Field Crops Research 165 (2014) 111–124

Contents lists available at ScienceDirect

Field Crops Research

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

Root genetic research, an opportunity and challenge to rice improvement

Weiming Wu, Shihua Cheng *

Chinese National Center for Rice Improvement and State Key Laboratory of Rice Biology, China National Rice Research Institute, 359 Tiyuchang Road, Hangzhou 310006, PR China

ARTICLE INFO

Article history:
Received 10 January 2014
Received in revised form 14 April 2014
Accepted 16 April 2014
Available online 16 May 2014

Keywords:
Rice (*Oryza sativa* L.)
Root
Genetic research

ABSTRACT

Rice is one of the most important cereal crops, feeding more than 50% population of the world. To meet the demand of increasing population, rice production has to be improved continually. As a very important part of rice plant, root system plays multiple roles in rice growth: anchorage of the plant, acquisition of water and nutrient elements, and biosynthesis of amino acids and hormones, etc. Almost all of the hot spots about rice research are associated with rice root: drought tolerance, lodging resistance, and efficient use of nutrition, the goal is to increase the grain yield with desirable seed quality. Although the understanding about rice root has been expanded in the last decades, there remain much to be done about root morphology and physiology, especially in root genetics. Rice root research is an exciting and focusing field in recent years. More and more researches on rice root genetics have been made. There is a close relation between above ground traits and underground roots, providing an alternative approach for rice genetic improvement. A number of genes associated with root architecture and physiological functions have been identified, or cloned. It provides an opportunity to further improve rice based on molecular assisted selection. Root traits improvement should be taken into account in future breeding programs in rice. However, root research is still a consuming and difficult work, because it was largely influenced by the complex underground environment. This paper reviewed the progress in rice root genetic research, and discussed its prospects.

1. Introduction

Rice is one of the most important food crop, feeding more than half of the world's population. The increasing population and economic development have been posing a growing pressure for increase in food production (Zhang, 2007). Meanwhile, rice yield increase eventually slowed in China as well as in other countries. The average yearly increase in yield dropped from 3.7% in 1980s to 0.9% in 1990s (Katsura et al., 2007). To meet the demand of food for increasing population, raising the yield ceiling of rice remains a priority task for rice breeders (Cheng et al., 2007b).

As an important organ of rice plant, root performs vital functions: acquisition of resources and anchorage of rice plant. In addition, root systems serve the secondary functions, such as propagation, synthesis of growth regulators, storage (Fitter, 2002). The synthesis of organic substances is very important to rice growth. The release of the organic substances from roots can modify the physical, chemical and biochemical characteristics of the soil in the rhizosphere (Grayston et al., 1996). Roots sense and response to abiotic and biotic stresses, and communicate with the shoot via signaling pathway. Hormones play a pivotal role in root/shoot communications. ABA (abscisic acid), ethylene and auxin serve as the signals for communication between root and shoot in rice (Konings and Jackson, 1979; Bano et al., 1993). Roots can regulate not only stomatal conductance, and also affect the posture of leaf blade and photosynthesis rate under soil impedance, nutrient, drought and salt stresses.

Since Weaver (1919) performed a pioneering investigation on rice root, great progress has been made in rice root biology. It is well known that the functions of absorption and support of root system are an important guarantee for biological yield and grain yield of rice (Carvalhais et al., 2011). Therefore, root traits have been claimed to be critical for increasing yield under soil-related

* Corresponding author. Tel.: +86 571 63370188.
E-mail addresses: wmw5599@126.com (W. Wu), shcheng@mail.hz.zj.cn (S. Cheng).

http://dx.doi.org/10.1016/j.fcr.2014.04.013

stresses (Lynch, 2007). Root morphology and physiology are closely associated with the growth and development of above-ground part of plant (Yang, 2011).

Root researches have been paid more and more attentions in recent years. With the aid of novel molecular biology methods, continuing progress on root genetic research has been achieved in rice. A number of genes related to root morphological characteristics and physiological functions have been identified or cloned, which opened an opportunity for further improvement of rice productivity (Rebouillat et al., 2009; Uga et al., 2013).

2. Importance of root genetic improvement

2.1. Increasing rice productivity

It is the roots that absorb most nutrients and water (Russell, 1977). Among essential nutrient elements required for rice growth, inorganic carbon is absorbed mainly by leaves in the form of carbon dioxide, the other essential mineral elements are all absorbed mainly through root surface from the soil. Root is the foundation of rice development.

As described in the report by Zhang et al. (2009), the high grain yield was mainly due to a larger sink size (total number of spikelets) as a result of a larger panicle. The low percentage of filled grains was closely associated with a quick decreased root activity during grain filling. Further research is needed to understand the mechanism involved in the low percentage of filled grains and yield fluctuation and to improve the yield performance in elite hybrid lines. The yield of elite varieties can be further increased by an increase in filled grains through enhancing root activity during grain filling (Yang, 2011; Cheng et al., 2007c).

2.2. Enhancing tolerance to abiotic stresses

Drought is one of the most severe abiotic stresses limiting rice productivity in the world, and poses a serious threat to the sustainability of rice yields in rainfed agriculture. Development of drought resistant rice is one of the objectives in the water-saving agriculture programs (Dat, 1986). Acquisition of more water from soil is a mechanism for drought tolerance in rice. Improving the understanding of the interaction between root function and drought in rice could have a significant impact on global food security (Gowda et al., 2011). Therefore, improving root system with deep root and high water uptake ability would be the key to developing elite rice varieties suitable for water-saving farming system.

Soil salinity is another severe abiotic stress in agriculture worldwide (Fig. 1). About 20% of the world's cultivated land and nearly half of all irrigated lands are affected by salinity (Rhoades and Loveday, 1990). High salt stress disrupts homeostasis in water potential and ion distribution. This disruption of homeostasis occurs at both the cellular and the whole plant levels. Drastic changes in ion and water homeostasis lead to molecular damage, growth arrest and even death (Zhu, 2001). For plants growing in saline soils, the 'exclusion' of Na^+ and Cl^- by roots is of paramount importance (Barrett-Lennard, 2003). High-affinity K^+ transport systems are also essential for preventing Na^+ toxicity. Under NaCl-dominated salt stress, the key to plant survival is maintaining a low cytosolic Na^+ level or Na^+/K^+ ratio. Therefore, one way to engineer plant cells with improved salt tolerance is to enhance K^+ uptake activity of the cells, while keeping Na^+ out during salt stress (Horie et al., 2011). Developing salt tolerance varieties is also a task for rice breeders in the future.

2.3. Improving efficiency of nutrients

The use of fertilizer changed dramatically in the twentieth century, but excess nutrients have involved in many environmental problems. Unused fertilizer is washing off fields into rivers, poisoning coastal waters and causing acid rain (Nosengo, 2003).

Nitrogen use efficiency (NUE) for cereal production is approximately 33% worldwide. The remaining N from fertilizer is lost to the atmosphere or leached into the groundwater and other freshwater bodies (Raun and Johnson, 1999), which is causing serious N pollution and becoming a threat to global ecosystems (Nosengo, 2003). Nitrogen pollution is now claimed the third major threat to our planet after biodiversity loss and climate change (Giles, 2005).

On the other hand, nutrients deficiencies are most frequently encountered in agriculture practices. For example, low levels of plant-available P in soils are the major constraint for rice production. Only 10–20% of the P supplied in fertilizers is available to plants (Wada et al., 1990). The development of cultivars with an improved ability to utilize this large but hardly plant-available P pool could offer a more sustainable solution than relying on fertilizer application alone (Wissuwa et al., 1998).

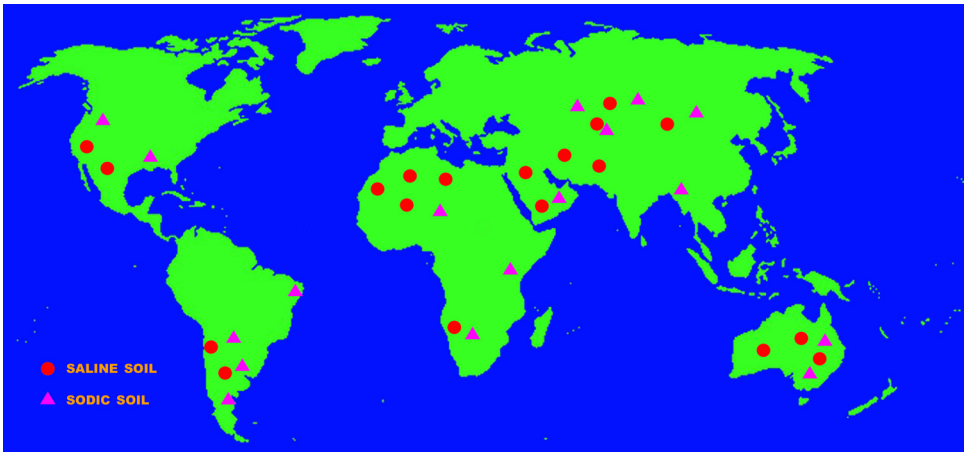

Fig. 1. Sodic and saline soils of the world.

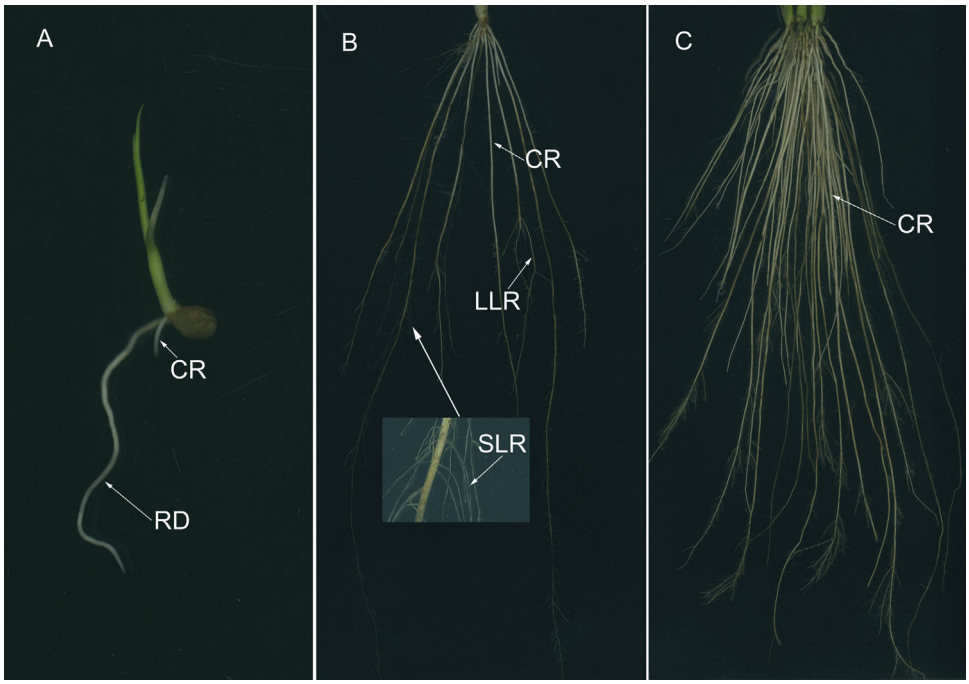

Fig. 2. Root system of rice. (A) 3 days after germination; (B, C) 20 and 50 days after germination. RD: radicle; CR: crown root (adventitious root); LLR: large lateral root; SLR: small lateral root.

3. Progress of molecular genetic research on rice root

3.1. Root development

Rice bears a shallow root system that is comprised of one seminal root (radicle), numerous adventitious roots (crown roots) arising from successive nodes, and large and small lateral root emerging from primary roots (Fig. 2). Dissecting genetic and molecular mechanisms controlling rice root development is critical for the development of new rice ideotypes that are better adapted to adverse conditions and for the production of sustainably achieved rice yield potential (Rebouillat et al., 2009). Early in 1980s, Chang et al. (1982) and Ekanayake et al. (1985) have made some genetic researches on rice root. Fustuhara and Kitano (1985) reported a crown root inhibiting gene *RT1*. To date, advances have been made in root genetics. Through the utilization of several mapping populations (including DH, RI, and F_2 population, such as Akihikari/IRAT109, CT9993/IR6226, Bala/Azucena, IR64/Azucena), more than 700 QTLs related to rice root architecture (root length, root number, and root thickness etc.) have been mapped (Horii et al., 2006; Kamoshita et al., 2002; Price et al., 2002; Nguyen et al., 2004). For more information, see Courtois et al., 2009, and http://www.gramene.org/. An increasing number of genes related to rice root have been identified or cloned (Rebouillat et al., 2009; E et al., 2012).

3.1.1. Adventitious root formation

There are four reported genes related to radicle development in rice. The *ral1* is the first mutant impaired in both procambium development and vascular patterning to be isolated in a monocot species, which produce normal adventitious roots after germination. Knockdown of *RADICLELESS1 (RAL1)* gene results in distinctive vascular pattern defects (Scarpella et al., 2003) (Table 1). The both *ral2* and *ral3* mutants also presented radicle inhibition (Hong et al., 1995). *OsCem* mutant develops Siamese polyembryos with multiple radicles. *OsCem* encodes a protein related to polar transport of auxin in the embryos and that is specifically expressed in embryo tissues and not in other vegetative tissues (Yang and Hwa, 2008).

Crown rootless1 (crl1) mutant is defective in crown root formation (Inukai et al., 2005). It showed auxin-related abnormal phenotypic traits in the roots, such as decreased lateral root number, auxin in sensitivity in lateral roots (LRs) formation, and impaired root gravitropism, whereas aboveground organs were normal. *ARL1* is the same gene with *CRL1* (Liu et al., 2005). *CRL1* encodes a protein with a LOB domain. It expresses in lateral and adventitious root primordia, tiller primordia, vascular tissues, scutellum, and young pedicels. CRL2 is involved in crown root formation, the initiation and subsequent growth of adventitious roots primordia of mutant are impaired (Inukai et al., 2001). *CRL3* is exclusively involved in the formation of the crown root primordia, but not in the formation of other types of root primordial and shoot apical meristem (Kitomi et al., 2008a). *CRL4* encodes OsGNOM1, which expressed in AR(adventitious root) primordia, vascular tissues, LRs, root tips, leaves, anthers and lemma veins (Kitomi et al., 2008b). *CRL4* is mediated by OsPINs family, such as OsPIN2, OsPIN5b, OsPIN9, and affected the formation of ARs through regulating PAT (polar auxin transport) (Liu et al., 2009). *CRL5* encodes a member of the large AP2/ERF transcription factor family protein. The auxin-induced *CRL5* promotes crown root initiation through repression of cytokinin signaling by positively regulating type-A *RR*, *OsRR1* (Kitomi et al., 2011).

