

Direct-Seeded Rice Root System Architecture

Subjects: **Plant Sciences**

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Direct-seeded rice (DSR) is such a system of rice cultivation that has the potential to decrease water consumption, in addition to lessening labor requirements and at the same time enhance resource-use efficiency and system productivity, and check greenhouse gas emissions. Identifying ideal traits and breeding new rice varieties with efficient root system architecture (RSA) has great potential to increase resource-use efficiency and grain yield, especially under direct-seeded rice, by adapting to aerobic soil conditions.

direct-seeded rice

root system architecture

root plasticity

1. Background

Rice (*Oryza sativa* L., family: Poaceae or Gramineae) is the most cultivated cereal globally (after wheat) is mostly associated with ample quantities of water, has very low water productivity (1 kg of grain requires 3000–5000 L of water). In recent years, direct-seeded rice (DSR) has been adopted on >25% of the area under rice cultivation worldwide [1]. Considering its benefits from sowing to harvesting, DSR as a whole saves about 50% of water and labor expenses [2], provides better temporal isolation for succeeding crops, and decreases emissions of greenhouse gases [3]. Furthermore, dry-DSR could effectively use the early-season monsoon in areas with limited moisture [4]. However, when assess the risks involved, yield in DSR is often diminished because of intrinsic problems such as poor seedling establishment owing to waterlogging immediately after sowing, heavy weed infestation, low nutrient- and water-use efficiency, and susceptibility to lodging [5]. Another major problem arises from the high seed rate involved in this type of cultivation practice compared with that of its counterpart, TPR (Transplanted rice).

Roots are the primary organs for sensing and buffering against several abiotic stresses (drought, flood, salinity, and mineral stress). The root system spreading inside the soil is the key player for maintaining the aboveground parts, enhancing their capacity to uptake more water and nutrient from the soil environment and yield higher. Designing root architecture befitting DSR has a high potential to break both the adaptability and yield barrier. This would effectively aid in developing genotypes on par/better performing under DSR conditions than under TPR conditions as the varieties suitable for TPR conditions are not fit for DSR [6].

2. Insights into Rice Root System Architecture

Being a monocot, the rice plant bears the fibrous root system mainly of three distinct types of roots; embryonic roots, seminal roots, and post-embryonic roots. The radicle is the first root to be formed from the embryo and, after

the seed germinates, the radicle is referred to as the seminal root. The parenchyma cells at the base of the stem give rise to shoot-borne roots called the crown roots. The lateral roots are borne initially on the seminal roots, and then the crown roots contribute to water and nutrient uptake activity [7]. Set apart from these structures are root hairs, fine tubular outgrowths of the epidermal layers. They are of prime importance in increasing the surface area and reaching out to the minute pore space in the soil to acquire moisture and nutrients (they also play a role in interaction with soil fauna) [8][9]. Therefore, it is essential to have an updated understanding of the genetic mechanism associated, the gene networks involved, and plant requirements at different stages of growth [10]. In a well-drained upland soil, the coleorhiza emerges first from the rice seed, whereas, in submerged conditions, the coleoptile arises before the coleorhiza. The first roots to come out of the seed are the embryonic roots (or radicle), which arise out of the coleorhiza [11]. Then, the secondary roots develop, which ultimately form the lateral roots. The embryonic roots by this stage are desiccated and are replaced by the secondary adventitious roots (or crown roots), generating from the meristematic cells of the culm's underground nodes. The crown roots are of two types: lower thick ones and thin upper ones. Their growth angle decides the fate of the distribution of the whole root system in the soil in the DSR system [12]. Short roots develop into a compact root system, whereas long roots help mine water and nutrients from a depth.

