Introduction

The availability of water and nutrients in the soil strongly constrains plant growth. These resources are heterogeneously distributed in the soil. For example, the topsoil tends to hold more immobile nutrients such as phosphorus (P) than the subsoil but conversely, it holds less water. Therefore, the distribution of a terrestrial plant’s root system determines its ability to efficiently capture water and nutrients from the soil (Gewin 2010, Lynch 1995).

Because nutrient constraints govern crop yield, researchers should consider genetic improvement of root system architectures (de Dorlodot et al. 2007). Recent simulations performed by Hammer et al. (2009) suggested that changes in maize (Zea mays L.) root system architecture had directly affected biomass accumulation and historical yield trends in the American Corn Belt region compared to changes in the leaf canopy. Higher dry matter production in rice can be achieved by increasing the uptake of nitrogen and water during the grain-filling stage in paddy fields (Ookawa et al. 2003, San-oh et al. 2004, 2006). Nitrate, which is the main form of nitrogen under upland (aerobic) conditions, is leached by precipitation into deeper soil layers because it dissolves well in water. Thus, deeper rooting achieved by modulation of the root growth angle (RGA) and root plasticity in response to the nitrogen distribution may enhance nitrogen acquisition from deep soil layers (Trachsel et al. 2013). Crops with a deeper root system are also thought to improve the soil structure, as well as its steady-state carbon, water, and nutrient retention, and therefore to contribute to sustainable crop production (Kell 2011). On the other hand, a shallow root system benefits crops by enabling plants to capture P distributed in the topsoil (Lynch and Brown 2001). In wheat (Triticum aestivum L.), root-length density in the topsoil was the most important trait for enhancing P absorption (Manske et al. 2000). In the common bean (Phaseolus vulgaris L.), P-efficient cultivars generated shallower basal roots and increased adventitious rooting in the topsoil (Lynch and Brown 2001). Root system architectures related to enhanced foraging within the topsoil include a shallower RGA of axial roots, enhanced adventitious rooting, a greater number of axial roots, and greater dispersion of lateral roots (Lynch 2011). Thus, the root distribution determines the ability of a plant to exploit nutrients that are unevenly distributed in soil.

Crop production is greatly affected by environmental stresses such as drought, high salinity, and submergence, as well as by nutrient deficiency. The global climate change that has occurred in recent years has exacerbated the effects of these stresses on plant growth. For example, global warming has caused serious drought damage in farmlands that rely on rainwater or that have limited access to irrigation (Scheffran and Battaglini 2011). Under drought conditions, drought-resistant plants tend to develop a deeper root
system, resulting in roots that can reach into still-moist deeper soil layers (Rich and Watt 2013). Thus, deeper rooting is thought to be a key factor in enhanced drought avoidance by crops (Fukai and Cooper 1995, Kirkegaard et al. 2007, Manschadi et al. 2006). Therefore, improving root system architectures to increase rooting in deep soil layers would be an effective strategy to avoid the negative impacts of drought on yield (de Dorlodot et al. 2007). Under waterlogged conditions, it is difficult for plant roots to obtain sufficient oxygen because soil oxygen levels become low. Rooting at the soil surface may help plants to avoid damage from reducing soil conditions because these roots can obtain dissolved oxygen more easily from above the soil surface (Omori and Mano 2007). In wheat, Oyanagi et al. (2004) reported that doubled haploid lines (DHLs) with shallow roots showed higher grain yield than DHLs with deep roots in a wet paddy field with a high groundwater level, suggesting that shallow-rooting lines can potentially resist waterlogging better than deep-rooting lines. Therefore, adventitious root formation near the soil surface may be an important trait for tolerating waterlogging in dry-field crops that are adapted to well-drained fields (Mano and Omori 2007).