It is known that *SCR (SCARECROWN)* and *SHR (SHORT-ROOT)* genes related with root initiation and root elongation in plants. OsSCR1 and OsSCR2 are involved in root development. They are essential for the asymmetric division of the cortex/endodermis progenitor cell in the root, and expressed in the endodermal cell layer and down-regulated in the daughter cortex cell after asymmetric division in the root tip (Kamiya et al., 2003). A SHR homolog from rice is a moving transcription factor essential for endodermis specification. SHR movement is limited to essentially one cell layer. SCARECROW (SCR) blocks SHR movement by sequestering it into the nucleus through protein-protein interaction and a safeguard mechanism that relies on a SHR/SCR-

Table 1
Reported root development-related genes.

Phenotype	Gene	Locus ID	Reference
Radicle initiation	*RAL1,RAL2,RAL3*		Scarpella et al. (2003); Hong et al. (1995)
	OsCEM		Yang and Hwa (2008)
Crown root formation	*OsCAND1*	LOC_Os02g7120	Wang et al. (2011)
	OsCOW1	LOC_Os03g6654	Woo et al. (2007)
	CRL1(ARL1)	LOC_Os03g5510	Inukai et al. (2005); Liu et al. (2005)
	CRL2,CRL3	LOC_Os03g46330	Inukai et al. (2005); Kitomi et al. (2008a)
	CRL4(OsGNOM1)	LOC_Os07g3250	Kitomi et al. (2008b); Liu et al. (2009)
	CRL5		Kitomi et al. (2011)
	OsMT2b	LOC_Os05g2070	Yuan et al. (2008)
	OsSHR1		Cui et al. (2007)
	OsSCR1, OsSCR2		Kamiya et al. (2003)
	WOX11	LOC_Os07g48560	Zhao et al. (2009)
	OsYUCCA1	LOC_Os01g45760	Yamamoto et al. (2007)
Root elongation	*OsAGAP*	LOC_Os02g10480	Zhuang et al. (2005)
	OsARF12	LOC_Os04g57610	Qi et al. (2012)
	OsCKI1	LOC_Os02g40860	Liu et al. (2003)
	OsCYT-INV1	LOC_Os02g34560	Jia et al. (2008)
	OsDGL1	LOC_Os07g10830)	Qin et al. (2013)
	GLR3.1	LOC_Os04g49570	Li et al. (2006b)
	OsRR1	LOC_Os04g36070	Kitomi et al. (2011)
	OsRR2	LOC_Os02g35180	Zhao et al. (2009)
	OsGNA1	LOC_Os09g31310	Jiang et al. (2005)
	OsGLU3	LOC_Os04g41970	Zhang et al. (2012a)
	KSR1		Ning et al. (2010)
	OsKSR2		Luo et al. (2012)
	RT1		Fustuhara and Kitano (1985)
	OsRAA1	LOC_Os01g15340	Ge et al. (2004)
	OsRMC	LOC_Os04g56430	Jiang et al. (2007)
	RRL1,RRL2,RRL3		Inukai et al. (2001, 2003)
	SRT1, SRT2, SRT3	LOC_Os02g34560	Ichii and Ishikawa (1997); Yi et al. (2002)
	SRT4		Liang and Ichii (1995)
	SRT5		Yao et al. (2002)
	SRT6		Yao et al. (2003)
	OsSPR1	LOC_Os01g67290	Jia et al. (2011)
	qRL6.1		Obara et al. (2010)
	qRL7		Wang et al. (2013a)
	OsPIN1	LOC_Os02g50960	Xu et al. (2005)
	OsPIN3t	LOC_Os01g45550	Zhang et al. (2012c)
Root angle	*DRO1*	LOC_Os09g26840	Uga et al. (2013)
Root thickness	*DES*		Wan et al. (1996)

dependent positive feedback loop for SCR transcription (Cui et al., 2007). OsKSR2 is responsible for root development. *Oksr2* shows a dwarf phenotype and the elongation of primary roots, adventitious roots and lateral roots are severely impaired (Luo et al., 2012).

OsCAND1 is an ortholog of *Arabidopsis CAND1*, required for crown root emergence. The defect of visible crown root in the *Oscand1* mutant is the consequence of a cessation of the G2/M cell cycle transition in the crown root meristem. During crown root primordium development, the expression of *OsCAND1* is confined to the root cap after the establishment of fundamental organization (Wang et al., 2011).

3.1.2. Root elongation

Root elongation is essentially driven by stem cells localized in apical meristems of roots. The mutants *rrl1, rrl2* both show shorter root, *RRL1*, *RRL2* inhibit the maintenance of root apical meristem and cell elongation (Inukai et al., 2001). The mutant *rrl3* with short roots is highly sensitive to mechanical stimulus. *RRL3* specifically regulates the cell production process in the root meristematic zone under mechanically impeded condition, and does not regulate the sensitivity to ABA (abscisic acid), IAA (indoleacetic acid) and ethylene (Inukai et al., 2003). *SRT1* is a short root gene. The *srt1* shows shorter length of root due to defective cell elongation (Ichii and Ishikawa, 1997). Subsequently, *srt2*, *srt3*, *srt4* and *srt5*were characterized (Liang and Ichii, 1995; Yi et al., 2002; Ichii and Ishikawa, 1997; Yao et al., 2002). The mutant *srt5* shows extreme inhibition of seminal root, crown root and lateral root elongation, and altere root hair formation at the seedling stage, due to the reduced cell size and cell number. *SRT6* is restricted specifically to the development of primary roots. Its expression is phase-specific, and greatly reduced primary root length and diameter (Yao et al., 2003).

ADP-ribosylation factor (ARF) proteins, which mediate vesicular transport, have little or no intrinsic GTPase activity. They rely on the action of GTPase-activating proteins (GAPs) and guanine nucleotide exchange factors (GEFs) for their function. *OsAGAP* encodes a protein with predicted structure similar to ARF-GAP. Transgenic *Arabidopsis* with *OsAGAP* constitutively expression shows reduced apical dominance, shorter primary roots, increasing number of longer adventitious roots (Zhuang et al., 2005).

Glu receptors are known to function as Glu-activated ion channels that mediate mostly excitatory neurotransmission in animals. Glu receptor-like genes have also been reported in higher plants, although their function is largely unknown. *GLR3.1* is a Glu receptor-like gene in rice, the root meristematic activity of mutant is distorted and accompanied by enhanced programmed cell death. *GLR3.1* is essential for the maintenance of cell division and individual cell survival in the root apical meristem at the early seedling stage (Li et al., 2006b).

OsGNA1 is involved in de novo UDPN-acetylglucosamine biosynthesis. It encodes a glucosamine-6-P acetyltransferase. The *gna1* mutant exhibited a temperature-sensitive defect in root elongation. The aberrant root morphology of the mutant includes shortening of roots, disruption of microtubules, and shrinkage of

cells in the root elongation zone (Jiang et al., 2005). *OsCyt-inv1* codes an alkaline/neutral invertase and is an ortholog of *Arabidopsis* gene *AtCyt-inv1*. The mutant showed short root under normal growth condition, the cell length along the longitudinal axis was reduced and the cell shape in the root elongation zone shrank. Map-based cloning revealed that a nucleotide substitution causing an amino acid change from Gly to Arg occurred in the predicted gene (Jia et al., 2008). *OsSPR1* encodes a mitochondrial protein with the Armadillo-like repeat domain. *Osspr1* mutant exhibited decreased root cell elongation (Jia et al., 2011). The iron and zinc content of the mutant shoots was significantly altered. A homolog of *KOR1* of rice, *OsGLU3,* encodes a putative membrane-bound endo-1,4-b-glucanase. OsGLU3 can affect root cell wall cellulose synthesis to modulate root elongation (Zhang et al., 2012a). *KSR1* is a short root gene, it is mapped to a 155 kb region, flanked by the InDel marker 4–24,725 K and the SSR marker RM17182 (Ning et al., 2010).

As an ortholog of *Arabidopsis DGL1*, human *OST48* and yeast *WBP1, OsDGL1* encodes the dolichyl-diphosphooligosaccharide-protein glycosyl- transferase 48 kDa subunit precursor (Qin et al., 2013). The *osdgl1* displayed a change of matrix polysaccharides in its root cell wall, shorter root cell length, smaller root meristem and cell death in the root. *OsCKI1* encodes a casein kinase, and plays an important role in formation and growth of adventitious root in rice (Liu et al., 2003).

A large number of QTLs related to root development in rice have been detected, but just few major QTLs have been cloned. *DEEPER ROOTING 1 (DRO1)*, a rice quantitative trait locus controlling root growth angle, was mapped and sequenced (Uga et al., 2013). *DRO1* is negatively regulated by auxin and is involved in cell elongation in the root tip that causes asymmetric root growth and downward bending of the root in response to gravity. *qRL7* is located between markers InDel11 and InDel17, which delimit a 657.35 kb interval in the reference cultivar Nipponbare. *qRL7* plays a crucial role in root length (Wang et al., 2013a). The major QTL, *qRL6.1*, greatly promoted root elongation under NH_4^+ condition, and was localized to the long-arm of chromosome 6 (Obara et al., 2010). *DES* is associated with adventitious root thickness (Wan et al., 1996).

3.1.3. Lateral root and root hair development

Lateral roots emerge from the primary roots (radicle and adventitious roots), it is the most important part of root system, and contributes to water and nutrient acquisition. Several genes associated with lateral root development have been identified (Table 2).

The mutant *lrt1* fails to form lateral roots and shows a reduced root gravity response. *Lrt1* displays resistance to 2,4-D, NAA, IBA, and IAA, due to the altered auxin activity in the root, thereby affecting root morphology (Chhun et al., 2003a). The mutant *lrt2* fails to form lateral roots and exhibits altered root response to gravity too (Wang et al., 2006). *LRT2* is localized to a 10.8 cM interval on the short arm of chromosome 2, flanked by two sequence-tagged site (STS) markers Lrt2P1 and Lrt2P2.

OsWOX3A plays important roles in organ development, including lateral-axis outgrowth and vasculature patterning in leaves, lemma and palea morphogenesis in spikelets, and the numbers of tillers and lateral roots. OsWOX3A is encoded by *NARROW LEAF2 (NAL2)* and *NAL3*, a pair of duplicated genes. It also acts in the control of root hair formation (Cho et al., 2013). A G → A mutation in the 9th exon of *OsORC3* (Origin Recognition Complex subunit 3) is responsible for the mutant (*orc3*) phenotype. OsORC3 is strongly expressed in regions of active cell proliferation, including the primary root tip, stem base, lateral root primordium, emerged lateral root primordium, lateral root tip, young shoot, anther and ovary (Chen et al., 2013).

Arm1 and *Arm2* function in different processes in the auxin response pathways leading to lateral root formation. The *arm1* displays a variety of morphological defects including reduced lateral root formation, increased seminal root elongation, reduced root diameter, and impaired xylem development in roots, while the *arm2* reduces slightly lateral root formation, impaired xylem development in roots and an enhanced plant height (Chhun et al., 2003b).

Root hairs differentiate from epidermal cells of root, and serve to acquisition of nutrients and water from the rhizosphere. Eight genes related to root hair development have been reported in last decade (For more information, see http://www.iroothair.org/). The mutant *roothairless 1* (*rth1*) shows absence of root hair (Yuo et al., 2009). It is caused by a mutation of *OsAPY*, an important gene for root hair elongation and plant growth in rice. *Root hairless 2 (rh2)* is complete absence of root hairs, and with a strong reduction in root length among all root types, as well as a strong reduction in plantheight. The mutation does not affect the number of crown roots or the morphology of leaves (Suzuki et al., 2003). *OsCSLD1* is required for hair elongation but not initiation (Kim et al., 2007). It expresses in only root hair cells, and is the only member of the four rice *CSLD* genes that shows root-specific expression. OsRHL1 is a novel basic helix-loop-helix (bHLH) transcription factor involved in the regulation of plant root hair development, and belongs to subfamily

Table 2
Genes related to development of lateral root and root hair.

Phenotype	Gene	Locus ID	Reference
Lateral root development	*ALF1*		Debi et al. (2003)
	ARM1,ARM2		Chhun et al. (2003b)
	OsIAA3,	LOC_Os12g40900	Nakamura et al. (2006)
	OsIAA11,	LOC_Os03g43400	Zhu et al. (2011)
	OsIAA13	LOC_Os03g53150	Kitomi et al. (2012)
	OsIAA23	LOC_Os06g39590	Ni et al. (2011)
	LRT1, LRT2		Chhun et al. (2003a); Wang et al. (2006)
	OsORC3		Chen et al. (2013)
	OsWRKY31	LOC_Os03g20550	Zhang et al. (2008)
	OsWOX3A(NAL2)	LOC_Os11g1130	Cho et al. (2013)
Root hair development	*OsAPY(RTH1)*	LOC_Os07g48430	Yuo et al. (2009)
	OsCSLD1	LOC_Os10g42750	Kim et al. (2007)
	OsEXPB5,	LOC_Os04g46650	Won et al. (2010)
	OsEXPA17	LOC_Os06g1920	Yu et al. (2011)
	RH2	LOC_Os01g32460	Suzuki et al. (2003)
	OsSRH1, OsSRH3		Ding et al. (2011, 2012)
	OsRHL1	LOC_Os06g8500	Ding et al. (2009)

C of the rice bHLH. It is highly homologous to members of subfamily 17 of the bHLH family in *Arabidopsis* (Ding et al., 2009).

OsSRH1 and *OsSRH3 are* two short hair genes. *OsSRH1* was mapped between markers T1757 and T1768 with a distance of 115 kb on chromosome 6. *OsSRH3* flanked by markers S38,978 and S39,016 on chromosome 1. The elongation of root hairs in both mutant is severely impaired (Ding et al., 2011, 2012). *OsEXPB5* is a root hair-specific *EXPB* gene that contains root hair-specific *cis*-elements (RHEs). It is thought to encode proteins that function more efficiently on cell wall modification during root hair morphogenesis (Won et al., 2010). *OsEXPA17* expresses in root hair cells. *OsexpA17* contains a point mutation, causing a change in the amino acid sequence. The mutant has short root hairs (Gly104 → Arg) (Yu et al., 2011).

3.1.4. Phytohormones controlling root growth

Phytohormones play vital functions in root growth. They not only control the initiation and elongation of radicle and adventitious roots, and also regulate the development of lateral roots and root hairs.

3.1.4.1. Auxin. The mutant *alf1* (altered lateral root formation) with shorter lateral roots displayed reduction in both the number and length of root hairs. It is related to altered auxin response or transport in which IBA is playing an important role (Debi et al., 2003).