3. RSA: Infant to Early Vegetative Stage and Associated Traits

3.1. Root Requirements and Nutrient Uptake

The desirable architecture at the initial stage of growth after germination is preferably a shallow and well-spread surface–subsurface root system on the nutrient-use front. Studies have confirmed the accumulation of phosphorus (P), one of the essential macronutrients, in the shallow soil layers vis-à-vis subsurface/deeper layers [13], and the same applies to other immobile nutrients such as potassium (K), manganese (Mn), and iron (Fe). P uptake starts as early as 2 days after germination (DAG) [14]. Primarily, OsPT8 and OsPT1 genes are involved at the initial stage and contribute to P uptake by roots as early as 2–3 DAG [15][16]. Phosphorus starvation tolerance 1 (PSTOL1), a significant gene identified in the phosphorus-deficiency tolerance QTL, phosphorus uptake 1 (Pup1), aids in the uptake of P and enhances early root growth [17]. It helps the plant in P uptake under rainfed/upland conditions in rice [18] and was reported in an aus-type variety Kasalath [17]. Sandhu et al. [19] have identified QTLs regulating P uptake and length of root hair on chromosome 5. The key player in developing different types of the root system in the early seedling growth are the genes controlling root angle, which determine the development of surface and shallow subsurface roots. However, root growth angle as a trait is determined by multiple environmental factors such as gravity, light, and water potential [20][21]. An actin-binding protein, Rice Morphology Determinant (RMD), has been found to govern root angle by linking actin filaments with statoliths producing shallower crown root angle [22]. This also leads to a low intensity of auxin-driven gravitropism of the root. Another QTL, qSOR1 (QTL for SOIL SURFACE ROOTING 1), an 812-kb long segment located on chromosome 7 expressed in the columella cells, also operates similarly working antagonistically with auxin [23]. It induces shallow root formation beneficial for the uptake of nutrients from the top layers [24]. DEEPER ROOTING 1 (DRO1), a major QTL responsible for root growth angle,

is also involved in gravitropism [25] and is negatively regulated by auxin signaling and is involved in root tip cell elongation leading to gravitropic bending [26]. Besides the above, the crown root has an important role in P acquisition. A large number of crown roots (adventitious roots) contribute to shallower rooting depth, in turn increasing P uptake from deficient soils [27].

Nitrogen (N) deficiency at the early stages of seedling growth can lead to the development of long but thinner roots [28]. Rice roots can uptake N in both the nitrate and ammonium form. Under limited-moisture DSR conditions, the availability of nitrate would be higher than the ammoniacal form of N. Nitrate uptake has been reported to be facilitated by transporters such as OsNRT1.1 allele OsNPF6.5 (OsNRT1.1B), OsNPF2.4 (OsNRT1.6), OsNPF8.9 (OsNRT1.1, Os3g13274, or AF140606) and OsNRT1.1b (AK066920) in rice [29][30][31] under high nitrate availability, whereas, in a soil environment with low nitrate, OsNRT2.1, OsNRT2.2, and OsNAR2.1 come into play [32][33][34]. The partner protein of the NRT family, OsNAR2.1, also helps in promoting root growth. Under oxygen-limiting conditions, rice can also rely on ammonia for its N source. A range of transporters for ammonium intake by the plant cells have been reported such as OsAMT1.1, OsAMT1.2, OsAMT1.3, OsAMT2.1, OsAMT2.2, OsAMT2.3, OsAMT3.1, OsAMT3.2, and OsAMT3.3 [35][36][37]. A major QTL on chromosome 12, Tolerance of Nitrogen Deficiency 1 (TOND1) contributes to N deficiency tolerance in plants, also manifesting increased root length [38]. QTLs for N uptake and root hair density has been identified on chromosome 2 (a stretch of 3.4 Mb) [19]. Yet another QTL, NITRATE TRANSPORTER 1.1, has been reported, which transports both nitrogen and auxin, and this was one of the first studies to suggest a connecting link between the auxin pathway and nitrate availability in soil [39].