Cereal crops are members of the grass family (Poaceae). They are monocotyledonous and have a root system that consists of one or more seminal roots that originate from the seed embryo and nodal roots that originate from nodes along the stem (Rich and Watt 2013). In cereal crops, the combination of the RGA and root length in seminal and nodal roots determines the region of the soil that can be exploited by the roots (Abe and Morita 1994, Araki et al. 2002). For example, the combination of a near-vertical growth axis (i.e., high RGA) with increased root length along that axis can lead to the development of a deeper root system. In particular, because RGA determines the direction of root elongation, it determines whether a plant develops shallow or deep rooting.

How is RGA controlled?

RGA is affected by several environmental factors such as gravity, light, and water potential (Oyanagi et al. 1993). Gravitropism is one of the major factors that determine RGA: roots show positive gravitropism by growing downward along the gravity vector. Researchers have proposed that, in root columella cells, sedimentation of the starch-filled amyloplasts, which act as statoliths, allows vascular plants to sense the direction of gravity (Haberlandt 1900, Němec 1900). This starch-statolith hypothesis has been supported by several experiments. For example, an Arabidopsis thaliana mutant lacking phragmoplasts (Miz1) produces no starch and shows a severely reduced gravitropic response. In wild-type Arabidopsis, physical elimination of columella cells also greatly disturbs the gravitropic response (Blancaflor et al. 1998, Tsugeki and Fedoroff 1999). After the gravity vector is experimentally changed by rotating a plant, amyloplasts in the columella cells begin to fall to the new bottom side of the cells, where they distort the endoplasmic reticulum (Leitz et al. 2009). This stimulus likely appears to open mechanosensitive ion channels and change the concentration of Ca2+ in the columella cells, and the resulting cytoplasmic pH change might triggers the re-localization of auxin efflux-carrier PIN-FORMED (PIN) proteins to change polar auxin signaling. This mechanism differs from that in columella cells because cells of the elongation zone do not contain statoliths.

Light also changes the direction of RGA. Arabidopsis roots exhibit negative phototropism in response to unilateral blue light. Two Arabidopsis mutants, phototropin 1 (phot1) and phot2 deficient in the phototropin blue light receptors display a lack of response in roots against the blue light (Liscum and Briggs 1995, Sakai et al. 2001). In contrast, red light, which is absorbed by phytochrome A (phyA), can induce a weak positive phototropic bending in the primary root of Arabidopsis (Kiss et al. 2003). It is reported that red light treatment of dark-grown seedlings can significantly alter subsequent blue light-mediated bending response (Briggs 1963). Since phyA can absorb both red and blue light (Pratt and Coleman 1974) and phyA appears to regulate the distribution of phot1 (Han et al. 2008), it is conceivable that phot1 and phyA functionally interact also in roots.

Roots show positive hydrotropism and can follow a moisture gradient to reach water (Takahashi et al. 2002). Several mutants related to hydrotropism have been reported: roots of no hydrotropic response1 (nhr1) cannot develop a hydrotropic curvature, mizu-kussei1 (miz1) and miz2 show impaired hydrotropic response, and altered hydrotropic response1 (ahr1) develops a larger root system due to the hydrotropic response in the presence of water potential gradients (Eapen et al. 2003, Kobayashi et al. 2007, Miyazawa et al. 2009, Saucedo et al. 2012). Hydrotropism and phototropism appear to be closely related. Moriwaki et al. (2012) demonstrated that light enhances the hydrotropic response in Arabidopsis roots and LONG HYPOCOTYL 5 (HY5)-mediated light signaling is required for MIZ1 expression and hydrotropism. HY5 is a bZIP type transcription factor that functions as a key regulator for light signaling downstream of red and blue light receptors, and the kinetics of hydrotropic curvature of hy5 roots is reduced relative to the wild type (Moriwaki et al. 2012). This light-enhanced hydrotropism should enable plant roots to grow downward to anchor the plant’s body to the ground and avoid drought stress, which would improve plant survival.