There are 24 rice Aux/IAA homologous genes in the rice genome. *OsIAA3* is the first identified Aux/IAA gene that functions in lateral root development. *Osiaa3* showed auxin insensitivity, abnormal shoot and root gravitropism, and a defect in lateral root initiation (Nakamura et al., 2006). *OsIAA11* causes the inhibition of lateral root development (Zhu et al., 2011). It strictly blocks the initiation of lateral root primordia, but it does not affect crown root development. Expression of *OsIAA11* is located in root tips, lateral root caps, steles, and lateral root primordia. *Osiaa13* is a rice gain-of-function mutant. The number of lateral roots of mutant was significantly reduced, and the root gravitropic response was defective. OsIAA13 is involved in auxin signaling and controls the expression of genes that are required for lateral root initiation in rice (Kitomi et al., 2012).

The quiescent center (QC) is crucial to root development. *Osiaa23* is a semi-dominant mutant related QC development. It exhibits pleiotropic defects in root tissues, which includes the root cap, lateral and crown roots. Expression of *OsIAA23* is specific to the QC of the root tip during the development of primary, lateral and crown roots. The maintenance of the QC is dependent on OsIAA23-mediated auxin signaling (Ni et al., 2011).

The rice genome contains 12 putative *PIN* genes encoding auxin efflux transporters, including four *PIN1* and one *PIN2* genes. *OsPIN1* plays an important role in auxin-dependent adventitious root emergence and tillering. *OsPIN1* expresses in the vascular tissues and root primordial in a manner similar to *AtPIN1*(Xu et al., 2005). OsPIN3t acts in auxin polar transport but is also involved in the drought stress response. Overexpression of *OsPIN3t* led to improved drought tolerance, while knockdown of *OsPIN3t* caused crown root abnormalities in the seedling stage (Zhang et al., 2012c). OsARF12 is a transcription activator on auxin response genes, regulates root elongation and affects iron accumulation (Qi et al., 2012).

OsYUCCA1 is characterized to function in root formation. Over-expressing *OsYUCCA1* results in increased IAA level and adventitious root number, whereas rice expressing antisense *OsYUCCA1* cDNA displayed decreased adventitious root number (Yamamoto et al., 2007). *OsCOW1* encodes a member of the YUCCA protein family causes a phenotype of reduced adventitious root number and lower root to shoot ratios in rice (Woo et al., 2007).

WRKY transcription factors have many regulatory roles in response to biotic and abiotic stresses. *OsWRKY31* is a rice *WRKY* gene that encodes a polypeptide of 211 amino-acid residues and belongs to a subgroup of the rice *WRKY* gene family. Over-expression of the *OsWRKY31* exhibits reduced lateral root formation and elongation. *OsWRKY31* might alter the auxin response or transport and the defense response (Zhang et al., 2008).

OsRAA1 encodes a 12.0 kD protein that has 58% homology to the *AtFPF1* (Flowering Promoting Factor 1) in *Arabidopsis*. *OsRAA1* expresses specifically in the apical meristem, the elongation zone of root tip, steles of the branch zone, and the young lateral root. *OsRAA1* constitutive expression was induced by auxin, and caused longer leaves and sterile florets at the last stage of plant development. Over-expression of *OsRAA1* caused endogenous indole-3-acetic acid to increase (Ge et al., 2004). *OsRR2* is also an auxin response gene RR2 involved in rice adventitious root elongation (Zhao et al., 2009).

3.1.4.2. Cytokinin. As a WUSCHEL-related homeobox gene, *WOX11* is involved in the CK-regulated development of adventitious root. *WOX11* expresses in emerging crown roots and later in cell division regions of the root meristem, and its expression could be induced by exogenous application of auxin or cytokinin (Zhao et al., 2009). *WOX11* and *CRL5* are involved in different developmental stages of crown root formation through the regulation of cytokinin signaling. *WOX11* could be part of the positive feedback loop of auxin signaling.

OsMT2b is also involved in cytokinin-regulated adventitious root emergence and development, it encodes a metallothionein (Yuan et al., 2008). *OsMT2b* RNAi transgenic plants have serious defects in plant growth and root formation, whereas *OsMT2b* overexpressing transgenic plants are dwarfed with more adventitious roots and bigger lateral roots. Expression of *OsMT2b* could be suppressed by exogenous application of cytokinin.

3.1.4.3. Jasmonic acid. Jasmonic acid can also affect rice root growth. *OsRMC* affects rice root system development through a negative JA (jasmonic acid) pathway. It encodes a JA induced putative receptor-like protein of the DUF26 subfamily. RNAi transgenic rice cultured in the dark inhibits lateral root initiation and primary root elongation, but promotes the initiation and development of adventitious roots (Jiang et al., 2007).

3.2. Root physiological functions

3.2.1. Macro-mineral elements uptake

Although some progress on root physiological genetics has been achieved in recent years, a large number of genes involved in acquisition of nutrients through roots have been discovered (Table 3), it is still insufficient for understanding the functions of rice root at molecular level.

3.2.1.1. Nitrogen. There are three transport systems for the uptake of NO_3^- in plants roots: two high affinity transport systems (HATS: constitutive HATS, cHATS, and inducible HATS, iHATS) and one low-affinity transporter system (LATS) (King et al., 1993), and two for uptake of NH_4^+, one HATS and one LATS (Miller et al., 2001). Ammonium in comparison to nitrate as N source for rice promoted uptake and translocation of total N from root to shoot and resulted in higher shoot yield. Supply of the two forms of N showed the highest biomass yield of both roots and shoots and total N uptake (Li et al., 2006a).

In many natural and agricultural ecosystems, NH_4^+ is the predominant N source (Bijlsma and Lambers, 2000). NH_4^+ uptake

Table 3
Genes related to physiological functions of root.

Phenotype	Gene	Locus ID	Reference
N utilizaiton	*OsAMT1;1*	LOC_Os04g43070	Kumar et al. (2003)
	OsAMT1;2,	LOC_Os02g40730	Suenaga et al. (2003)
	OsAMT1;3	LOC_Os02g40710	Sonoda et al. (2003)
	OsAMT2;1	LOC_Os05g39240	Gaur et al. (2012)
	OsAMT2;3	LOC_Os01g61550	Gaur et al. (2012)
	OsGS1;1	LOC_Os02g50240	Tabuchi et al. (2005)
	OsGS1;2		Ishiyama et al. (2004)
	OsNR1		Li et al. (2006a)
	NRR	LOC_Os05g51690	Zhang et al. (2012b)
	OsNRT1	LOC_Os10g40600	Lin et al. (2000)
	OsNRT2	LOC_Os01g50820	Yan et al. (2011a)
P uptake	*OsLPT1*		Ming et al. (2005)
	OsMYB2P-1	LOC_Os05g4820	Dai et al. (2012)
	OsPAP10a	LOC_Os01g56880	Tian et al. (2012)
	Pup1 (PSTOL1)		Wissuwa et al. (1998); Gamuyao et al. (2012)
	OsPI1		Wasaki et al. (2003)
	OsPHT2;1		Shi et al. (2013)
	OsPHO2		Secco et al. (2012)
	OsPHR1	LOC_Os03g21240	Zhou et al. (2008)
	OsPHR2	LOC_Os07g25710	Liu et al. (2010)
	OsPT1-OsPT13		Sun et al. (2012); Ai et al. (2009); Shi et al. (2013); Paszkowski et al. (2002); Goff et al. (2002); Guimil et al. (2005); Wang et al. (2013b)
	OsPTF1	LOC_Os06g9370	Yi et al. (2005)
	OsSPX1	LOC_Os06g40120	Wang et al. (2009a)
	OsSPX2-OsSPX6		Wang et al. (2009b); Secco et al. (2012)
K uptake	*OsAKT1*		Fuchs et al. (2005)
	OsHAK1,3,4,6–17		Banuelos et al. (2002); Okada et al. (2008); Horie et al. (2011)
	OsHAK5		
K and Na uptake	*OsHAK2*	LOC_Os01g70940	Horie et al. (2011)
	OsHKT1 (OsHKT2;1)	LOC_Os06g48810	Kader et al. (2006)
	OSHKT2(OsHKT2;2);OsVHA		Horie et al. (2001)
	OsHKT4 (OsHKT;1)	LOC_Os04g51820	Garciadeblas et al. (2003)
	OsHKT8 (OsHKT1;5; SKC1)	LOC_Os01g20160	Ren et al. (2005)
	OsHKT1;4	LOC_Os04g51830	Cotsaftis et al. (2012)
	OsHKT2;4	LOC_Os06g48800	Sassi et al. (2012)
	OsNHX1	LOC_Os07g47100	Fukuda et al. (1999)
S uptake	*OsST1, OsST2*		Godwin (2002)
Mg uptake	*OsMGT*	LOC_Os01g64890	Cai et al. (2011)

by plant roots is mainly mediated by ammonium transporters (AMTs). There are 10 putative *OsAMT* genes, which are subdivided into four clades, three each for *OsAMT1*, *OsAMT2* and *OsAMT3*, and one for *OsAMT4.* Among them, *OsAMT2;1* encodes functional ammonium transporters and constitutively expresses in both roots and shoots irrespective of the supply of inorganic nitrogen to the medium, whereas OsAMT3;1 expression is relatively weak (Suenaga et al., 2003). *OsAMT1* is belong to the *AMT1* family, including *OsAMT1;1-1;3*, which plays a key role in the influx of NH_4^+ from low external NH_4^+ concentration (Kumar et al., 2003). Similar to its ortholog *AtAMT1;2* in *Arabidopsis* roots, OsAMT1;1 is abundantly expressed in rice roots and is little affected by change of the N supply form or N starvation (Gazzarrini et al., 1999). *OsAMT2*;3 belongs to *AMT2* family, its expression is affected by different doses of nitrogen (Gaur et al., 2012).

Nitrate transporters (NRTs) mediate nitrate uptake. There are seven *NRT2* genes encoding high-affinity nitrate transporters (Orsel et al., 2002) and over 50 *NRT1* genes encoding low affinity nitrate transporters (Williams and Miller, 2001) in *Arabidopsis thaliana*. *OsNRT1* is a constitutive low-affinity nitrate transporter gene (Lin et al., 2000). *OsNRT2* has the highest similarity to *AtNRT2;5* in protein sequence level (62%) among all members of *AtNRT2* in *Arabidopsis* (Li et al., 2006a). A two-component system for nitrate transport including NRT2s with a partner protein (NAR2 or NRT3.1) has been identified in *Arabidopsis*. Yan et al. (2011a) reported the physiological function of another member of the *NAR2* family, *OsNAR2.1* (Nipponbare), which mainly expressed in roots and induced by nitrate and suppressed by ammonium and some amino acids. NR (Nitrate reductase) responses to environments and circadian clock (Lillo et al., 2001). *OsNR1* was induced expression by exposure to nitrate. It might be regulated by nitrate in the short term and by both nitrate and total N supply status in the long term (Li et al., 2006a).

Rice plants possess three homologous but distinct genes for cytosolic glutamine synthetase (GS1): *OsGS1;1*, *OsGS1;2*, and *OsGS1;3*. OsGS1;1 is expressed in all organs tested with higher expression in leaf blades, while *OsGS1;3*, and *OsGS1;3* are expressed mainly in roots and spikelets, respectively (Sonoda et al., 2003; Tabuchi et al., 2005). In the report of Ishiyama et al. (2004), OsGS1;1 accumulated in dermatogens, epidermis and exodermises in rice roots under N-limited condition, while OsGS1;2 was abundantly expressed in the same cell layers under N (ammonium)-sufficient conditions. OsGS1;1 and OsGS1;2 were both induced by ammonium within the central cylinder of the elongating zone.

NRR (nutrition response and root growth) is alternatively spliced, producing two 5'-coterminal transcripts, *NRRa* and *NRRb*. Expression of *NRR* in rice seedling roots is significantly influenced by deficiency of macronutrients. *NRRa* and *NRRb* play negative regulatory roles in rice root growth, modulate the rice root architecture with the availability of macronutrients (Zhang et al., 2012b).

3.2.1.2. Phosphorus. The uptake and distribution of P in plants requires multiple P transport systems throughout growth and development. Vance et al. (2003) considered that an effective adaptation for enhancing P uptake was to increase root growth.

Wissuwa et al. (1998) mapped a major QTL, *pup1,* for P uptake to a 13-cM marker interval on the long arm of chromosome 12. Gamuyao et al. (2012) characterized this gene and named *PSTOL1*, it is the first phosphorus-efficiency gene identified in plants. The gene encodes a protein kinase enzyme that significantly enhances grain yield from rice plants grown on phosphorus-deficient soils.

The PHT1 and PHT2 families in plant function absorption and transportation of P. Thirteen putative high-affinity P transporter genes belonging to the Pht1 family (*OsPT1–OsPT13*) have been identified in the rice genome (Goff et al., 2002). OsPT1is involved in the OsPHO2-regulated P pathway (Sun et al., 2012). OsPT1 is a key member of the Pht1 family involved in P uptake and translocation under P-replete conditions. Expression of *OsPT13* is constitutively independent of P supply. OsPT2 is a low-affinity P transporter, expressed abundantly in P-starved roots and facilitate the transport of P from roots to shoot. OsPT6 plays a broad role in P uptake and translocation throughout the plant (Ai et al., 2009). *OsPT9* and *OsPT10* express in the root epidermis, root hairs and lateral roots, with their expression being specifically induced by P starvation (Wang et al., 2013c). OsPT8 is expressed in various tissues and organs and involved in P homeostasis in rice (Jia et al., 2011). OsPT11 and OsPT13, are exclusively induced in roots by inoculation with arbuscular mycorrhiza fungi. OsPT11 activation is independent of the nutritional status of the plant and phosphate availability in the rhizosphere (Paszkowski et al., 2002; Guimil et al., 2005). *OsPHT2;1*, a putative low affinity phosphate transporter gene, is involved in the P accumulation in leaves and P translocation through plants (Shi et al., 2013).

AtPHR1 plays a central role in phosphate (P)-starvation signaling in *Arabidopsis thaliana*. Two *OsPHR* genes *OsPHR1* and *OsPHR2* are involved in P-starvation signaling pathway by regulation of the expression of P-starvation-induced genes, whereas only *OsPHR2* over-expression results in the excessive accumulation of P in shoots under P-sufficient conditions. Under P-sufficient conditions, over-expression of *OsPHR2* mimics P-starvation stress in rice with enhanced root elongation and proliferated root hair growth (Zhou et al., 2008). As a ortholog of *AtPHR1, OsPHR2* positively regulates the low-affinity P transporter gene *OsPT2* by physical interaction and upstream regulation of *OsPHO2* in roots (Liu et al., 2010).