Besides N and P, iron (Fe) can greatly influence and limit plant growth. The aerobic conditions under DSR lead to oxidation of iron from its available ferrous (Fe^{2+}) form to its unavailable ferric (Fe^{3+}) form [40]. Under normal conditions, rice proceeds through the biosynthesis and secretion of root exudates, compounds called phytosiderophores (PSs), through the roots to facilitate the uptake of Fe. These PSs form soluble complexes with iron (Fe(III)-PS) in the rhizosphere and taken up by the root cells with the help of YELLOW STRIPE-LIKE PROTEINS (YSLs) [41]. Besides this, rice acquires Fe^{2+} directly from the surrounding rhizosphere through multiple transporters such as OsIRT1 and OsIRT2 [42]. Zinc (Zn) is one of the most critical regulatory cofactors and its deficiency can cause multiple irregularities, including chlorosis and hampering auxin and chlorophyll activity. Plants tolerant to Zn deficiency in soil show rapid crown root development [43]. Zn uptake by plants is facilitated by one of two ways: directly from the soil via root epidermal cells or associations with arbuscular mycorrhizal fungi (AMF). The direct uptake from the soil is similar to that of iron. Like iron, response to Zn deficiency is related to root exudates, phytosiderophores (MA). ZmYS1, a yellow stripe gene, identified in maize, has a range of specificity for metals, including Zn, and thus helps in uptake and transport [44]. Many Zn transporters of the ZIP (Zrt, Irt-like protein) family have been reported that sense become activated in response to Zn deficiency: OsZIP1, OsZIP3, OsZIP4, and OsZIP5 [42,45,46]. These ZIP transporters are also involved in the transport of iron and manganese [45]. Besides root exudation, zinc uptake is facilitated by mycorrhizal fungi (as is phosphorus). These fungi colonize the root cortical cells, extending their hyphae into the rhizosphere [46].

3.2. Early Uniform Emergence and Early Root Vigor

Early uniform emergence (EUE), seedling establishment, and development are major determinants of crop growth and subsequent yield. Two significant major QTLs (qEMM_{1.1} on chromosome 1 and qEMM_{11.1} on chromosome 11) for EUE derived from Moroberekan (BC₂F₃; Moroberekan × Swarna) were reported by Dixit et al. [47]. QTLs for early uniform emergence (qEUE11.1) [47] and early vigor (qEVV9.1) [48] can be used for the improvement of dry-DSR varieties. Mesocotyl, the portion between the coleoptile node and the base of the seminal root, is one of the key players in pushing the germinating seedlings out of the soil. Its length determines the seedling emergence and establishment [49]. GWAS study for mesocotyl elongation in 208 accessions of rice has identified six novel loci explaining up to 15.9% of phenotypic variations [50]. In the DSR environment, EVV is associated with yield stability [51]. Several researchers [49][52][53][54][55] have already identified many QTLs for these traits using mapping populations. Two major QTL hotspots have been identified in relation to vigor traits: QTL hotspot A on chromosome 3 (qEV3.1, qEUE3.1, qSHL3.1, qSL3.1, qSFW3.1, qTFW3.1, qRDW3.1) and hotspot B on chromosome 5 (qEV5.1, qEUE5.1, qSHL5.1, qSL5.1, qSFW5.1, qSDW5.1, qTDW5.1) [56].

Another aspect of seedling vigor is the proper and early development of crown roots, a major trait in rice that controls nutrient and water acquisition in the initial days of seedling growth. Thus, their number and distribution are deciding factors of ESV, and they also help in P uptake due to their shallow rooting. Rapid nodal root growth, longer root, and high density of roots are imperative for EUE under DSR [19]. For their timely normal emergence from the shoot base, seedlings with high vigor have been reported to utilize the WUSCHEL-related homeobox (WOX) gene, WOX11 [57]. They found its action to be in coordination with both auxin and cytokinin activity. Both crown root (CR) and lateral root (LR) developmental processes follow many common pathways and gene actions. For instance, the WOX genes, OsIAA23, OsARM1, OsARM2, and CRL4/OsGNOM1, have a regulatory function in both LR and CR development [58]. It is interesting to note that crown root regulating significant gene, crown rootless1 gene also positively regulates the development of LRs [10]. LRs are regulated by the auxin in their growth and gravitropism [59]. A recent report on *lateral rootless 1* (*lrt1*) and *lrt2* mutants suggested that they had less sensitivity to auxin and lacked LRs [60]. Similar auxin involvement is also seen in the OsWOX3A-encoding genes NARROW LEAF 2 (NAL2) and NAL3, which regulate LR development. NAL1 has also been identified with a role in crown root development [61].