Recent analyses have revealed the detailed mechanisms that
control gravitropic bending of roots. This bending results from differential elongation of the cells in the distal elongation zone (DEZ), which results from the differential accumulation of auxins on opposite sides of the root (Cholodny 1927, Ishikawa and Evans 1993, Went 1926). As mentioned above, columella-sensed changes in the gravity vector during gravistimulation cause relocalization of the auxin-efflux carrier PIN proteins. PIN3 and PIN7 relocate on the new bottom sides of the columella cells and establish an asymmetrical flow of auxins from columella cells to the lateral root cap (Friese et al. 2002, Kleine-Vehn et al. 2010). PIN2 transports auxins from the root cap to the epidermal cells in the DEZ, which is necessary for gravitropic bending (Müller et al. 1998). The auxin influx carrier AUXIN RESISTANT 1 (AUX1) also functions in the root gravitropic response (Swarup et al. 2005). The auxins transported by these carriers initiate cell elongation in the DEZ.

It is well known that auxin signaling is mediated by the interactions between AUXIN (Aux)/INDOLE-3-ACETIC ACID (IAA) and AUXIN RESPONSE FACTOR (ARF) proteins (Liscum and Reed 2002). An auxin signal captured by TRANSPORT INHIBITOR RESPONSE1 (TIR1)/AUXIN SIGNALING F-BOX (AFB), which is an auxin receptor, promotes the ubiquitination of Aux/IAA proteins, which are repressors of auxin-responsive transcription, through the SCFTIR1/AFB complex (Gray et al. 2001). The ubiquitinated Aux/IAA proteins are then degraded by the 26S proteasome, allowing auxin-responsive transcription regulated by ARF proteins that function as transcriptional activators or repressors (Gray et al. 2001). Signal transduction by numerous transcription factors that act downstream of Aux/IAA and ARF proteins leads to a variety of auxin-induced morphological changes in plants, including gravitropic bending. The defective gravitropic response in each Arabidopsis mutant related to auxin signaling mediated by Aux/IAA and ARF proteins indicates the strong contributions of auxins to environmental adaptation through morphological modification (Fukaki et al. 2002, Leyser et al. 1996, Nagpal et al. 2000, Tian and Reed 1999, Yang et al. 2004).

Reduced gravitropic responses have also been observed in rice mutants. CROWN ROOTLESS4 (CRL4)/OsGNOM1, which encodes a guanine exchange factor for ADP ribosylation factor GTPases (Arf-GEF), is essential for maintaining an appropriate auxin accumulation and gradient (Kitomi et al. 2008, Liu et al. 2009). CRL4/ADVENTITIOUS ROOTLESS1 (ARL1) and CRL5 encode plant-specific LATERAL ORGAN BOUNDARIES DOMAIN (LBD)/ASYMMETRIC LEAVES LIKE (ASL) and APETALA2 (AP2)/ETHYLENE RESPONSIVE FACTOR (ERF) transcription factors, respectively, and function downstream of auxin signaling pathways mediated by Aux/IAA and ARF (Inukai et al. 2005, Kitomi et al. 2011, Liu et al. 2005). In gain-of-function mutants of OsIAAs, auxin signaling was blocked because of a single amino acid substitution in the core sequence of domain II, which is responsible for rapid degradation of Aux/IAA proteins (Jun et al. 2011, Kitomi et al. 2012, Zhu et al. 2012). Recently, the quantitative trait locus DEEPER ROOTING 1 (DRO1), which controls the RGA, was isolated. The expression of DRO1 has been shown to be negatively regulated by auxin signaling downstream of Aux/IAA and ARF, and is involved in cell elongation in the root tip that causes gravitropic bending (Uga et al. 2013a).

These results suggest that polar auxin transport and auxin signal transduction during the gravitropic response is an important determinant of the RGA in rice plants, as it is in Arabidopsis.