Arabidopsis thaliana SPX (SYG/PHO81/XPR1) domain genes have recently been shown to be involved in the phosphate signaling pathway. In plants, proteins harboring the SPX domain are classified into four families based on the presence of additional domains in their structure, namely the SPX, SPX–EXS, SPX–MFS and SPX–RING families. The genome of rice contains at least six genes exclusively with an SPX(SYG1/PHO81/XPR1) domain at the N-terminal, designated as *OsSPX1–6*. *OsSPX1* occurs downstream of *OsPHR2* and *PHO2*. OsSPX1 acts via a negative feedback loop to optimize growth under phosphate-limited conditions (Wang et al., 2009a). Meanwhile, Wang et al. (2009b) reported the diverse expression patterns of the *OsSPX* genes in different tissues and their responses to P-starvation. Among them, five genes, *OsSPX1,2,3,5* and *6* are responsive to P-starvation in shoots and/or in roots. OsSPX1 and OsSPX2 are exclusively located in nucleus, OsSPX3 is in the cytoplasm, and OsSPX4 is a membrane localized protein. OsSPX1 regulates OsSPX2,3 and 5 at the transcription level and is positively involved in the responses of the genes to P-starvation. OsSPX3 negatively regulates the PSI (P-starvation induced) gene *OsIPS1,* and is involved in the responses of *miR399* and *OsPHO2* to P-starvation (Secco et al., 2012).

An R2R3 MYB transcription factor, *OsMYB2P-1,* is induced by P-starvation. It is also associated with the regulation of root system architecture. Over-expression of *OsMYB2P-1* led to greater expression of P-responsive genes such as *Oryza sativa* UDP-sulfoquinovose synthase, *OsIPS1, OsPAP10, OsmiR399a*, and *OsmiR399j* (Dai et al., 2012). *OsLPT1* was a putative high-affinity phosphate (P) transporter gene with 1635-bp nucleotide sequence and encoding a polypeptide of 535 amino acids. Expression of *OsLPT1* in both leaves and roots was enhanced by P deprivation (Ming et al., 2005). Yi et al. (2005) cloned a P uptake gene *OsPTF1*. Wasaki et al. (2003) isolated P utilization gene *OsPI1* in root.

OsPAP10a belongs to group Ia of purple acid phosphatases (PAPs), and clusters with the principal secreted PAPs in a variety of plant species including *Arabidopsis*. Constitutive over-expression of *OsPAP10a* results in a significant increase of phosphatase activity in both shoot and root. *OsPAP10a* is a root-associated APase. *OsPAP10a* can potentially be used for crop breeding to improve the efficiency of P use (Tian et al., 2012).

3.2.1.3. Potassium and sodium. Potassium is an essential nutrient element for rice growth. K^+ plays vital roles in many aspects of cellular homeostasis including competing with sodium ion (Na^+) during potassium starvation and salt stress (Horie et al., 2011). Membrane transport of potassium can be mediated by potassium channels and secondary potassium transporters. Plant potassium transporters are presented in three families of membrane proteins: the K^+ uptake permeases (KT/HAK/KUP), the K^+ transporter (Trk/HKT) family and the cation proton antiporters (CPA) (Gierth and Mäser, 2007). In plants, the KT/HAK/KUP transporters form a large family. KT/HAK/KUP transporters serve various functions in various K traffic, but their physiological roles are still unclear.

At least seventeen genes (*OsHAK1–17*) encoding KT/HAK/KUP transporters are presented in the genome of rice. *OsHAK1* and *OsHAK16* are KT/HAK/KUP transporters of cluster I in rice, expression of the *OsHAK16* is induced by K starvation (Banuelos et al., 2002). The expression of *OsHAK1*, *OsHAK7*, and *OsHAK16* is much higher than that of other *OsHAK* genes (Okada et al., 2008). *OsHAK1* (cluster I) and *OsHAK12* (cluster III) are candidates for high-affinity Kuptake transporters in root. *OsHAK11* and *OsHAK12* (cluster III) are significantly induced by salt stress and K^+ starvation. OsHAK5 functions as a Na^+-insensitive K^+ transporter, while OsHAK2 is sensitive to extracellular Na^+ and exhibits higher Na^+ over K^+ transport activities. OsHAK5 is localized to the plant plasma membrane, it could be used as a tool to enhance salt tolerance in plant cells (Horie et al., 2011).

OsAKT1 is a potassium channel homologous of *AKT/KAT* subfamily. Expression of *AKT/KAT* is down-regulated under salt stress, and predominantly localized in root epidermis and endodermis. It encodes a K^+ uptake channel protein (Fuchs et al., 2005).

Excessive accumulation of sodium in plants causes toxicity. High-affinity K^+ transport systems are essential for preventing Na^+ toxicity. Under NaCl-dominated salt stress, the key for plant to survive is to maintain a low cytosolic Na^+ level or Na^+/K^+ ratio. In rice, eight functional HKT homologues (*OsHKT1, OsHKT3–9*) have been identified (Garciadeblas et al., 2003). OsHKT2;1 (OsHKT1) is a Na^+ transporter, and OsHKT2; 2 (OsHKT2) is a K^+/Na^+ cotransporter (Horie et al., 2001). *OsHKT2;1* is mainly expressed in the cortex and endodermis of roots. Na^+ can enhance growth of rice under K^+ starvation conditions, and that *OsHKT2;1* is the central transporter for nutritional Na^+ uptake into K^+-starved rice roots (Horie et al., 2007). OsHKT1, OsHKT2, and OsVHA (the vacuolar H^+-ATPase) also are sodium transporters, which function in maintaining cytosolic Na^+ homeostasis (Kader et al., 2006). *SKC1* (*OsHKT8*) functions as a Na^+-selective transporter. *OsHKT8* is involved in regulating K^+/Na^+ homeostasis under salt stress, providing a potential tool for improving salt tolerance in crops (Ren et al., 2005). OsHKT1;4 and OsHKT2;4 are responsive to K and Na accumulation and transporter (Cotsaftis et al., 2012; Sassi et al., 2012).

OsNHX1 functions as a Na^+/H^+ exchanger, it has high homology with a putative Na^+/H^+ exchanger in *Saccharomyces cerevisiae*, NHX1. *OsNHX1* is 2330 bp in length with an open reading frame of 1608 bp. The deduced amino acid shares high similarity with that of NHX1 and NHE isoforms in mammals. Expression of *OsNHX1* can be induced by salt stress (Fukuda et al., 1999).

3.2.1.4. Magnasium and sulphur. *OsST1* and *OsST2* encode putative sulfate transporters. Both proteins with predicted topologies of 12 membrane spanning domains and possess signature sequences of the $H^+/ H_2S0_4^{2-}$ symporter family of transporters. *OsST1* expresses strongly in roots with levels of expression being strongly enhanced by sulphate starvation. Expression of *OsST1* is localized in the main absorptive region of roots especially in all cells within a few millimeters of the root tip, and the tips of emerging laterals. It is responsible for uptake of sulfate from the soil solution. *OsST1* is predicted to be a plastidic sulfate transporter possessing a typical plastid-targeting transit peptide (Godwin, 2002).

A putative Mg absorption gene *OsMGT* showed down- and up-regulation in the rice root by K starvation (Cai et al., 2011).

3.2.2. Micro-mineral elements uptake

3.2.2.1. Iron. As an essential micro mineral element, iron plays a vital role in rice production. *OsIRT1* is highly homologous with Fe (II) transport gene *IRT1* of *Arabidopsis*. *OsIRT1* is induced by Fe and Cu deficiency and expressed in root (Bughio et al., 2002) (Table 4).

Nicotianamine (NA) is a chelator of metals. It is a biosynthetic precursor of phytosiderophores and is thus a crucial component for iron (Fe) acquisition in graminaceous plants. Three rice NA synthase (NAS) genes, *OsNAS1, OsNAS2*, and *OsNAS3* express in cells and are involved in long-distance transport of Fe, and differentially regulated by Fe. *OsNAS1* and *OsNAS2* transcripts were detected in Fe-sufficient roots but not in leaves, while *OsNAS2* transcript was present in leaves but was very low in roots of Fe-sufficient plants. *OsNAS2* expression was induced in roots but was suppressed in leaves in response to Fe deficiency (Inoue et al., 2003). *NAAT1* encodes nicotianamine aminotransferase in rice. The mutant failed to produce deoxymugineic acid and could not absorb Fe(III) efficiently. The disruption of deoxymugineic acid biosynthesis can stimulate Fe(II) acquisition and increase iron accumulation in rice (Cheng et al., 2007a).

There are 18 putative *yellow stripe 1* (*YS1*)-*like* genes (*OsYSLs*) in rice, that exhibited 36–76% sequence similarity to maize iron(III)-phytosiderophore transporter YS1. *OsYSL2* encodes a polypeptide of 674 amino acids containing 14 putative transmembrane domains, and expresses in companion cells in iron sufficient roots. OsYSL2 transports iron(II)-nicotianamine (NA) and manganese(II)-NA, but did not transport iron(III)- phyosiderophore (Koike et al., 2004). *OsYSL15* expresses in the epidermis/exodermis and phloem cells under conditions of iron deficiency in roots. OsYSL15 is the dominant iron(III)-deoxymugineic acid transporter responsible for iron uptake from the rhizosphere and is also responsible for phloem transport of iron (Inoue et al., 2009). OsYSL16 has 85% similarity to both OsYSL15 and the iron(II)-nicotianamine transporter OsYSL2 (Kakei et al., 2012). *OsYSL18* is predicted to encode a polypeptide of 679 amino acids containing 13 putative transmembrane domains. OsYSL18 is an iron phytosiderophore transporter involved in the translocation of iron in reproductive organs and phloem in joints. In vegetative organs, OsYSL18 is specifically expressed in lamina joints, the inner cortex of crown roots, and phloem parenchyma and companion cells at the basal part of every leaf sheath (Aoyama et al., 2009). *OsIRO2* is a key gene in Fe(III)-MAs (Mugineic acid family phytosiderophores) transport and absorption system. Its over-expression will increases MAs secretion in root system. Once this gene is restricted, the rice plant will present symptoms of iron deficiency. It functions as a transcriptional activator and regulated 59 Fe-deficiency-induced genes in roots (Ogo et al., 2007).

Multidrug and toxic compound extrusion (MATE) transporters represent a large family in plants. A rice MATE gene, *OsFRDL1*, the closest ortholog of barley *HvAACT1* (aluminum [Al]-activated citrate transporter 1), is a citrate transporter localized at the pericycle cells, which is necessary for efficient translocation of Fe to the shoot. It mainly expressed in the roots and the expression level was not affected by either Fe deficiency or Al toxicity (Yokosho et al., 2009).

OsbHLH133 is induced by Fe-deficiency. Insertional inactivation of *OsbHLH133 (bhlh133)* resulted in growth retardation, with enhanced Fe concentration in shoots, and reduced Fe concentration

Table 4
Genes related to utilization of water and micronutrients.

Phenotype	Gene	Locus ID	Reference
Fe utilization	*OsbHLH133*	LOC_Os12g32400	Wang et al. (2013b)
	OsFRDL1	LOC_Os03g11734	Yokosho et al. (2009)
	OsIRO2	LOC_Os01g72370	Ogo et al. (2007)
	OsIRT1	LOC_Os03g46470	Bughio et al. (2002)
	OsNAS1	LOC_Os03g19427	Inoue et al. (2003)
	OsNAS2	LOC_Os03g19420	Inoue et al. (2003)
	OsNAS3	LOC_Os07g48980	Inoue et al. (2003)
	NAAT1	LOC_Os02g20360	Cheng et al. (2007a)
	OsYSL2	LOC_Os02g43370	Koike et al. (2004)
	OsYSL15	LOC_Os02g43410	Inoue et al. (2009)
	OsYSL16	LOC_Os04g45900	Kakei et al. (2012)
	OsYSL18	LOC_Os01g61390	Aoyama et al. (2009)
Si acquisition	*LSI1*	LOC_Os02g51110	Ma et al. (2006)
Cd accumulation	*OsHMA2*	LOC_Os06g48720	Takahashi et al. (2012)
	OsHMA3(qCdT7)	LOC_Os07g12900	Ueno et al. (2010)
	OsHMA9	LOC_Os06g45500	Lee et al. (2007)
Water acquisition	*OsPIP1,2,4,5,7;*		Guo et al. (2006)
	OsTIP4;1		Sakura et al. (2005)
Abiotic stress tolerance	*MAIF1*		Yan et al. (2011b)
	OsMSR2	LOC_Os01g72530	Xu et al. (2013)
	OsNAC9	LOC_Os03g60080	Redillas et al. (2012)
	OsNAC10	LOC_Os11g3300	Jeong et al. (2010)
	OsNAC45		Zheng et al. (2009)

in roots. Over-expression of *OsbHLH133* had the opposite effect, resulted in an enhanced Fe concentration in roots and reduced Fe concentration in shoots and also in xylem sap (Wang et al., 2013b).

3.2.2.2. Silicon. Rice is a typical silicon-accumulating plant. Silicon is essential for high and sustainable production of rice, it is helpful to overcome abiotic and biotic stresses by preventing lodging and increasing resistance to pests and diseases, as well as other stresses. *Low silicon rice 1* (*Lsi1*) gene controls silicon accumulation. *Lsi1* belongs to the aquaporin family and is constitutively expressed in the roots. Lsi1 is localized on the plasma membrane of the distal side of both exodermis and endodermis cells, where casparian strips are located. Suppression of *Lsi1* expression resulted in reduced silicon uptake (Ma et al., 2006).

3.2.3. Water acquisition

It is well known that plant aquaporins serve to water uptake in root and water transport through whole plant. Aquaporins are membrane proteins that belong to the major intrinsic protein (MIP) family, with members found in nearly all living organisms (Agre et al., 1998). Plant aquaporins include four major subfamilies: plasma-membrane intrinsic proteins (PIPs), tonoplast intrinsic proteins (TIPs), Nod26-like intrinsic proteins (NIPs), and small and basic intrinsic proteins (SIPs), which enable fast and controlled translocation of water across the membrane. Researches on aquaporins in rice mostly focused on PIPs. Thirty-three genes for aquaporins in rice have been identified, of which six genes, including *OsPIP2;4* and *OsPIP2;5*, express predominantly in roots. 14 genes, including *OsPIP2;7* and *OsTIP1;2*, are found in leaf blades. Eight genes, such as *OsPIP1;1* and *OsTIP4;1*, express in leaf blades, roots and anthers (Sakura et al., 2005). There are 10 rice *PIP* genes (*OsPIPs*) that are classified into two subgroups (*OsPIP1* and *OsPIP2*), of which three members *OsPIP1–3*, *OsPIP2–2*, and *OsPIP2–7* are root specific in seedlings (Guo et al., 2006).