4. Stress during Germination

4.1. Anaerobic Germination and Regulation of Associated Root Traits

Water, when available in excess, can be a limiting factor in the early stages, hampering the pathway of germination. This is one of the most common stresses that a germinating seed faces, i.e., anaerobic soil conditions. Few rice cultivars can germinate, grow, and survive under such oxygen-deficient conditions is commonly known as anaerobic germination (AG) tolerance in the crop. [62][63][64][65][66][67][68][69] The Os-EXP4 expansin gene helps in seed germination in anaerobic conditions or submergence. This gene might be involved in the expansion of the epidermal cells to form long coleorhizal hairs [70]. Among the several QTLs detected for anaerobic germination, qAG-9-2 was traced to the locus AG1 (trehalose-6-phosphate phosphatase gene family) controlling coleoptile elongation under submergence [71]. A similar coleoptile elongating gene (AG2)

has also been reported. These genes (AG1 and AG2) have displayed surprisingly higher survivability under anaerobic conditions in the introgressed lines than in the recurrent parent, Dongan, a japonica cultivar [72]. However, SOR1 (SOIL SURFACE ROOTING 1) remains the most useful gene adapted to anaerobic conditions under DSR. Its mechanism enables roots to grow toward the soil surface and acquire oxygen directly from the air [73]. Uga et al. [74] identified an 812-kb interval (7L), delimited by markers RM21941 and RM21976, and it was designated as QTL qSOR1. This SOR gene is reported explicitly in the Bulu genotype from Indonesia. A similar mechanism is adopted by Arabidopsis using an allele of CYTOKININ OXIDASE 2 (CKX2), which promotes shallower root growth aiding in surviving hypoxia due to snow [75]. Other genes have also been reported, such as the QTLs qAG-9-2 (AG1) and qAG-7-2 (AG2) [76]. QTLs located on the short arm of chromosome 7, qAG7.1 and qAG7.2 [77], and the functional allele of qLTG3-1 in Ouu 365 and Arroz da Terra inbred lines [78] were found to promote efficient germination under anaerobic conditions.

4.2. Limited Moisture during Germination and Regulation of Associated Root Traits under DSR

It has been seen that rice roots respond to drought or water stress in the following ways: osmotic adjustment within the root cells, enhanced root penetration into the soil by increasing root length, increased root density, and a higher root-to-shoot ratio [79]. However, the basic adaptive response in the DSR system lies with traits such as root length, root thickness, and root hair growth to reach moisture at greater depths. Root elongation is facilitated by auxin signaling and the expansion of the cells. Several factors control root length as a trait, for instance, cell wall loosening regulated by the endo-1,4- β -D-glucanase protein encoded by the gene ROOT GROWTH INHIBITING (RT)/OsGLU3 regulates root length [80]. Kitomi et al. [81] identified two QTLs for maximal root length, QUICK ROOTING 1 (QRO1) on chromosome 2 and QRO2 on chromosome 6. The rt/osglu3 mutants exhibit short roots as a decrease in longitudinal cell elongation occurs but with no effect on root differentiation, root cell division, or shoot development. OsEXPA8, a turgor-driven cell elongation root-specific α -expansin, works similarly by loosening the cell wall and then resulting in an increased seminal, crown, and lateral root length [82]. Many other genes controlling root elongation have also been found to be effective, such as GNA1, which encodes a glucosamine-6-P acetyltransferase; OsCYT-INV1 (an alkaline/neutral invertase) [9]; OsGlu3-1 (a putative membrane-bound endo-1,4-beta-glucanase) [83]; OsRPK1 (a Ca^{2+} -independent Ser/Thr kinase [84]; QTL Dro1 (DEEP ROOTING 1) for deep rooting (with an increased gravitropic response) [74]; and *O. sativa* CELLULOSE SYNTHASE-LIKE D1 (OsCSLD1) [85]. Root thickness determines the water uptake, nutrient acquisition, and penetration of the roots [59][86]. QTL qRT9 that has a function regulating both root length and root thickness has been identified. It encodes a basic helix-loop-helix (bHLH) transcription factor, OsbHLH120. Its level of expression is in turn steered by drought-response phytochemicals such as salt, polyethylene glycol, and ABA [87]. In addition to these traits, increased root hair can increase the surface area and enhance moisture and nutrient acquisition from the finest soil pores that remain inaccessible to the root apex [88]. Like root length and thickness, root hair is also linked to a bHLH transcription factor encoded by *O. sativa* ROOT HAIRLESS 1 (OsRHL1) controlling cell epidermal transformation [89].

