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Root Development Genes in Rice: Regulation of Root-Soil Interactions for Stress Tolerance and Yield Improvement

Ruchun Chen, Dapeng Zhang
Hier Rice Research Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China
Corresponding email: dapeng.zhang@hitar.org

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Abstract The structure and growth of the root system of rice directly affect its ability to absorb water and nutrients. In adverse environments such as drought and high salt content, the role of the root system becomes particularly significant. This study mainly collated the key genes and regulatory relationships related to the formation of the crown roots, lateral roots, changes in root length, root angles, and root hair development. By combining transcriptome, epigenetic, and population genetics research results, it analyzed the response characteristics of these root development-related genes under drought and salt stress conditions, and discussed how to utilize important root development genes and their excellent allelic variations to provide references for the improvement of rice root traits, genetic breeding, and the enhancement of resource utilization efficiency.

Keywords Rice (*Oryza sativa*); Root development; Root-soil interaction; Stress tolerance; Yield formation

1 Introduction

The root system of rice is a typical fibrous root system. It mainly consists of the radicle, the adventitious roots growing from the stem nodes, and a large number of lateral roots and root hairs. In mature plants, the adventitious roots constitute the main structure of the entire root system. The number of lateral roots and root hairs is large, which can significantly increase the contact area between the roots and the soil (Seo et al., 2020). The distribution depth, branching number, and thickness of the roots in the soil jointly determine the root system structure. If the root system is distributed deeper and has more branches, it is more likely to continuously absorb water and nitrogen from the deep soil.

Hormone signaling-related genes (auxin, cytokinin, ethylene, abscisic acid, jasmonic acid, strigolactone, etc.) and their downstream transcription factors, such as RRS1-OsIAA3, OsNAC41-RoLe1-OsAGAP, OsEIL1-OsWOX11, and JAUP1, shape deeper, thicker, or more highly branched root systems by finely regulating the initiation and elongation of crown roots and lateral roots (Gao et al., 2023; Li et al., 2024). Genes related to reactive oxygen species (ROS) homeostasis, cell wall modification, and root barrier structure, such as WOX11-OsPRX130, OsDIR55, and OsHyPRP06/OsR3L1, directly affect drought and salt tolerance and ion balance by regulating the ROS gradient at the root tip, Casparian strip, and lignification barrier development, thereby altering the flux and selectivity of water and ions at the root-soil interface (Zhao et al., 2021).

The regulatory modules such as DRO1, RRS1, OsNAC41-RoLe1-OsAGAP, and WOX11-OsPRX130 can alter the growth angle of roots, the length of roots, and the development of the root crown. After the root structure changes, the water absorption capacity will increase (Han et al., 2024). Under salt stress conditions, root growth is usually significantly inhibited. Salt causes osmotic stress; the accumulation of Na^+ and Cl^- can have toxic effects on the roots. The root tip and different types of roots are often the first sites to sense changes in salt concentration and respond.

This study summarizes the structural characteristics and functional roles of the rice root system at the plant-soil interface, and summarizes the key developmental genes and regulatory modules related to root crown formation, lateral root formation, root length, root growth angle, and root zone structure. It assesses the use of important root development genes and their excellent allelic variations, and discusses how to minimize the risk of yield loss during the improvement of stress resistance, providing research ideas for rice to achieve stable yield and efficient resource utilization through root system improvement.