There are 140 *NAC* (NAM–ATAF–CUC) genes predicted in rice, 18 are identified to be induced by stress conditions. *OsNAC9* may account for the altered root architecture conferring increased drought resistance phenotype (Redillas et al., 2012). *OsNAC10* expresses predominantly in roots and panicles and is induced by drought, high salinity, and abscisic acid (ABA). The root-specific over-expression of *OsNAC10* enlarges roots, enhancing drought tolerance of transgenic plants, which increases grain yield significantly under field drought conditions (Jeong et al., 2010). *OsNAC045* is induced by drought, high salt, and low temperature stresses, and ABA. It encodes a novel stress-responsive NAC transcription factor and is potentially useful for engineering drought and salt tolerant rice (Zheng et al., 2009).

OsMSR2 is a calmodulin-like gene induced by cold, drought and heat, mainly expresses in root, leaf, seedling, lamina joint, base of stem and spikelet. Over-expression of *OsMSR2* showed more tolerance to salt stress (Xu et al., 2013).

F-box domain proteins is one of the largest gene families, they have important roles in regulating various developmental processes and stress responses. Expression of rice F-box domain gene, *MAIF1,* is induced rapidly and strongly by ABA and abiotic stresses. *MAIF1* expression is also induced in root tips by sucrose, independent of its hydrolytic hexose products, glucose and fructose, and the plant hormones auxin and cytokinin. Over-expression of *MAIF1* reduces rice ABA sensitivity and abiotic stress tolerance and promotes rice root growth (Yan et al., 2011b).

3.2.4. Accumulation of toxic trace elements

Toxic trace elements (Pb, As, Hg and Cd, etc.) pollutions in food have posed a threat to human health. Cadmium (Cd) is highly toxic for all organisms. It has been elucidated that the Cd was associated with cancers of the prostate, lungs, and testes, kidney tubule damages, rhinitis, emphysema, and bone fractures (Nawrot et al., 2006; Bertin and Averbeck, 2006). Therefore, it is necessary to limit Cd into the food chain from soil to reduce potential health risks to humans. As an important staple food, rice is a major source of Cd intake (Cheng et al., 2006; Watanabe et al., 2004). Some genetic studies on Cd accumulation in rice grain have been done, and several QTLs were detected and mapped (Ishikawa et al., 2010; Xue et al., 2009). There are several families of transporters that mediate Cd uptake and transport, including Zip and Nramp, ABC, Ysl, Copt, Heavy metal ATPases (CPX-type), Ca_2^+-ATPases, Cation/H^+ antiporters, and GNGC (Clemens, 2001; Colangelo and Guerinot, 2006; Williams et al., 2000). More than 30 genes related to Cd uptake, transportation and accumulation have been characterized in rice (Sebastian and Prasad, 2014). Among them, P_{1B}-type heavy metal ATPase (HMAs) play a very important role in Cd uptake and accumulation. Expression of *OsHMA9* is induced by a high concentration of Cu, Zn, and Cd (Lee et al., 2007). *OsHMA2* is related to Cd transportation, and also response to Zn transportation through rice plant (Takahashi et al., 2012). *OsHMA3* is responsible for low Cd accumulation. It encodes a transporter belonging to the P_{1B}-type ATPase family, shares low similarity with other members. It is fascinating that over-expression of the functional gene from the low Cd-accumulating cultivar selectively decreased accumulation of Cd, but not other micronutrients in the grain. OsHMA3 limits translocation of Cd from the roots to the above-ground tissues by selectively sequestrating Cd into the root vacuoles (Ueno et al., 2010). This gene would contribute to selection and breeding of rice cultivars with low Cd accumulation in the grain.

4. Problems and prospects

Although increasing knowledge on rice root has given an insight into mechanisms of root development, it remains unclear what root traits should be taken into account in rice breeding programs. There are difficulties that hampered progress of root genetics: research efforts devoted to the root system have been much less than to the above ground part. Lacking stable and credible morphological data makes it difficult to perform genetic research on rice root traits (De Dorlodot et al., 2007).

Since Hales carried out root research with excavation method as early as 1727, a number of approaches, such as root box, pin-board, minirhizotrons, CT scans, gel-based imaging have been improved for root studies. Recent years, computer assistant image analysis have been developed quickly (see Root Methods, Smit et al., 2000). The synchrotron X-ray computed tomography has been used as a noninvasive method to observe how aerenchyma develops from rice primary root (Karahara et al., 2012). A three-dimensional imaging technique allows to perform a quantitative morphological analysis and time-course, and also in-situ observations of aerenchyma formation to phenotype root traits during seedlings development (Clark et al., 2011).

However, many methods are still time-consuming and laborious, and largely influenced by the complex underground environments. Root sampling procedures are often destructive. It is impossible to sample intact root system from plants in field environments. Soilless culture techniques have provided a simple and convenient methods with which the whole root system could be extracted from the plants. But the soilless culture system could not completely mimic the environments of paddy field, thus the information obtained in soilless culture usually do not exactly reflect root feature under natural conditions. For identifying and screening the root traits, more facilitated and effective methods, especially the large-scale screening techniques for root measurement in paddy field are urgently required.

Quantitative trait loci (QTL) mapping is a major approach for investigating complex genetic traits such as root, but QTL were not

fine-mapped with appropriate selectable markers, the desired gene might have been lost in the selection process (Gowda et al., 2011). To cope with this problem, association mapping(meta-analysis) as a promising method was introduced to genetic dissection of complex traits. Using association mapping, it is possible to locate QTLs with better precision than using a mapping population (Courtois et al., 2009, 2013). Among the large number of root QTLs identified in past decades, few major QTLs have been cloned and introgressed into another background (Shen et al., 2001). Introduction of *DRO1* into a shallow-rooting rice cultivar was a successful practice. It enabled the resulting line to avoid drought by increasing deep rooting, which maintained high yield performance under drought conditions relative to the recipient cultivar(Uga et al., 2013). *SUBMERGENCE 1 (SUB1)* is a robust quantitative trait locus from the submergence tolerant FR13A landrace. The marker-assisted introgression of the *SUB1* region has successfully improved submergence tolerance in a wide range of mega-varieties without any penalties on development, yield, and grain quality (Bailey-Serres et al., 2010).

Compared with QTL mapping, exploring beneficial genes with root mutants is a more efficient approach, and a number of genes reported are explored through root mutants. In addition, a number of genome-wide large-scale studies have been performed (Takehisa et al., 2012; Zhai et al., 2013). These provide researches useful techniques to unveil molecular mechanisms of root development. For example, transcriptome analysis of rice mature root tissue and root tips at two time points identified 1761 root-enriched transcripts and 306 tip-enriched transcripts involved in different physiological processes (Kyndt et al., 2012).

As mentioned by Den Herder et al. (2010), now is the time to improve the plant's capacity for uptake and fixation of nutrients and the focus should be on improving the root system. To achieve a high-yield and eco-friendly agriculture, an enormous effort on a political, economical and social level will be required. With the increasing number of the identified genes related with root traits, the combination of MAS (marker-assisted selection), conventional approaches, and genetic engineering, would make it possible to develop further grain yield varieties with ideal type root system in the near future.

Acknowledgement

The work was supported by grants from the National Program on Super Rice Breeding, the Ministry of Agriculture of China.

References

Agre, P., Bonhivers, M., Borgnia, M.J., 1998. The aquaporins, blueprints for cellular plumbing systems. J. Biol. Chem. 273, 14659–14662.
Ai, P.H., Sun, S.B., Zhao, J.N., Fan, X.R., Xin, W.J., Guo, Q., Yu, L., Shen, Q.R., Wu, P., Miller, A.J., Xu, G.H., 2009. Two rice phosphate transporters, OsPht1;2 and OsPht1;6, have different functions and kinetic properties in uptake and translocation. Plant J. 57, 798–809.
Aoyama, T., Kobayashi, T., Takahashi, M., Nagasaka, S., Usuda, K., Kakei, Y., Ishimaru, Y., Nakanishi, H., Mori, S., Nishizawa, N.K., 2009. OsYSL18 is a rice iron(III)-deoxymugineic acid transporter specifically expressed in reproductive organs and phloem of lamina joints. Plant Mol. Biol. 70, 681–692.
Bailey-Serres, J., Fukao, T., Ronald, P., Ismail, A., Heuer, S., Mackill, D., 2010. Submergence tolerant rice: SUB1's journey from landrace to modern cultivar. Rice 3, 138–147. doi:http://dx.doi.org/10.1007/s12284-010-9048-5.
Bano, A., Dorffling, K., Bettin, D., Hahn, H., 1993. Abscisic acid and cytokinins as possible root-to-shoot signals in xylem sap of rice plants in drying soil. Aus. J. Plant Physiol. 20, 109–115.
Banuelos, M.A., Garciadeblas, B., Cubero, B., Rodríguez-Navarro, A., 2002. Inventory and functional characterization of the HAK potassium transporters of rice. Plant Physiol. 130, 784–795.
Barrett-Lennard, E.G., 2003. The interaction between waterlogging and salinity in higher plants: causes, consequences and implications. Plant Soil 253, 35–54.
Bertin, G., Averbeck, D., 2006. Cadmium: cellular effects, modifications of biomolecules, modulation of DNA repair and genotoxic consequences (a review). Biochimie 88, 1549–1559.
Bijlsma, R.J., Lambers, H., 2000. A dynamic whole-plant model of integrated metabolism of nitrogen and carbon. 2. Balanced growth driven by C fluxes and regulated by signals from C and N substrate. Plant Soil 220, 71–87.
Bughio, N., Yamaguchi, H., Nishizawa, N.K., Nakanishi, H., Mori, S., 2002. Cloning an iron-regulated metal transporter from rice. J. Exp. Bot. 53, 1677–1682.
Cai, J., Chen, L., Qu, H.Y., Lian, J., Liu, W., Hu, Y.B., Xu, G.H., 2011. Alteration of nutrient allocation and transporter genes expression in rice under N, P, K, and Mg deficiencies. Acta Physiol. Plant 34, 939–946.
Carvalhais, L.C., Dennis, P.G., Fedoseyenko, D., Hajirezaei, M.R., Borriss, R., Von Wirén, N., 2011. Root exudation of sugars, amino acids, and organic acids by maize as affected by nitrogen, phosphorus, potassium, and iron deficiency. J. Plant Nutr. Soil Sci. 174, 3–11.
Chang, T.T., Loresto, G.C., Toole, O', Armenta-soto, J.L., 1982. Strategy and methodology of breeding rice for drought-prone areas. Drought resistance in crops with emphasis on rice. IRRI 217–244.
Chen, X., Shi, J., Hao, X., Liu, H., Shi, J., Wu, Y., Wu, Z., Chen, M., Wu, P., Mao, C., 2013. *OsORC3* is required for lateral root development in rice. Plant J. 74, 339–350. doi:http://dx.doi.org/10.1111/tpj.12126.
Cheng, F., Zhao, N., Xu, H., Li, Y., Zhang, W., Zhu, Z., Chen, M., 2006. Cadmium and lead contamination in japonica rice grains and its variation among the different locations in southeast China. Sci. Total Environ. 359, 156–166.
Cheng, L., Wang, F., Shou, H., Huang, F., Zheng, L., He, F., Li, J., Zhao, F.J., Ueno, D., Ma, J.F., Wu, P., 2007a. Mutation in nicotianamine aminotransferase stimulated the Fe(II) acquisition system and led to iron accumulation in rice. Plant Physiol. 145, 1647–1657.
Cheng, S.H., Cao, L.Y., Zhuang, J.Y., Chen, S.G., Zhan, X.D., Fan, Y.Y., Zhu, D.F., Min, S. K., 2007b. Super hybrid rice breeding in China: achievements and prospects. J. Integr. Plant Biol. 49, 805–810.
Cheng, S.H., Zhuang, J.Y., Fan, Y.Y., Du, J.H., Cao, L.Y., 2007c. Progress in research and development on hybrid rice: a super-domesticate in China. Ann. Bot. 100, 959–966.
Chhun, T., Taketa, S., Tsurumi, S., Ichii, M., 2003a. The effects of auxin on lateral root initiation and root gravitropism in a lateral rootless mutant *Lrt1* of rice (*Oryza sativa* L.). Plant Growth Regul. 39, 161–170.
Chhun, T., Taketa, S., Tsurumi, S., Ichii, M., 2003b. Interaction between two auxin-resistant mutants and their effects on lateral root formation in rice (*Oryza sativa* L.). J. Exp. Bot. 54, 2701–2708.
Cho, S.H., Yoo, S.C., Zhang, H., Pandeya, D., Koh, H.J., Hwang, J.Y., Kim, G.T., Paek, N.C., 2013. The rice narrow leaf2 and narrow leaf3 loci encode WUSCHEL-related homeobox 3A (OsWOX3A) and function in leaf, spikelet, tiller and lateral root development. New Phytol. 198, 1071–1084.
Clark, R.T., MacCurdy, R.B., Jung, J.K., Shaff, J.E., McCouch, S.R., Aneshansley, D.J., Kochian, L.V., 2011. Three-dimensional root phenotyping with a novel imaging and software platform. Plant Physiol. 156, 455–465.
Clemens, S., 2001. Molecular mechanisms of plant metal tolerance and homeostasis. Planta 212, 475–486.
Colangelo, E.P., Guerinot, M.L., 2006. Put the metal to the petal: metal uptake and transport throughout plants. Curr. Opin. Plant Biol. 9, 322–330.
Cotsaftis, O., Plett, D., Shirley, N., Tester, M., Hrmova, M., 2012. A two-staged model of Na^+ exclusion in rice explained by 3D modeling of HKT transporters and alternative splicing. PLoS One 7, e39865.
Courtois, B., Ahmadi, N., Khowaja, F., Price, A.H., Rami, J.F., Frouin, J., Hamelin, C., Ruiz, M., 2009. Rice root genetic architecture: meta-analysis from a drought QTL database. Rice 2, 115–128.
Courtois, B., Audebert, A., Dardou, A., Roques, S., Ghneim-Herrera, T., Droc, G., Frouin, J., Rouan, L., Gozé, E., Kilian, A., Ahmadi, N., Dingkuhn, M., 2013. Genome-wide association mapping of root traits in a Japonica rice panel. PLoS One 8, e78037. doi:http://dx.doi.org/10.1371/journal.pone.0078037.
Cui, H.C., Levesque, M.P., Vernoux, T., Jung, J.W., Paquette, A.J., Gallagher, K.L., Wang, J.Y., Blilou, I., Scheres, B., Benfey, P.N., 2007. An evolutionarily conserved mechanism delimiting SHR movement defines a single layer of endodermis in plants. Science 316, 421–425. doi:http://dx.doi.org/10.1126/science.1139531.
Dai, X.Y., Wang, Y.Y., Yang, A., Zhang, W.H., 2012. *OsMYB2P-1*, an R2R3 MYB transcription factor, is involved in the regulation of phosphate-starvation responses and root architecture in rice. Plant Physiol. 159, 169–183.
Dat, T.V., 1986. An overview of upland rice in the world. Progress in Upland Rice Research. Proceeding of Jakarta Conference, IRRI Los Banos, Philippines.
De Dorlodot, S., Forster, B., Pages, L., Price, A., Tuberosa, R., Draye, X., 2007. Root system architecture: opportunities and constraints for genetic improvement of crops. Trends Plant Sci. 12, 474–481.
Debi, B.R., Mushika, J., Taketa, S., Miyao, A., Hirochika, H., Ichii, M., 2003. Isolation and characterization of a short lateral root mutant in rice (*Oryza sativa* L.). Plant Sci. 165, 895–903.
Den Herder, G., Van Isterdael, G., Beeckman, T., De Smet, I., 2010. The roots of a new green revolution. Trends Plant Sci. 15, 600–607.
Ding, W.N., Yu, Z.M., Tong, Y.L., Huang, W., Chen, H.M., Wu, P., 2009. A transcription factor with a bHLH domain regulates root hair development in rice. Cell Res. 19, 1309–1311.
Ding, N., Tong, Y.L., Wu, J.R., Zhu, S.H., 2011. Identification and gene mapping of a novel short root hair mutant in rice. Sci. Agr. Sinica 4333–4339. doi:http://dx.doi.org/10.3864/j.issn.0578-1752.2011.21.001.
Ding, W.N., Huang, W., Ning, Y.Q., Zhu, S.H., 2012. Genetic analysis and gene mapping of a novel short root hair mutant in rice. Acta Agron. Sinica 38, 240–244.
E, Z.G., Ge, L., Wang, L., 2012. Molecular mechanism of adventitious root formation in rice. Plant Growth Regul. 68, 325–331.