Root length-controlling expansin genes OsEXPA17, OsEXPA30, and OsEXPB5 are all conserved domains for root hair-specific elements (RHEs) tightly linked with root hair initiation [82][83]. Reduced or short root hair has been observed in mutants of *O. sativa* SEC14-NODULIN DOMAIN PROTEIN (OsSNP1) that encodes a phosphatidylinositol transfer protein [84] and short root hair 2 (srh2) mutant, with a mutation in the XYLOGLUCAN XYLOSYLTRANSFERASE 1 (OsXXT1) gene [85]. Root pulling resistance, a trait that has a high positive correlation with root length, root thickness, branching number, and dry mass in rice [86], is also an indication of drought tolerance (possessing a larger root system).

5. RSA: Vegetative to Reproductive Stage

When the plant reaches the vegetative stage, ground cover occurs faster due to EVV, and this lessens soil evaporation and weed growth and accelerates root uptake of soil water and nutrients. The root length, root number, root density, root thickness, and lateral branching or lateral roots are important at the later stages of plant growth. A QTL controlling linear lateral root number, L-LRN (qLLRN-12), on chromosome 12 guided the development of long-type LR production [87]. Root volume also has a role for auxin in it, and a candidate gene (NAL1) regulates both leaf and root growth [88]. This gene is associated with the QTL qFSR4, which has a role in root volume per tiller, with a 38-kb segment fine mapped on chromosome 4 [89]. LR regulation and root thickness have already been reviewed in previous sections. Another important root organ that not many have focused on is the root tip. According to Robinson et al. [90], continued growth and production of root tips for mobile resource uptake might be more important than total root length. Because of suberisation with time and also exposure to dry soil [91], roots tend to be more apoplastic in nature. However, if the root tips are regenerated or remain unsuberised, then this loss in water uptake can be compensated to some extent [92]. Both auxins (OsIAA23, OsARF16, OsWOX11, and OsWOX12) and cytokinin play a role in root cap regeneration [85].

During the later stages of plant growth, demand for nutrient uptake increases vis-à-vis the seedling and early vegetative stage. Thus, there is a need for the development of new roots to decrease nutrient demand per unit volume of roots. This specifically is required at the flowering and grain-filling stage to facilitate higher grain filling. Lodging tolerance should be another major objective when breeding DSR. Strengthening the culm and lower positioning of panicles can aid in decreasing the risks of root lodging. The QTL STRONG CULM3 (SCM3) develops culm strength in rice [93]. QTLs for higher nutrient uptake with lodging tolerance (qLDG_{3.1}, qLDG_{4.1}) are already reported [47]. They have identified a major QTL, qLR1 (~80 kb), that increases stem length diameter and breaking strength, qLR8 (~120 kb) that improves breaking strength, and many others using sequencing through SNP markers. It is noteworthy to mention that deep sowing in direct-seeded rice has also become a phenomenon wherein it helps the plant to have better anchorage and imparts lodging tolerance.

The grain-filling stage would require more carbon sources diverted to the grains from different parts of the plant. Especially in drought conditions, root carbon can act as a source for grain assimilates [94]. Thus, a higher carbon source accumulation in the roots could be a desirable trait during the grain-filling stage. Additionally, this stage requires continuous uptake of nutrients, so longer roots to acquire more N and enhance the active photosynthesis period of the leaves are more desirable [95].