2 Molecular Architecture of Rice Root Development

2.1 Developmental origin and structural components of the rice root system

The primary/embryonic root originates from the hypocotyl and is the first root to grow in the seedling. After rice emerges from the soil, the primary root only grows for a few days before its growth slows down and its function gradually weakens. The main function of the root system will be replaced by adventitious roots. These adventitious roots mostly grow from the stem nodes and the hypocotyl, and are also called crown roots. They are responsible for absorbing water and nutrients, and also play a role in stabilizing the plant. On the primary root and the crown roots, lateral roots will continue to grow. The number of lateral roots is large, which can significantly increase the number and surface area of the roots (Meng et al., 2019). Root hairs are formed by the differentiation of epidermal cells in the mature zone. Root hairs can expand the contact area between the root and the soil, and are very important for absorbing nutrients such as phosphorus that are not easily mobile. Looking from the root tip upwards, the rice root can be divided into the root cap, meristematic zone, elongation zone and mature zone. Different regions correspond to processes such as cell division, cell elongation and cell differentiation. In the transverse structure, the rice root includes structures such as the cortex, vascular cylinder and conducting tissue. These structures facilitate the adaptation of the rice root to soil environments with strong reductivity, hypoxia or high salt content (Jiang et al., 2025).

2.2 Genetic control of root initiation, elongation, and branching

Rice crown root initiation is mainly regulated by genes such as ARL1/CRL1 and CRL5, which are mostly auxin-responsive LBD or AP2/ERF transcription factors, mediating the transformation of axillary meristems into root primordia. Lateral root initiation and development depend on auxin signaling components such as AUX/IAA, ARF, and LBD, and their downstream cell cycle genes. GWAS and QTL analyses have revealed multiple genes and loci related to maximum root length and root number (Zhang et al., 2020). Root elongation is regulated by the activity of the root apical meristem and cell elongation. The OsRLR4–OsAUX1 module negatively controls primary root length by regulating auxin accumulation in the root tip and OsAUX1 transporter expression (Sun et al., 2021); overexpression of OsARD4 promotes rapid elongation of the radicle, early crown root/lateral root development, and higher root biomass (Ramanathan et al., 2018). Deep rooting and root angle are controlled by the IGT family gene DRO1 and its homologs. DRO1 and others not only affect root growth angle and depth but are also closely related to yield performance under drought and saline conditions (Kitomi et al., 2020).

2.3 Spatial and temporal expression patterns of root development genes in soil-grown rice

Deep-rooting rice varieties, such as Azucena, usually show higher gene activity in the Z1 root zone. Most of these genes are related to root growth. They also affect how the root system is formed. Shallow-rooting varieties, like IR64, show a different situation. In these varieties, more genes linked to oxidative stress are turned on. This suggests that shallow roots respond more to stress in the environment (Abdirad et al., 2022). When researchers put together gene expression data from several platforms, they found hundreds of genes that mainly work in roots. Many of these genes are important for root development. They also help rice plants handle different kinds of soil stress. What is interesting is that these genes stay quite stable. This is true even when rice varieties or growing conditions change (Moon et al., 2018). As roots start to form, different root types do not follow the same rules. Radicles, crown roots, and lateral roots each show their own gene expression patterns. Their CHH methylation patterns are also not the same at the early stages. This shows that root formation is under tight methylation control. Factors such as DNG702 and DRM2 play a key role in this process. They help decide where important regulatory genes are switched on (Zhang et al., 2021). In real field soil, root growth is influenced by many outside factors. Water supply, salt levels, and soil hardness all matter. These signals affect crown root development through the ethylene–OsEIL1–OsWOX11 pathway. Through this pathway, rice plants can quickly change how many crown roots they produce and where these roots grow. This response is especially useful when the soil is compacted (Li et al., 2024).