Genetic dissection of natural variation in RGA

To understand genetic control of root system architectures and the resulting potential for using this knowledge to improve crop production, many quantitative trait locus (QTL) analyses have been performed in crop species to dissect the control of root traits such as maximum length, thickness, volume, and distribution. In rice, 675 QTLs for root traits have been reported (summarized by Courtois et al. 2009). On the other hand, there have been few reports of RGA QTLs in crops. To improve drought adaptation in sorghum (Sorghum bicolor L. Moench), Mace et al. (2012) detected four QTLs for RGA in recombinant inbred lines (RILs) that had been developed from a cross between accessions with small and large root angles. To develop a flooding-tolerant maize variety, Omori and Mano (2007) investigated QTLs for RGA in two F2 populations derived from different crosses between deep-rooted maize and shallow-rooted teosinte (Zea luxurians (Durieu & Asch.) R.M. Bird). They found 10 QTLs with moderate or minor genetic effects. In wheat, Hamada et al. (2012) found two QTLs for the deep root ratio (which represents the proportion of total roots with an RGA > 45°) in DHLs derived from a cross between shallow- and deep-rooting accessions. Christopher et al. (2013) reported six QTLs for RGA in DHLs derived from a cross between two wheat accessions with small and large seminal root angles. However, none of these genes has been cloned yet.

In rice (Oryza sativa L.), two QTLs for the root gravitropic response, which is a component of RGA, have been reported (Norton and Price 2009). Recently, we found six major QTLs for RGA in rice (Kitomi et al. in press, Uga et al. 2011, 2012, 2013a, 2013b, 2015). DRO1 has been detected on chromosome 9 in RILs derived from a cross between the lowland cultivar ‘IR64’, which has shallow rooting, and the upland cultivar ‘Kinandang Patong’, which has deep rooting (Uga et al. 2011), and has been cloned (Uga et al. 2013a). ‘Kinandang Patong’ has a functional allele of DRO1, whereas ‘IR64’ has a non-functional allele of this gene, indicating that the ‘IR64’ allele of DRO1 causes shallow rooting in rice. We also found a major QTL for RGA (DRO2) on chromosome 4 in three F2 populations derived from crosses between each of three shallow-rooting cultivars (‘ARC5955’, ‘Pinulupot1’, and ‘Tupa729’) and ‘Kinandang Patong’ (Uga et al. 2013b). Based on these results, we hypothesize that ‘Kinandang Patong’ has positive
alleles of \textit{DRO1} and \textit{DRO2} that lead to downward growth of rice roots, although further study will be needed to determine the genetic relationship between \textit{DRO1} and \textit{DRO2}. \textit{qSOR1} (quantitative trait locus for \textit{SOIL SURFACE ROOTING}) has been fine-mapped on chromosome 7 in RILs derived from a cross between ‘Gemdjah Beton’, a lowland rice cultivar with a high proportion of roots that run along or near the soil surface, and ‘Sasanishiki’, a lowland rice cultivar that lacks soil-surface roots (Uga \textit{et al.} 2012). To understand the genetic mechanism responsible for natural variation of RGA in rice, it will be important to identify and further characterize these QTLs.

\textbf{Prospects of genetic improvement for RGA}

Genetic improvement of the root system architecture has been recognized as an important approach to enhance crop production. The existence of wide natural variation in root system architectures has been reported in various crops (reviewed by O’Toole and Bland 1987). In cultivated rice, varietal differences in root traits such as root length, root thickness, and root volume have been found in many previous studies (Henry \textit{et al.} 2011, Lafitte \textit{et al.} 2001, O’Toole and Bland 1987, Uga \textit{et al.} 2009), but few studies of the genetic variation in RGA have been published (Kato \textit{et al.} 2006, Uga \textit{et al.} 2009). This natural variation represents a useful breeding resource that can be used to improve crop productivity. However, it is more laborious and time-consuming to evaluate root traits than aboveground traits in a large number of plants grown under natural field conditions in a breeding program. In addition, root growth is strongly affected by soil conditions and their variations, such as unevenly distributed water and nutrients within the surrounding rhizosphere. Therefore, breeding of crops to improve their root traits has shown little progress.