Ekanayake, I.J., O'Toole, J.C., Garrity, D.P., Masajo, T.M., 1985. Inheritance of root characters and their relations to drought resistance in rice. Crop Sci. 25, 927–933. doi:http://dx.doi.org/10.2135/cropsci1985.0011183X002500060007.x.

Fitter, A., 2002. Characteristics and functions of root system, Plant Root. Third Edition Marcel Dekker Inc, New York.

Fuchs, I., Stölzle, S., Ivashikina, N., Hedrich, R., 2005. Rice K^+ uptake channel OsAKT1 is sensitive to salt stress. Planta 221, 212–221.

Fukuda, A., Nakamura, A., Tanaka, Y., 1999. Molecular cloning and expression of the Na^+/H^+ exchanger gene in *Oryza sativa*. Biochimi. Biophys. Acta (BBA) Gene Struct. Expr. 1446, 149–155.

Fustuhara, Y., Kitano, H., 1985. Inheritance of a root-growth inhibiting mutant in rice. Rice Genet. Newslett. 2, 70–71.

Gamuyao, R., Chin, J.H., Pariasca-Tanaka, J., Pesaresi, P., Catausan, S., Dalid, C., Slamet-Loedin, I., Tecson-Mendoza, E.M., Wissuwa, M., Heuer, S., 2012. The protein kinase Pstol1 from traditional rice confers tolerance of phosphorus deficiency. Nature 488, 535–539. doi:http://dx.doi.org/10.1038/nature11346.

Garciadeblas, B., Senn, M.E., Banuelos, M.A., Rodriguez-Navarro, A., 2003. Sodium transport and HKT transporters: the rice model. Plant J. 34, 788–801.

Gaur, V.S., Singh, U.S., Gupta, A.K., Kumar, A., 2012. Influence of different nitrogen inputs on the members of ammonium transporter and glutamine synthetase genes in two rice genotypes having differential responsiveness to nitrogen. Mol. Biol. Rep. 39, 8035–8044. doi:http://dx.doi.org/10.1007/s11033-012-1650-8.

Gazzarrini, S., Lejay, L., Gojon, A., Ninnemann, O., Frommer, W.B., Von Wiren, N., 1999. Three functional transporters for constitutive, diurnally regulated, and starvation-induced uptake of ammonium into *Arabidopsis* roots. Plant Cell 11, 937–948.

Ge, L., Chen, H., Jiang, J.F., Zhao, Y., Xu, M.L., Xu, Y.Y., Tan, K.H., Xu, Z.H., Chong, K., 2004. Overexpression of *OsRAA1* causes pleiotropic phenotypes in transgenic rice plants, including altered leaf, flower, and root development and root response to gravity. Plant Physiol. 135, 1502–1513.

Gierth, M., Mäser, P., 2007. Potassium transporters in plants—involvement in K acquisition, redistribution and homeostasis. FEBS Lett. 581, 2348–2356.

Giles, J., 2005. Nitrogen study fertilizes fears of pollution. Nature 433, 791.

Godwin, R.M., 2002. Cloning and characterization of genes encoding phosphate and sulphate transporters from rice. Ph.D. Thesis. The University of Queensland.

Goff, S.A., Ricke, D., Lan, T.H., Presting, G., Wang, R., Dunn, M., Glazebrook, J., Sessions, A., Oeller, P., Varma, H., Hadley, D., Hutchison, D., Martin, C., Katagiri, F., Lange, B.M., Moughamer, T., Xia, Y., Budworth, P., Zhong, J., Miguel, T., Paszkowski, U., Zhang, S., Colbert, M., Sun, W.L., Chen, L., Cooper, B., Park, S., Wood, T.C., Mao, L., Quail, P., Wing, R., Dean, R., Yu, Y., Zharkikh, A., Shen, R., Sahasrabudhe, S., Thomas, A., Cannings, R., Gutin, A., Pruss, D., Reid, J., Tavtigian, S., Mitchell, J., Eldredge, G., Scholl, T., Miller, R.M., Bhatnagar, S., Adey, N., Rubano, T., Tusneem, N., Robinson, R., Feldhaus, J., Macalma, T., Oliphant, A., Briggs, S., 2002. A draft sequence of the rice genome (*Oryza sativa* L. ssp. japonica). Science 296, 92–100.

Gowda, V.R.P., Henry, A., Yamauchi, A., Shashidhar, H.E., Serraj, R., 2011. Root biology and genetic improvement for drought avoidance in rice. Field Crops Res. 122, 1–13.

Grayston, S.J., Vaughan, D., Jones, D., 1996. Rhizosphere carbon flow in trees, in comparison with annual plants: the importance of root exudation and its impact on microbial activity and nutrient availability. Appl. Soil Ecol. 5, 29–56.

Guimil, S., Chang, H.S., Zhu, T., Sesma, A., Osbourn, A., Roux, C., Ioannidis, V., Oakeley, E.J., Docquier, M., Descombes, P., Briggs, S.P., Paszkowski, U., 2005. Comparative transcriptomics of rice reveals an ancient pattern of response to microbial colonization. Proc. Natl. Acad. Sci. 102, 8066–8070.

Guo, L., Wang, Z.Y., Lin, H., Cui, W.E., Chen, J., Liu, M.H., Chen, Z.L., Qu, L.J., Gu, H.Y., 2006. Expression and functional analysis of the rice plasma-membrane intrinsic protein gene family. Cell Res. 16, 277–286.

Hong, S.K., Aoki, T., Kitano, H., Satoh, H., Nagato, Y., 1995. Phenotypic diversity of 188 rice embryo mutants. Dev. Genet. 16, 298–310.

Horie, T., Yoshida, K., Nakayama, H., Yamada, K., Oiki, S., Shinmyo, A., 2001. Two types of HKT transporters with different properties of Na^+ and K^+ transport in *Oryza sativa*. Plant J. 27, 129–138.

Horie, T., Costa, A., Kim, T.H., Han, M.J., Horie, R., Leung, H.Y., Miyao, A., Hirochika, H., An, G., Schroeder, J.I., 2007. Rice OsHKT2;1 transporter mediates large Na^+ influx component into K^+ starved roots for growth. EMBO J. 26, 3003–3014.

Horie, T., Sugawara, M., Okada, T., Taira, K., Kaothien-Nakayama, P., Katsuhara, M., Shinmyo, A., Nakayama, H., 2011. Rice sodium-insensitive potassium transporter, OsHAK5, confers increased salt tolerance in tobacco BY2 cells. J. Biosci. Bioeng. 111, 346–356.

Horii, H., Nemoto, K., Miyamoto, N., Harada, J., 2006. Quantitative trait loci for adventitious and lateral roots in rice. Plant Breed. 125, 198–200.

Ichii, M., Ishikawa, M., 1997. Genetic analysis of newly induced short-root mutants in rice (*Oryza sativa*). Breed. Sci. 47, 121–125.

Inoue, H., Higuchi, K., Takahashi, M., Nakanishi, H., Mori, S., Nishizawa, N.K., 2003. Three rice nicotianamine synthase genes, *OsNAS1, OsNAS2*, and *OsNAS3* are expressed in cells involved in long-distance transport of iron and differentially regulated by iron. Plant J. 36, 366–381.

Inoue, H., Kobayashi, T., Nozoye, T., Takahashi, M., Kakei, Y., Suzuki, K., Nakazono, M., Nakanishi, H., Mori, S., Nishizawa, N.K., 2009. Rice OsYSL15 is an iron-regulated iron(III)-deoxymugineic acid transporter expressed in the roots and is essential for iron uptake in early growth of the seedlings. J. Biol. Chem. 284, 3470–3479. doi:http://dx.doi.org/10.1074/jbc.M806042200.

Inukai, Y., Miwa, M., Nagato, Y., Kitano, H., Yamauchi, A., 2001. *RRL1, RRL2* and *CRL2* loci regulating root elongation in rice. Breed. Sci. 51, 231–239.

Inukai, Y., Miwa, M., Nagato, Y., Kitano, H., Yamauchi, A., 2003. Mechanical stimulus-sensitive mutation, *rrl3*, affects the cell production process in the root meristematic zone in rice. Plant Prod. Sci. 6, 265–273.

Inukai, Y., Sakamoto, T., Ueguchi-Tanaka, M., Shibata, Y., Gomi, K., Umemura, I., Hasegawa, Y., Ashikari, M., Kitano, H., Matsuoka, M., 2005. *Crown rootless1*, which is essential for crown root formation in rice, is a target of an AUXIN RESPONSE FACTOR in a Auxin signaling. Plant Cell 17, 1387–1396.

Ishikawa, S., Abe, T., Kuramata, M., Yamaguchi, M., Ando, T., Yamamoto, T., Yano, M., 2010. A major quantitative trait locus for increasing cadmium specific concentration in rice grain is located on the short arm of chromosome 7. J. Exp. Bot. 61, 923–934. doi:http://dx.doi.org/10.1093/jj/erp360.

Ishiyama, K., Inoue, E., Tabuchi, M., Yamaya, T., Takahashi, H., 2004. Biochemical background and compartmentalized functions of cytosolic glutamine synthetase for active ammonium assimilation in rice roots. Plant Cell Physiol. 45, 1640–1647.

Jeong, J.S., Kim, Y.S., Baek, K.H., Jung, H., Ha, S.H., Choi, Y.D., Kim, M., Reuzeau, C., Kim, J.K., 2010. Root-specific expression of *OsNAC10* improves drought tolerance and grain yield in rice under field drought conditions. Plant Physiol. 153, 185–197.

Jia, L.Q., Zhang, B., Mao, C.Z., Li, J., Wu, Y., Wu, P., Wu, Z.C., 2008. OsCYT-INV1 for alkaline/neutral invertase is involved in root cell development and reproductivity in rice (*Oryza sativa* L.). Planta 228, 51–59. doi:http://dx.doi.org/10.1007/s00425-008-0718-0.x.

Jia, L.Q., Wu, Z.C., Hao, X., Carrie, C., Zheng, L.B., Whelan, J., Wu, Y.R., Wang, S.F., Wu, P., Mao, C.Z., 2011. Identification of a novel mitochondrial protein, short postembryonic roots 1 (SPR1), involved in root development and iron homeostasis in Oryza sativa. New Phytol. 189, 843–855. doi:http://dx.doi.org/10.1111/j.1469-8137.2010.03513.

Jiang, H.W., Wang, S.M., Dang, L., Wang, S.F., Chen, H.M., Wu, Y.R., Jiang, X.H., Wu, P., 2005. A novel short-root gene encodes a flucosamine-6-phosphate acetyltransferase required for maintaining normal root cell shape in rice. Plant Physiol. 138, 232–242.

Jiang, J.F., Li, J.H., Xu, Y.Y., Han, Y., Bai, Y., Zhou, G.X., Lou, Y.G., Xu, Z.H., Chong, K., 2007. RNAi knockdown of *Oryza sativa* root meandercurling gene led to altered root development and coiling which were mediated by jasmonic acid signalling in rice. Plant Cell Environ. 30, 690–699.

Kader, M.A., Seidel, T., Golldack, D., Lindberg, S., 2006. Expressions of OsHKT1, OsHKT2, and OsVHA are differentially regulated under NaCl stress in salt-sensitive and salt-tolerant rice (*Oryza sativa* L.) cultivars. J. Exp. Bot. 57, 4257–4268.

Kakei, Y., Ishimaru, Y., Kobayashi, T., Yamakawa, T., Nakanishi, H., Nishizawa, N.K., 2012. OsYSL16 plays a role in the allocation of iron. Plant Mol. Biol. 79, 583–594. doi:http://dx.doi.org/10.1007/s11103-012-9930-1.

Kamiya, N., Nagasaki, H., Morikami, A., Sato, Y., 2003. The *SCARECROW* gene's role in asymmetric cell divisions in rice plants. Plant J. 36, 45–54.

Kamoshita, A., Wade, L.J., Ali, M.L., Pathan, M.S., Zhang, J., Sarkarung, S., Nguyen, H.T., 2002. Mapping QTL for root morphology of a rice population adapted to rainfed lowland conditions. Theor. Appl. Genet. 104, 880–893.

Karahara, I., Umemura, K., Soga, Y., Akai, Y., Bando, T., Ito, Y., Tamaoki, D., Uesugi, K., Abe, J., Yamauchi, D., Mineyuki, Y., 2012. Demonstration of osmotically dependent promotion of aerenchyma formation at different levels in the primary roots of rice using a 'sandwich' method and X-ray computed tomography. Ann. Bot. 110, 503–509.