3 Core Root Development Genes and Functional Modules

3.1 Key genes regulating root meristem maintenance and cell differentiation

Several transcription factors involved in cell division and cell fate are mainly found in the root apical meristem, particularly around the quiescent center (QC). Typical examples include OsGATA6, OsGRF6, as well as genes from other transcription factor families. These genes do not stay highly expressed throughout the whole root. Instead, their expression becomes weaker as cells move away from the meristematic region and enter the elongation zone, following the developmental progression of the root. At the hormone level, ORR3, a cytokinin response regulator, is strongly expressed in young root meristems. When ORR3 is artificially overexpressed, obvious changes in root growth can be observed. The primary root becomes shorter, and the same trend is seen in adventitious roots. Meanwhile, the meristematic zone is clearly reduced in size. These observations indicate that ORR3 limits meristem activity rather than promoting it. This effect appears to be linked to cytokinin signaling and may further influence auxin synthesis, auxin transport, and processes related to cell wall metabolism (Wei et al., 2025). The RING-H2 finger protein MAL (MERISTEM ACTIVITYLESS) shows a more localized expression pattern and is mainly detected in the crown root meristem. When MAL expression is suppressed using RNAi, crown root development is strongly affected. Both root number and root length are reduced. In addition, cell division in the meristematic zone slows down. At the molecular level, changes are also observed in genes associated with cell wall metabolism and redox regulation, suggesting that MAL is required for maintaining normal meristem function (Jiang et al., 2020).

3.2 Transcription factor networks involved in rice root development

The NAC transcription factor OsNAC2 is an important upstream integrator, mainly expressed in the primary root tip, crown roots, and lateral root primordia. Its overexpression inhibits primary root elongation and crown root formation, while RNAi or CRISPR knockout significantly increases primary root length and the number of crown roots. OsNAC2 can directly bind to the promoters of IAA inactivation-related genes GH3.6/GH3.8, IAA signaling gene OsARF25, and cytokinin oxidase OsCKX4, integrating auxin and cytokinin pathways, and upstream regulating CROWN ROOTLESS (CRL) and CDK-like genes (Mao et al., 2019). The LBD/ASL family member CRL1/ARL1 and its network are core modules of crown root development. Downstream genomic analysis shows that the gene regulatory network controlled by CRL1 includes a large number of auxin signaling elements, root primordia initiation factors, and genes for root meristem specification and maintenance, such as QUIESCENT-CENTER-SPECIFIC HOMEOBOX, etc. (Lavarenne et al., 2019). The WOX-LBD module refines the spatiotemporal control of crown root development. WOX11 is recruited to the LBD16 promoter region by forming a complex with the histone demethylase JMJ706, removing H3K9me2 and activating LBD16 transcription, thus promoting crown root development; while the LBD16 protein interacts with WOX11, feedback interfering with the formation of the WOX11-JMJ706 complex (Geng et al., 2024). Besides NAC, LBD, and WOX, the TOPLESS-related corepressor OsTPR1 regulates auxin distribution and sensitivity by regulating the expression of PIN family efflux carriers (OsPIN1a/b/c, OsPIN2, OsPIN5a), with its overexpression reducing and RNAi increasing lateral root density (Hou et al., 2025).

3.3 Natural genetic variation and functional diversity of root development genes

Researchers used GWAS, TWAS, and eGWAS to study root traits in rice. In total, 12 root traits were analyzed using 57 rice accessions. The analysis identified several genes that are likely important for root development. One of these genes is OsENT1. This gene encodes a nucleoside transporter. The results show that OsENT1 is negatively related to several crown root and lateral root traits. In simple terms, higher OsENT1 activity is linked to weaker root development. Another gene, OsEXPA31, is an α-expansin gene. It shows a close relationship with crown root diameter. Root diameter is also affected by OsSPL14. In addition, OsDEP1 is linked to nitrogen use efficiency and drought tolerance, which are important traits under stress conditions (Wei et al., 2023). When individual genes were examined, OsRLR4 showed clear differences between wild rice and cultivated rice. This gene displays strong selection signals during domestication. Different OsRLR4 alleles have a direct impact on primary root growth. They also affect how auxin is distributed at the root tip. These findings suggest that OsRLR4 played an important role in helping rice adapt during domestication (Wang et al., 2025). Further GWAS analysis focused on root hair traits, including root hair length and density. This analysis identified 18 new genomic regions. These regions mainly influence root hair density. They do this by controlling epidermal cell differentiation, rather than changing cell size. Most of the candidate genes are involved in basic developmental processes. Many of these genes have not been reported before in studies on rice or Arabidopsis (Hanlon et al., 2023).