Marker-assisted selection (MAS) is a promising breeding strategy for improving complex traits. Many QTLs for aboveground traits have been identified as single genes, and MAS has been used to identify promising genetic resources (reviewed by Yamamoto and Yano 2008, Yamamoto \textit{et al.} 2014). In rice roots grown underground, six root QTLs have recently been fine-mapped as single loci (Ding \textit{et al.} 2011, Obara \textit{et al.} 2010, Uga \textit{et al.} 2010, 2011, 2012, Wang \textit{et al.} 2013). These QTLs may be promising genetic resources that can be used to alter the root system architecture. Some QTLs have been applied for MAS in breeding to improve drought resistance in rice (Shen \textit{et al.} 2001, Steele \textit{et al.} 2006). Steele \textit{et al.} (2006) performed MAS to introduce the ‘Azucena’ (upland \textit{japonica}) alleles of four root QTLs into ‘Kalinga III’ (upland \textit{indica}) based on DNA marker information reported in previous studies, but have not yet performed QTL analysis using mapping population derived from the parent accessions. Some advanced progenies with the selected QTL alleles showed significantly improved root traits, although other lines with these alleles did not show positive effects on root morphology. Likewise, there have been no genetic studies in which crop productivity was increased by genetic improvement of the root system architecture.

We developed a near-isogenic line (Dro1-NIL) that carries a functional allele of \textit{DRO1} derived from the deep-rooting cultivar ‘Kinandang Patong’ in the genetic background of the shallow-rooting parent variety ‘IR64’, which has a non-functional allele of \textit{DRO1}. The maximum root depth of Dro1-NIL plants (ca. 45 cm) was more than twice that of ‘IR64’ plants (ca. 20 cm) under upland conditions (Uga \textit{et al.} 2013a). We observed a similar difference in the root distribution between the two accessions under paddy fields with drought stress (\textbf{Fig. 1}). \textit{DRO1}, which controls the gravitropic curvature in roots, predominantly influences RGA, but shows no marked differences in other root and shoot traits. In the rest of this section, we describe the potential genetic improvement of RGA based on our recent studies using Dro1-NIL, which is a homogeneous genetic material that differs from the parent variety only in terms of the RGA.

\textbf{Drought avoidance}

Many QTLs for drought resistance have been reported in rice (Bernier \textit{et al.} 2007, Courtois \textit{et al.} 2000, Lanceras \textit{et al.} 2004, Yue \textit{et al.} 2005, Zou \textit{et al.} 2005). Bernier \textit{et al.} (2007) reported a major QTL (\textit{qtl12.I}) on chromosome 12 that increased grain yield under drought conditions. However, we do not know whether RGA influences crop yield under natural field conditions when drought stress occurs. To determine the effect of \textit{DRO1} on drought resistance, we compared the yield performance of ‘IR64’ and Dro1-NIL plants under upland field conditions with no drought,
 moderat drought, or severe drought (Uga et al. 2013a). The drought treatments were imposed from panicle initiation to heading, since rice is most sensitive to drought stress during this period. Both accessions had similar yields under no-drought conditions. In contrast, moderate drought significantly decreased the grain weight per plant in ‘IR64’, whereas Dro1-NIL had almost the same grain weight per plant as in the unstressed Dro1-NIL plants. In addition, under severe drought, the percentage of filled grains in ‘IR64’ was nearly zero, whereas Dro1-NIL maintained >30% filled grains. This experiment demonstrates that the larger RGA conferred by the functional allele of DRO1 contributes to avoiding drought stress, resulting in higher yield under up-land conditions with drought stress.