Katsura, K., Maeda, S., Horie, T., Shiraiwa, T., 2007. Analysis of yield attributes and crop physiological traits of Liangyoupeijiu, a hybrid rice recently bred in China. Field Crops Res. 103, 170–177.

Kim, C.M., Park, S.H., Je, B.I., Park, S.H., Park, S.J., Piao, H.L., Eun, M.Y., Dolan, L., Han, C. D., 2007. *OsCSLD1*, a cellulose synthase-like D1 gene, is required for root hair morphogenesis in rice. Plant Physiol. 143, 1220–1230.

King, B.J., Siddiqi, M.Y., Ruth, T.J., Warner, R.L., Glass, A.D.M., 1993. Feedback regulation of nitrate influx in barley roots by nitrate, nitrite, and ammonium. Plant Physiol. 102, 1279–1286.

Kitomi, Y., Kitano, H., Inukai, Y., 2008a. Mapping of the *CROWNROOTLESS3* gene, *CRL3*, in rice. Rice Genet. Newslett 24, 31–32.

Kitomi, Y., Ogawa, A., Kitano, H., Inukai, Y., 2008b. *CRL4* regulates crown root formation through auxin transport in rice. Plant Root 2, 19–28.

Kitomi, Y., Ito, H., Hobo, T., Aya, K., Kitano, H., Inukai, Y., 2011. The auxin responsive AP2/ERF transcription factor *CROWN ROOTLESS5* is involved in crown root initiation in rice through the induction of *OsRR1*, a type-A response regulator of cytokinin signaling. Plant J. 67, 472–484.

Kitomi, Y., Inahashi, H., Takehisa, H., Sato, Y., Inukai, Y., 2012. OsIAA13-mediated auxin signaling is involved in lateral root initiation in rice. Plant Sci. 190, 116–122.

Koike, S., Inoue, H., Mizrno, D., Takahashi, M., Nakanishi, H., Mori, S., Nishizawa, N.K., 2004. OsYSL2 is a rice metal-nicotianamine transporter that is regulated by iron and expressed in phloem. Plant J. 39, 415–424.

Konings, H., Jackson, M.B., 1979. A relationship between rates of ethylene production by roots and the promoting or inhibiting effects of exogenous ethylene and water on root elongation. Zeitschrift für Pflanzenphysiologie (Continued as J. Plant Physiol.) 92, 385–397.

Kumar, A., Silim, S.N., Okamoto, M., Siddiqi, M.Y., Glass, A.D.M., 2003. Differential expression of three members of the *AMT1* gene family encoding putative high-affinity NH_4^+ transporters in roots of *Oryza sativa* subspecies indica. Plant Cell Environ. 26, 907–914.

Kyndt, T., Denil, S., Haegeman, A., Trooskens, G., De Meyer, T., Van Criekinge, W., Gheysen, G., 2012. Transcriptome analysis of rice mature root tissue and root

tips in early development by massive parallel sequencing. J. Exp. Bot. 63, 2141–2157. doi:http://dx.doi.org/10.1093/jxb/err435.
Lee, S., Kim, Y.Y., Lee, Y., An, G., 2007. Rice P_{1B}-type heavy-metal ATPase, OsHMA9, is a metal efflux protein. Plant Physiol. 145, 831–842. doi:http://dx.doi.org/10.1104/pp.107.102236.
Li, B.Z., Xin, W.J., Sun, S.B., Shen, Q.R., Xu, G.H., 2006a. Physiological and molecular responses of nitrogen-starved rice plants to re-supply of different nitrogen sources. Plant Soil. 287, 145–159.
Li, J., Zhu, S.H., Song, X.W., Shen, Y., Chen, H.M., Yu, J., Yi, K.K., Liu, Y.F., Karplus, V.J., Wu, P., Deng, X.W., 2006b. A rice glutamate receptor-like gene is critical for the division and survival of individual cells in the root apical meristem. Plant Cell 18, 340–349.
Liang, Z.W., Ichii, M., 1995. Morphological characterization of the seedling of short-root mutant *LM10* selected from rice (*Oryza sativa* L., IR8). Jpn. J. Crop Sci. 65, 473–478.
Lillo, C., Meyer, C., Ruoff, P., 2001. The nitrate reductase circadian system. The central clock dogma contra multiple oscillatory feedback loops. Plant Physiol. 125, 1554–1557.
Lin, C.M., Koh, S., Stacey, G., Yu, S.M., Lin, T.Y., Tsay, Y.F., 2000. Cloning and functional characterization of a constitutively expressed nitrate transporter gene, *OsNRT1*, from rice. Plant Physiol. 122, 379–388.
Liu, W., Xu, Z.H., Luo, D., Xue, H.W., 2003. Roles of *OsCKI*1, a rice casein kinase I, in root development and plant hormone sensitivity. Plant J. 36, 189–202.
Liu, H.J., Wang, S.F., Yu, X.B., Yu, J., He, X.W., Zhang, S.L., Shou, H.X., Wu, P., 2005. ARL1, a LOB-domain protein required for adventitious root formation in rice. Plant J. 43, 47–56.
Liu, S.P., Wang, J.R., Wang, L., Wang, X.F., Xue, Y.H., Wu, P., Shou, H.X., 2009. Adventitious root formation in rice requires OsGNOM1 and is mediated by the OsPINs family. Cell Res. 19, 1110–1119.
Liu, F., Wang, Z.Y., Ren, H.Y., Shen, C.J., Li, Y., Ling, H.Q., Wu, C.Y., Lian, X.M., Wu, P., 2010. OsSPX1 suppresses the function of OsPHR2 in the regulationof expression of *OsPT2* and phosphate homeostasis in shoots of rice. Plant J. 62, 508–517.
Luo, L.L., Shi, J.Y., Xiang, X.B., Ding, W.N., Zhu, S.H., 2012. Mapping of a short root-related gene *OsKSR2* in rice (*Oryza sativa* L.). Acta Agron. Sinica 38, 429–435.
Lynch, J.P., 2007. Roots of the second green revolution. Aust. J. Bot. 55, 493–512.
Ma, J.F., Tamai, K., Yamaji, N., Mitani, N., Konishi, S., Katsuhara, M., Ishiguro, M., Murata, Y., Yano, M., 2006. A silicon transporter in rice. Nature 440, 688–691.
Miller, A.J., Cookson, S.J., Smith, S.J., Wells, D.M., 2001. The use of microelectrodes to investigate compartmentation and the transport of metabolized inorganic ions in plants. J. Exp. Bot. 52, 541–549.
Ming, F., Mi, G.H., Lu, Q., Yin, S., Zhang, S.S., Guo, B., Shen, D.L., 2005. Cloning and characterization of cDNA for the *Oryza sativa* phosphate transporter. Cell Mol. Biol. Lett. 10, 401–411.
Nakamura, A., Umemura, I., Gomi, K., Hasegawa, Y., Kitano, H., Sazuka, T., Matsuoka, M., 2006. Production and characterization of auxin-insensitive rice by overexpression of a mutagenized rice IAA protein. Plant J. 46, 297–306.
Nawrot, T., Plusquin, M., Hogervorst, J., Roels, H.A., Celis, H., Thijs, L., Vangronsveld, J., Van Hecke, E., Staessen, J.A., 2006. Environmental exposure to cadmium and risk of cancer: a prospective population-based study. Lancet 7, 119–126.
Nguyen, T.T.T., Klueva, N., Chamareck, V., Aarti, A., Magpantay, G., Millena, A.C.M., Pathan, M.S., Nguyen, H.T., 2004. Saturation mapping of QTL regions and identification of putative candidate genes for drought tolerance. Mol. Genet. Genomics 272, 35–46.
Ni, J., Wang, G.H., Zhu, Z.X., Zhang, H.H., Wu, Y.R., Wu, P., 2011. OsIAA23-mediated auxin signaling defines postembryonic maintenance of QC in rice. Plant J. 68, 433–442. doi:http://dx.doi.org/10.1111/j.1365-313X.2011.04698.x.
Ning, Y.Q., Ding, W.N., Zhu, S.H., Yu, H.W., Yu, H., Lu, K.X., 2010. Genetic analysis and gene mapping of a short root mutant *ksr1* in rice. Chin. J Rice Sci. 24, 652–654.
Nosengo, N., 2003. Fertilized to death. Nature 425, 894–895.
Obara, M., Tamura, W., Ebitani, T., Yano, M., Sato, T., Yamaya, T., 2010. Fine-mapping of *qRL6.1*, a major QTL for root length of rice seedlings grown under a wide range of NH_4^+ concentrations in hydroponic conditions. Theor. Appl. Genet. 121, 535–547. doi:http://dx.doi.org/10.1007/s00122-010-1328-3.
Ogo, Y., Itai, R.N., Nakanishi, H., Kobayashi, T., Takahashi, M., Mori, S., Nishizawa, N. K., 2007. The rice bHLH protein OsIRO2 is an essential regulator of the genes involved in Fe uptake under Fe-deficient conditions. Plant J. 51, 366–377.
Okada, T., Nakayama, H., Shinmyo, A., Yoshida, K., 2008. Expression of *OsHAK* genes encoding potassium ion transporters in rice. Plant Biotechnol. 25, 241–245.
Orsel, M., Filleur, S., Fraisier, V., Daniel-Vedele, F., 2002. Nitrate transport in plants: which gene and which control? J. Exp. Bot. 53, 825–833.
Paszkowski, U., Kroken, S., Roux, C., Briggs, S.P., 2002. Rice phosphate transporters include an evolutionarily divergent gene specifically activated in arbuscular mycorrhizal symbiosis. PNAS 99, 13324–13329.
Price, A.H., Steele, K.A., Moore, B.J., Jones, R.G.W., 2002. Upland rice grown in soil-filled chambers and exposed to contrasting water-deficit regimes II. Mapping quantitative trait loci for root morphology and distribution. Field Crops Res. 76, 25–43.
Qi, Y.H., Wang, S.K., Shen, C.J., Zhang, S.N., Chen, Y., Xu, Y.X., Liu, Y., Wu, Y.R., Jiang, D. A., 2012. OsARF12, a transcription activator on auxin response gene, regulates root elongation and affects iron accumulation in rice (*Oryza sativa*). New Phytol. 193, 109–120.
Qin, C., Li, Y., Gan, J., Wang, W., Zhang, H., Liu, Y., Wu, P., 2013. OsDGL1, a homolog of an oligosaccharyltransferase complex subunit, is involved in *N*-glycosylation and root development in rice. Plant Cell Physiol. 54, 129–137. doi:http://dx.doi.org/10.1093/pcp/pcs159.
Raun, W.R., Johnson, G.V., 1999. Improving nitrogen use efficiency for cereal production. Agron. J. 91, 357–363.
Rebouillat, J., Dievart, A., Verdeil, J.L., Escoute, J., Giese, G., Breitler, J.C., Gantet, P., Espeout, S., Guiderdoni, E., Périn, C., 2009. Molecular genetics of rice root development. Rice. 2, 15–34.
Redillas, M.C.F.R., Jeong, J.S., Kim, Y.S., Jung, H., Bang, S.W., Choi, Y.D., Ha, S.H., Reuzeau, C., Kim, J.K., 2012. The overexpression of *OsNAC9* alters the root architecture of rice plants enhancing drought resistance and grain yield under field conditions. Plant Biotechnol. J. 10, 792–805. doi:http://dx.doi.org/10.1111/j.1467-7652.2012.00697.x.
Ren, Z.H., Gao, J.P., Li, L.G., Cai, X.L., Huang, W., Chao, D.Y., Zhu, M.Z., Wang, Z.Y., Luan, S., Lin, H.X., 2005. A rice quantitative trait locus for salt tolerance encodes a sodium transporter. Nat. Genet. 37, 1141–1146.
Rhoades, J.D., Loveday, J., 1990. Salinity in irrigated agriculture. In: Rhoades, J.D., Loveday, J. (Eds.), In Salinity in Irrigated Agriculture. American Society of Agronomy, Madison,WI, pp. 1089–1142.
Russell, R.S., 1977. Plant root systerms. Their function and interaction with the soil. McGraw Hill, Maidenhead.
Sakura, J., Ishikawa, F., Yamaguchi, T., Uemura, M., Maeshima, M., 2005. Identification of 33 rice aquaporin genes and analysis of their expression and function. Plant Cell Physiol. 46, 1568–1577.
Sassi, A., Mieulet, D., Khan, I., Moreau, B., Gaillard, I., Sentenac, H., Véry, A.A., 2012. The rice monovalent cation transporter OsHKT2;4: revisited ionic selectivity. Plant Physiol. 160, 498–510.
Scarpella, E., Rueb, S., Meijer, A.H., 2003. The *RADICLELESS1* gene is required for vascular pattern formation in rice. Development 130, 645–658.
Sebastian, A., Prasad, M.N.V., 2014. Cadmium minimization in rice. A review. Agron. Sustain. Dev. 34, 155–173. doi:http://dx.doi.org/10.1007/s13593-013-0152-y.
Secco, D., Wang, C., Arpat, B.A., Wang, Z.Y., Poirier, Y., Tyerman, S.D., Wu, P., Shou, H. X., Whelan, J., 2012. The emerging importance of the SPX domain-containing proteins in phosphate homeostasis. New Phytol. 193, 842–851. doi:http://dx.doi.org/10.1111/j.1469-8137.2011.04002.x.
Shen, L., Courtois, B., Nally, Mc, Robin, K.L., Li, S., Z, 2001. Evaluation of near-isogenic lines of rice introgressed with QTLs for root depth through marker-aided selection. Theor. Appl. Genet. 103, 75–83.
Shi, S.L., Wang, D.F., Yan, Y., Zhang, F., Wang, H.D., Gu, M., Sun, S.B., Xu, G.H., 2013. Function of phosphate transporter OsPHT2;1 in improving phosphate utilization in rice. Chin. J. Rice Sci. 27, 457–465.
Smit, A.L., Bengough, A.G., Engels, C., Van Noordwijk, M., Pellerin, S., Van De Geijn, S., C, 2000. Root Methods, A Handbook. Springer, Berlin.
Sonoda, Y., Ikeda, A., Saiki, S., von Wirén, N., Yamaya, T., Yamaguchi, J., 2003. Distinct expression and function of three ammonium transporter genes (*OsAMT1;1-1;3*) in rice. Plant Cell Physiol. 44, 726–734.
Suenaga, A., Moriya, K., Sonoda, Y., Ikeda, A., von Wirén, N., Hayakawa, T., Yamaguchi, J., Yamaya, T., 2003. Constitutive expression of a novel-type ammonium transporter *OsAMT2* in rice plants. Plant Cell Physiol. 44, 206–211. doi:http://dx.doi.org/10.1093/pcp/pcg017.
Sun, S.B., Gu, M., Cao, Y., Huang, X.P., Zhang, X., Ai, P.H., Zhao, J.N., Fan, X.R., Xu, G.H., 2012. A constitutive expressed phosphate transporter, OsPht1;1, modulates phosphate uptake and translocation in phosphate-replete rice. Plant Physiol. 159, 1571–1581.
Suzuki, N., Takeda, S., Ichii, M., 2003. Morphological and physiological characteristics of a root-hairless mutant in rice (*Oryza sativa* L.). Plant Soil. 255, 9–17.
Tabuchi, M., Sugiyama, K., Ishiyama, K., Inoue, E., Sato, T., Takahashi, H., Yamaya, T., 2005. Severe reduction in growth rate and grain filling of rice mutants lacking OsGS1;1, a cytosolic glutamine synthetase1;1. Plant J. 42, 641–651.
Takahashi, R., Ishimaru, Y., Shimo, H., Ogo, Y., Senoura, T., Nishizawa, N.K., Nakanishi, H., 2012. The OsHMA2 transporter is involved in root-to-shoot translocation of Zn and Cd in rice. Plant Cell Environ. 35, 1948–1957. doi:http://dx.doi.org/10.1111/j.1365-3040.2012.02527.x.
Takehisa, H., Sato, Y., Igarashi, M., Abiko, T., Antonio, B.A., Kamatsuki, K., Minami, H., Namiki, N., Inukai, Y., Nakazono, M., Nagamura, Y., 2012. Genomewide transcriptome dissection of the rice root system: implications for developmental and physiological functions. Plant J. 69, 126–140. doi:http://dx.doi.org/10.1111/j.1365-313X.2011.04777.x.
Tian, J.L., Wang, C., Zhang, Q., He, X.W., Whelan, J., Shou, H.X., 2012. Overexpression of *OsPAP10a*, a root-associated acid phosphatase, increased extracellular organic phosphorus utilization in rice. J. Integr. Plant Biol. 54, 631–639.
Ueno, D., Yamaji, N., Kono, I., Huang, C.F., Ando, T., Yano, M., Ma, J.F., 2010. Gene limiting cadmium accumulation in rice. PNAS 107, 16500–16505.
Uga, Y., Sugimoto, K., Ogawa, S., Rane, J., Ishitani, M., Hara, N., Kitomi, Y., Inukai, Y., Ono, K., Kanno, N., Inoue, N., Takehisa, H., Motoyama, R., Nagamura, Y., Wu, J.Z., Matsumoto, T., Takai, T., Okuno, K., Yano, M., 2013. Control of root system architecture by *DEEPER ROOTING 1* increases rice yield under drought conditions. Nat. Genet. 45, 1097–1102.
Vance, C.P., Uhde-Stone, C., Allan, D.L., 2003. Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol. 157, 423–447.
Wada, K., Li, X.Y., Moody, P.W., 1990. Chemistry of adverse upland soils. Proceedings of a symposium, 6–10 March 1989, IRRI. Phosphorus requirements for sustainable agriculture in Asia and Oceania, IRRI, Philippines. , pp. 243–253.
Wan, J., Nakazaki, T., Ikehashi, H., 1996. Analyses of genetic loci for diameter of seminal root with marker genes in rice. Breed. Sci. 46, 75–77.
Wang, H., Taketa, S., Miyao, A., Hirochika, H., Ichii, M., 2006. Isolation of a novel lateral-rootless mutant in rice (*Oryza sativa* L.) with reduced sensitivity to auxin. Plant Sci. 170, 70–77.