6. Root Growth and the Role of Phytohormones

Auxin is involved in almost all root trait expressions either directly or indirectly. The inactive or quiescent center (QC) region of the root apical meristematic zone is maintained by auxin. As reported by Friml et al. [96], auxin is also responsible for root cap growth. It was observed that mutant plants with an impaired AUXIN (Aux)/INDOLE-3-ACETIC ACID (IAA) gene family, OsIAA23, developed damaged root caps, thereby inhibiting root growth [97]. Auxin-cytokinin ratio regulates root morphology: a high ratio favors root growth, whereas a low value or higher cytokinin level favors shoot growth [98]. Moreover, crown root development has been found to be controlled by this relation of auxin and cytokinin, which works antagonistically with each other as observed in the case of cytokinin signaling gene WUSCHEL-RELATED HOMEBOX GENE 11 (WOX11). The mutant WOX11 shows a decrease in the number of crown roots [10][57]. YUCCA 1 (OsYUC1) is the key enzyme in auxin biosynthesis [99], whose overexpression enhances crown root formation [100]. Several PIN-FORMED (PIN) genes, OsPIN10a and OsPIN3a [101][102], OsPIN2 [103], and OsPID [104], control the auxin efflux regulating polar transport and also help in crown root development. Mutants linked with auxin-related defects also affect the lateral roots to some extent, for example, lateral rootless 1 (lrl1), lrl2, auxin-resistant mutant 1 (arm1), and arm2 [59,60]. Under low rates of nitrogen, the cytokinin signal decreases; as a result, higher root biomass is achieved [105]. The auxin–cytokinin ratio determines the development of lateral roots. Ethylene primarily inhibits root growth. This hormone either enhances or represses root growth, depending on its concentration. Mainly during drought stress, its concentration is regulated and induces different stress responses. Transcription factor OsEIL1 promotes root elongation, which is also a component in the ethylene signalling pathway [106]. The mutant of *O. sativa* ethylene-responsive factor 2 (Oserf2) developed shorter roots than the wild type [107]. Abscisic acid has a significant role under moisture stress as it regulates the expression of several genes to restrict water loss and at the same time increases water uptake that enhances root growth. This root growth refers to the formation of lateral roots and root hairs, root tip swelling, and increasing water permeability [108].

7. Modeling DSR with Root-Specific Traits

Even though several QTLs have been identified for RSA in rice, an ideal root model for DSR is still lacking. Therefore, amalgamating all the available information from diverse research works on root traits to develop and propose a root model for DSR. The desirable traits and the concerned genes/transporters expressed in the roots and that have shown promising effects (cited in previous sections) are included. The foremost trait is early root vigor, to provide the shoot with the optimum level of nutrients and moisture along with a uniform stand. The gene PSTOL1, an enhancer of early root growth, can facilitate this. QTLs such as qEUE11.1 and qEVV9.1 can also aid in the course. The next is the seedling crown root or the nodal roots: a higher number of nodal roots, are required to uptake immobile soil nutrients such as P, Fe, and Zn from topsoil. The QTL qSOR1 would also produce more surface rooting. On the nutrient uptake front, high-affinity P transporters are required as early as 2 DAG, and OsPT1 and OsPT8 genes can aid in P uptake from 2 to 3 DAG. Unlike for other nutrients, N requirement and uptake continue throughout the crop growth stages, so nitrate transporters active during the entire life cycle are more desirable. Nitrogen transporters such as OsNPF7.2 and OsAMT1;3 can be used for nitrate and ammonium,

respectively. Nitrogen uptake in the later stages of plant growth would require deep roots, and candidate gene DRO1 would satisfy the need for both deep roots and exploiting root angles to generate surface roots. Low xylem diameter for lower hydraulic conductivity with more conservative water-use efficiency and the maximum number of roots should be within a 45° spreading angle. Inverted V-shaped roots are suitable for a DSR deep-dimorphic root system. This new root development at the post-anthesis stage can also aid in proper supply to cater to the high nutrient demand by the growing reproductive organs. During this stage, grain filling would rely on carbon sources present in the vegetative parts of the plant, and thus a higher amount of carbon in the roots is desirable. High root density with fine root hairs can aid in the uptake of moisture from the finest of the pores. The genes and QTLs involved in these post-heading vigor traits are yet to be identified. Higher root number and density would also enhance the root plate, thus imparting lodging tolerance. The QTLs qLDG_{3.1} and qLDG_{4.1} identified in relation to this trait should also be exploited. Already, QTL information has been confirmed for most of the abovementioned traits. Therefore, the further need is pyramiding desirable QTLs together into a required genotype to develop a range of superior cultivars with suitable root architecture for DSR to meet future rice demand under the scenario of climate change.

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