Yield performance and lodging resistance

The genetic aspects of whether high RGA contributes to high yield in paddy fields are not yet clear, but previous studies suggested that deeper roots increase grain yield in paddy fields (Kawata et al. 1978, Morita 1993, Morita et al. 1988). We investigated the effect of DRO1 on rice yield in an irrigated paddy field using ‘IR64’ and Dro1-NIL (Arai-Sanoh et al. 2014). Uptake of nitrogen by Dro1-NIL after heading was higher than that of ‘IR64’, resulting in higher grain yield. This suggests that the deep roots conferred by DRO1 enhanced nitrogen uptake from lower soil layers, resulting in better grain filling. Lodging resistance influences grain yield and dry matter production in paddy rice, since plant productivity decreases when lodging occurs (Kono 1995). Previous studies showed that deep root was associated with high lodging resistance based on comparisons of different cultivars or examination of the effects of root pruning (Sakata et al. 2004, Terashima 1997, Terashima et al. 1994, 1995). Dro1-NIL showed higher pushing resistance, which can be used as an index of lodging resistance, than ‘IR64’ in wet soil, suggesting that roots in lower soil layers increase lodging resistance (Arai-Sanoh et al. 2014). The increased RGA conferred by DRO1 improved yield performance and lodging resistance, although further research is necessary because we examined the effects of DRO1 on these traits under only a single set of environmental conditions.

Phytoremediation and avoidance of contamination by heavy metals

The pollution of soils by toxic metals is a major environmental and human health problem. Phytoremediation using plants capable of high metal accumulation is a promising environmental clean-up technology (Salt et al. 1998). Conversely, the development of plants that accumulate low levels of these metals is expected to reduce the daily intake of heavy metals such as cadmium (Cd) from crops (Ishikawa et al. 2005). Cd is a highly toxic metal for most living organisms, including humans. Recently, the physiological and molecular mechanisms of Cd transport in plants have been studied in some depth (Uraguchi and Fujiwara 2012). In rice, lines with low Cd accumulation have been developed using the mutant osnramp5, which controls Mn, Fe, and Cd transport; plants with the mutant allele exhibit decreased Cd uptake by the roots (Ishikawa et al. 2012, Ishimaru et al. 2012). On the other hand, we have little knowledge of the relationship between RGA and the efficiency of heavy metal uptake. We used ‘IR64’ and Dro1-NIL to evaluate whether the difference in RGA affected Cd uptake (Ishikawa et al. 2005). To increase the bioavailable Cd concentration in the soil, irrigation water was withheld after the vegetative growth period. Consequently, the bioavailable Cd concentration increased in the upper soil layer because of oxidizing conditions in the soil. In plants grown under these conditions, the grain and straw Cd concentrations were significantly lower in Dro1-NIL than in ‘IR64’ (Fig. 2). This suggests that the shallow-rooting cultivar is a potential genetic resource for developing plants with high Cd accumulation, whereas the deep-rooting cultivar may be able to avoid absorbing the bioavailable Cd from the upper soil layers.

Conclusions and future prospects

Our DRO1 experiments demonstrate that modulation of RGA provides several potential advantages for rice cultivation under certain soil conditions (Fig. 3). Farmers seek the highest possible grain yields under both stressed and non-stressed conditions, and breeding for high or low RGA may reduce the frequency of stress that is sufficiently severe to reduce yield. Breeding for RGA based on DRO1 might meet farmer desires for high yield, since DRO1 only alters the
RGA and does not decrease either shoot or root biomass (Uga et al. 2013a). However, root system architectures exhibit complex interactions with environmental and cultivation conditions, so breeding for RGA may lead to tradeoffs among the acquisition of different resources that are unevenly distributed in the soil. For example, the available P is located primarily in the upper soil layers in upland fields, whereas water and nitrate are generally located in lower soil layers (Lynch 2011), and irrigated paddy fields show a different pattern. Ho et al. (2005) reported that shallow-rooting beans grew well under a P deficiency, whereas deeper-rooting plants grew better under drought stress. To develop a range of varieties that are adapted to a range of environmental stresses, which differ both from region to region and from soil to soil, it will be necessary to both identify and characterize RGA QTLs and to improve our understanding of the interactions between QTLs and environmental factors.

**Acknowledgements**

We thank Drs. A. Singh, A. Kumar, and A. Henry (International Rice Research Institute, IRRI) for their support and suggestions regarding the root evaluation studies in the paddy fields. This work was supported by two grants from the Ministry of Agriculture, Forestry, and Fisheries of Japan (Genomics for Agricultural Innovation QTL-4003, and Genomics-based Technology for Agricultural Improvement RBS-2009).

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