Wang, C., Ying, S., Huang, H., Li, K., Wu, P., Shou, H., 2009a. Involvement of *OsSPX1* in phosphate homeostasis in rice. Plant J. 57, 895–904.
Wang, Z.Y., Hu, H., Huang, H.J., Duan, K., Wu, Z.C., Wu, P., 2009b. Regulation of *OsSPX*1 and *OsSPX*3 on expression of *OsSPX* domain genes and Pi-starvation signaling in rice. J. Integr. Plant Biol. 51, 663–674.
Wang, X.F., He, F.F., Ma, X.X., Mao, C.Z., Hodgman, C., Lu, C.G., Wu, P., 2011. OsCAND1 is required for crown root emergence in rice. Mol. Plant 4, 289–299.
Wang, H.M., Xu, X.M., Zhan, X.D., Zhai, R.R., Wu, W.M., Shen, X.H., Dai, G.X., Cao, L.Y., Cheng, S.H., 2013a. Identification of *qRL7*, a major quantitative trait locus associated with rice root length in hydroponic conditions. Breed. Sci. 63, 267–274. doi:http://dx.doi.org/10.1270/jsbbs.63.000.
Wang, L., Ying, Y.H., Narsai, R., Ye, L.X., Zheng, L.Q., Tian, J.L., Whelan, J., Shou, H.X., 2013b. Identification of OsbHLH133 as a regulator of iron distribution between roots and shoots in *Oryza sativa*. Plant Cell Environ. 36, 224–236.
Wang, X.F., Wang, Y.F., Pineros, M.A., Wang, Z.Y., Wang, W.X., Li, C.Y., Wu, Z.C., Kochian, L.V., Wu, P., 2013c. Phosphate transporters OsPHT1;9 and OsPHT1;10 are involved in phosphate uptake in rice. Plant Cell Environ. 17, 2013. doi:http://dx.doi.org/10.1111/pce.12224 Published online.
Wasaki, J., Yonetani, R., Shinano, T., Kai, M., Osaki, M., 2003. Expression of the *OsPI1* gene, cloned from rice roots using cDNA microarray, rapidly responds to phosphorus status. New Phytol. 158, 239–248.
Watanabe, T., Shimbo, S., Nakatsuka, H., Koizumi, A., Higashikawa, K., Matsuda-Inoguchi, N., Ikeda, M., 2004. Gender-related difference, geographical variation and time trend in dietary cadmium intake in Japan. Sci. Total Environ. 329, 17–27.
Weaver, J.E., 1919. The Ecological Relations of Roots. Carnegie Institution of Washington Publications, Washington, pp. 1–22.
Williams, L.E., Miller, A.J., 2001. Transporters responsible for the uptake and partitioning of nitrogenous solutes. Annu. Rev. Plant Physiol. Mol. Biol. 52, 659–688.
Williams, L.E., Pittman, J.K., Hall, J.L., 2000. Emerging mechanisms for heavy metal transport in plants. Biochim. Biophys. Acta 1465, 104–126.
Wissuwa, M., Yano, M., Ae, N., 1998. Mapping of QTLs for phosphorus-deficiency tolerance in rice (*Oryza sativa* L.). Theor. Appl. Genet. 97, 777–783.
Won, S.K., Choi, S.B., Kumari, S., Cho, M., Lee, S.H., Cho, H.T., 2010. Root hair-specific EXPANSIN B genes have been selected for graminaceae root hairs. Mol. Cells 30, 369–376.
Woo, Y.M., Park, H.J., Su'udi, M., Yang, J.I., Park, J.J., Back, K., Park, Y.M., An, G., 2007. Constitutively wilted 1, a member of the rice YUCCA gene family, is required for maintaining water homeostasis and an appropriate root to shoot ratio. Plant Mol. Biol. 65, 125–136.
Xu, M., Zhu, J., Shou, H.X., Wu, P., 2005. A PIN1 family gene, *OsPIN1*, involved in auxin-dependent adventitious root emergence and tillering in rice. Plant Cell Physiol. 46, 1674–1681.
Xu, G.Y., Cui, Y.C., Li, M.J., Wang, M.L., Yu, Y., Zhang, B., Huang, L.F., Xia, X.J., 2013. *OsMSR2*, a novel rice calmodulin-like gene, confers enhanced salt tolerance in rice *(Oryza sativa* L.). AJCS 7, 368–373.
Xue, D., Chen, M., Zhang, G., 2009. Mapping of QTLs associated with cadmium tolerance and accumulation during seedling stage in rice (*Oryza sativa* L.). Euphytica 165, 58–596.
Yamamoto, Y., Kamiya, N., Morinaka, Y., Matsuoka, M., Sazuka, T., 2007. Auxin biosynthesis by the *YUCCA* genes in rice. Plant Physiol. 143, 1362–1371.
Yan, M., Fan, X.R., Feng, H.M., Miller, A.J., Shen, Q.R., Xu, G.H., 2011a. Rice OsNAR2. 1 interacts with OsNRT2. 1, OsNRT2. 2 and OsNRT2. 3a nitrate transporters to provide uptake over high and low concentration ranges. Plant Cell Environ. 34, 1360–1372.
Yan, Y.S., Chen, X.Y., Yang, K., Sun, Z.X., Fu, Y.P., Zhang, Y.M., Fang, R.X., 2011b. Overexpression of an F-box protein gene reduces abiotic stress tolerance and promotes root growth in rice. Mol. Plant 4, 190–197.
Yang, X.C., Hwa, C.M., 2008. Genetic and physiological characterization of the *OsCem* mutant in rice: formation of connected embryos with multiple plumules or multiple radicles. Heredity 101, 239–246.
Yang, J.C., 2011. Relationships of rice root morphology and physiology with the formation of grain yield and quality and the nutrient absorption and utilization. Sci. Agr. Sinica. 44, 36–46.
Yao, S.G., Taketa, S., Ichii, M., 2002. A novel short-root gene that affects specifically early root development in rice (*Oryza sativa* L.). Plant Sci. 163, 207–215.
Yao, S.G., Taketa, S., Ichii, M., 2003. Isolation and characterization of an abscisic acid-insensitive mutation that affects specifically primary root elongation in rice (*Oryza sativa* L.). Plant Sci. 164, 971–978.
Yi, X., Liang, Z., Kawasaki, S., Kuroda, S., Ichii, M., Ashikawa, I., 2002. Animal and Microbe Genomes X Conference, San Diego, USA.
Yi, K.K., Wu, Z.C., Zhou, J., Du, L.M., Guo, L.B., Wu, Y.R., Wu, P., 2005. *OsPTF1*, a novel transcription factor involved in tolerance to phosphate starvation in rice. Plant Physiol. 138, 2087–2096.
Yokosho, K., Yamaji, N., Ueno, D., Mitani, N., Ma, J.F., 2009. OsFRDL1 is a citrate transporter required for efficient, translocation of iron in rice. Plant Physiol. 149, 297–305.
Yu, Z.M., Kang, B., He, X.W., Lü, S.L., Bai, Y.H., Ding, W.N., Chen, M., Cho, H.T., Wu, P., 2011. Root hair-specific expansins modulate root hair elongation in rice. Plant J. 66, 725–734.
Yuan, J., Chen, D., Ren, Y.J., Zhang, X.L., Zhao, J., 2008. Characteristic and expression analysis of a metallothionein gene, *OsMT2b*, downregulated by cytokinin suggests functions in root development and seed embryo germination of rice. Plant Physiol. 146, 1637–1650.
Yuo, T., Toyota, M., Ichii, M., Taketa, S., 2009. Molecular cloning of a root hairless gene *rth1* in rice. Breed. Sci. 59, 13–20.
Zhai, R.R., Feng, Y., Wang, H.M., Zhan, X.D., Shen, X.H., Wu, W.M., Zhang, Y.X., Chen, D. B., Dai, G.X., Yang, Z.L., Cao, L.Y., Cheng, S.H., 2013. Transcriptome analysis of rice root heterosis by RNA-Seq. BMC Genomics 14, 1–14. doi:http://dx.doi.org/10.1186/1471-2164-14-19.
Zhang, J., Peng, Y.L., Guo, Z.J., 2008. Constitutive expression of pathogen- inducible *OsWRKY31* enhances disease resistance and affects root growth and auxin response in transgenic rice plants. Cell Res. 508–521. doi:http://dx.doi.org/10.1038/cr.2007.104.
Zhang, H., Xue, Y., Wang, Z., Yang, J., Zhang, J., 2009. Morphological and physiological traits of roots and their relationships with shoot growth in super rice. Field Crops Res. 113, 31–40.
Zhang, J.W., Xu, L., Wu, Y.R., Chen, X.A., Liu, Y., Zhu, S.H., Ding, W.N., Wu, P., Yi, K.K., 2012a. OsGLU3, a putative membrane-bound endo-1,4-beta-glucanase, is required for root cell elongation and division in rice (*Oryza sativa* L.). Mol. Plant 5, 176–186.
Zhang, Y.M., Yan, Y.S., Wang, L.N., Yang, K., Xiao, N., Liu, Y.F., Fu, Y.P., Sun, Z.X., Fang, R. X., Chen, X.Y., 2012b. A novel rice gene, *NRR* responds to macronutrient deficiency and regulates root growth. Mol. Plant 5, 63–72.
Zhang, Q., Li, J.J., Zhang, W.J., Yan, S.N., Wang, R., Zhao, J.F., Li, Y.J., Qi, Z.G., Sun, Z.X., Zhu, Z.G., 2012c. The putative auxin efflux carrier *OsPIN3t* is involved in the drought stress response and drought tolerance. Plant J. 72, 805–816.
Zhang, Q., 2007. Strategies for developing green super rice. Proc. Natl. Acad. Sci. U. S. A. 104, 16402–16409.
Zhao, Y., Hu, Y.F., Dai, M.Q., Huang, L.M., Zhou, D.X., 2009. The WUSCHEL-related homeobox gene *WOX11* is required to activate shoot-borne crown root development in rice. Plant Cell 21, 736–748.
Zheng, X.N., Chen, B., Lu, G.J., Han, B., 2009. Overexpression of a NAC transcription factor enhances rice drought and salt tolerance. Biochem. Biophys. Res. Commun. 379, 985–989.
Zhou, J., Jiao, F.C., Wu, Z.C., Li, Y.Y., Wang, X.M., He, X.W., Zhong, W.Q., Wu, P., 2008. *OsPHR2* is involved in phosphate-starvation signaling and excessive phosphate accumulation in shoots of plants. Plant Physiol. 146, 1673–1686.
Zhu, Z.X., Liu, Y., Liu, S.J., Mao, C.Z., Wu, Y.R., Wu, P., 2011. A gain-of-function mutation in *OsIAA11* affects lateral root development in rice. Mol. Plant 5, 154–161.
Zhu, J.K., 2001. Plant salt tolerance. Trends Plant Sci. 6, 66–71.
Zhuang, X., Xu, Y., Chong, K., Lan, L., Xue, Y., Xu, Z., 2005. OsAGAP, an ARF-GAP from rice, regulates root development mediated by auxin in *Arabidopsis*. Plant Cell Environ. 28, 147–156.