. Gene expression analysis helps in identifying the functionally important genes and pathways involved in root architecture under water-deficit conditions (Breyne et al., 2003). Yang et al. (2004) conducted a tissue-specific gene expression study in drought-stressed rice roots, in which 66 transcripts were identified and cloned in roots of Azucena. Four transcripts were mapped within an interval containing QTLs for root growth under water deficit in the Azucena/IR1552 population. In another study, Wang et al. (2007) observed that the majority of genes expressed in upland rice and lowland rice are almost identical and that 13% of all the expressed sequence tags (ESTs) detected in leaves and 7% of those in roots were expressed differentially in transcripts between the two cultivar types. Combining our knowledge of genes involved in root development with those that are differentially expressed under drought could help identify important target traits or mechanisms for drought resistance.

Recent studies have indicated that, apart from conventional and marker-assisted selection, potential exists for the transgenic approach to enhance drought resistance in plants by incorporating genes that are involved in stress tolerance (Agarwal et al., 2006; Hervé and Serraj, 2009). Numerous transcription factors

have been reported across crops that are responsible for the regulation of signal transduction and the expression of stress-related genes that impart stress resistance to plants. Transgenic rice with the transcription factor *AtDREB1A* or its orthologue *OsDREB1A* (Dehydration-Responsive Element Binding gene) tested in pots demonstrated improved resistance to simulated drought, high salt, and low-temperature stresses (Yamaguchi-Shinozaki and Shinozaki, 2004). Transgenic lines carrying the *OsNAC045* transcription factor, whose functions include a role in the development of lateral roots, were reported to have a greater survival rate in rice after drought and salt treatments (Zheng et al., 2009) and *OsNAC10* lines with a root-specific promoter showed greater yield than the wild type under drought in the field (Jeong et al., 2010). Improved performance under drought was observed in transgenic plants of the gene *OsMT1a* (metallothionein) that is predominantly expressed in roots and is induced by dehydration (Yang et al., 2009). Root growth was enhanced in transgenics of BRX (BREVIS RADIX-like homologous genes; Liu et al., 2010a) and OsVP1 (H⁺ pyrophosphatase in tonoplasts) and OsNHX1 (Na⁺/H⁺ exchangers; Liu et al., 2010b) that were reported to confer drought tolerance. Except for the *OsNAC10* study by Jeong et al. (2010), root-related drought resistance in terms of grain yield in rice transgenics in field studies have not been reported.

Proteomics is also advancing as a tool for identifying drought-tolerance characters, yet its potential is not exploited fully in plant research, especially compared with other organisms such as yeast and humans (Jorin et al., 2007). A number of proteomic studies on drought have been conducted on rice leaves (Salekdeh et al., 2002a,b; Ali and Komatsu, 2006; Ke et al., 2009), but less work has been conducted on roots. A proteomic evaluation of rice under salt stress by Salekdeh et al. (2002b) revealed a large number of differences in root proteins between salt-tolerant and sensitive varieties, including proteins with antioxidant properties and proteins involved in lignification. Rabello et al. (2008) compared gene expression and proteome profiles in roots of drought-tolerant and drought-sensitive upland rice varieties, and reported the tolerant variety to have increased expression of genes or proteins involved in turgor, cell integrity, and oxidative stress. Coupled with physiologically relevant drought stress treatments, the functional insights from proteomics are promising for improving our understanding of rice root physiology under drought.

5. Conclusions

5.1. Root function for water uptake under drought

Oryza sativa L. includes large genetic diversity for root architecture, but the environmental response of root growth among genotypes is just as diverse. This highlights the importance of characterizing the growing environment in all rice root studies. To improve our understanding of the role of roots in rice response to drought, it is necessary to rethink carefully some of the common paradigms about rice root biology. Early reports on drought and rice roots generalized the idea that rice has shallow root growth (maximum root depth of 30 cm), and that improvement for drought should emphasize deep, coarse root growth. We now know that many rice genotypes have the potential for deep root growth (compared with other rice genotypes; not compared with other deep-rooted species), but this is strongly controlled by the environment (i.e., presence of hardpans, severity of the drought stress). Coarse nodal roots may be critical for penetrating hardpans, but not all drought environments contain distinct hardpans. Furthermore, fine roots present a large percentage of total root length in almost all conditions and thus are strongly expected to contribute greatly to water uptake by the entire root system,

but their relative contribution to water uptake compared with coarse roots is not yet precisely determined. Finally, the discrepancies between spatial distribution and function of rice roots under drought are poorly understood, and need to be addressed with more focus on the biology of root function under water-limited conditions.

5.2. Effectiveness of the QTL mapping strategy for root traits

Field-managed drought stress conditions are necessary for reliable phenotyping of root traits for drought resistance, as are physiologically relevant stress conditions (i.e., time to dry-down). A great number of root QTLs for drought have been identified, and, although there are a limited number of successful introgressions of these QTLs used to improve drought resistance, the large number of QTLs and populations make it difficult for breeders to validate these loci and use them in marker-assisted breeding. Two strategies stand out as most promising for the future: fine mapping of large-effect QTLs to narrow down the genomic region responsible for a specific root trait; and QTL meta-analysis, to identify the most consistent and relevant loci over many studies and populations. Regardless of the strategy, environmental effects and position effects within the genome are likely obstacles to a straightforward introgression or marker-assisted breeding for improving drought avoidance.

5.3. The way forward

Given the urgent need for improved drought resistance in rice, strategic use of our knowledge about rice root architecture and biology is necessary. A trait-based approach with precise understanding of the target environment, including temporal and spatial heterogeneity, is a possible path toward the use of roots and dehydration avoidance traits for improved drought-resistant rice. Potential to grow deep roots is currently the most accepted target trait, and other traits will likely be elucidated as our understanding of plant-soil interactions improves. Meanwhile, the large-effect markers linked to drought resistance/root QTLs could be used carefully to dissect the genetic basis of resistance, while improving the understanding of the physiological processes that control root function and its impact on crop performance in the field.

Acknowledgments

This work was funded by the Generation Challenge Program project “Targeting Drought-Avoidance Root Traits to Enhance Rice Productivity under Water-Limited Environments,” the Gates Foundation project “Stress-Tolerant Rice for Poor Farmers in Africa and South Asia,” and a Grant-in-Aid for Scientific Research (No. 22380013) from the Japan Society for the Promotion of Science to A.Y.

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