4 Hormonal and Signaling Pathways Linking Roots to Soil Conditions

4.1 Auxin-mediated signaling pathways in root growth and soil sensing

Under low phosphorus supply conditions, using the DR5 reporter system and IAA content measurement, the auxin response in the root hair zone was significantly enhanced; the auxin signal originates from the root tip and is transported to the differentiation zone via OsAUX1, driving root hair elongation to increase surface area and phosphorus acquisition from the topsoil layer. The osaux1 mutant showed significantly shorter root hairs and reduced phosphorus absorption under low phosphorus conditions (Giri et al., 2018). In the IAA13 dominant inhibitory mutant, both the number of lateral roots and the aerenchyma formed by cortical cell lysis were significantly reduced; further yeast two-hybrid and ChIP analyses showed that IAA13 interacts with ARF19, which directly activates downstream genes such as LBD1-8, which are highly expressed in the cortex and lateral root primordia. Inactivating mutations or inhibiting auxin transport simultaneously reduced the frequency of aerenchyma and lateral root formation (Yamauchi et al., 2019).

4.2 Roles of ABA, cytokinin, and ethylene in soil stress-responsive root development

Using ABA biosynthesis mutants and chemical inhibitors, it was found that ethylene-induced radial expansion of the root cortex was significantly reduced in the absence of ABA, and the root tip became thinner and more easily penetrated compacted layers; exogenous ABA treatment restored cortical expansion without changing ethylene levels (Huang et al., 2022). At low concentrations, ABA treatment can maintain the size of the root apical meristem to some extent, while at high concentrations or in compacted environments where endogenous ABA levels are elevated, it inhibits cell elongation and promotes radial expansion, leading to shorter main roots and a "swollen root" phenotype (Qin et al., 2022). The bZIP transcription factor OsbZIP46, downstream of the ABA signal, directly binds to the OsYUC8 promoter to activate its transcription. After blocking auxin synthesis, the inhibitory effect of ABA on main root elongation was significantly weakened, and the root diameter decreased. The roots of mhz4 and other ABA-deficient mutants are largely insensitive to ethylene treatment, with the primary root maintaining a length close to that of the control in the presence of ethylene; however, supplementing with ABA restores the inhibitory effect of ethylene on root elongation. Ethylene treatment induces the transcription of ABA synthesis genes such as MHZ4 and increases ABA content in the roots, forming an "ethylene → ABA → root growth inhibition" signaling cascade (Ma et al., 2014). Under drought conditions, CRISPR/Cas9 knockout of OsERA1 enhances ABA signaling sensitivity, leading to stronger expression of ABA-induced genes in the roots during osmotic stress treatment, but these mutants have longer primary roots under non-stress conditions (Ogata et al., 2020).

4.3 Crosstalk between hormonal signaling and transcriptional regulation of root development genes

Abscisic acid (ABA) and ethylene both affect the auxin synthesis gene OsYUC8, which is also called REIN7. ABA controls OsYUC8 through OsbZIP46. Ethylene works through OsEIL1. Because of this regulation, the level of indole-3-acetic acid (IAA) increases in the root tip. When root growth is inhibited, the osyuc8 mutant does not respond to either ABA or ethylene. Even when the amount of ABA or ethylene is very low, plants that overexpress OsYUC8 still develop short and thick roots (Huang et al., 2022). Ethylene also affects crown root formation through gene regulation. It activates WOX11 expression by OsEIL1. After that, WOX11 combines with the demethylase JMJ706. This complex is recruited to the LBD16 promoter. There, it removes the H3K9me2 mark and turns on LBD16 expression, which helps crown roots form. When LBD16 protein builds up, it binds back to WOX11. This binding prevents WOX11 from forming a complex with JMJ706, creating a negative feedback loop (Dabravolski and Isayenkov, 2025; Das et al., 2025). The shi1 mutant shows a typical root system with low auxin levels and is more sensitive to ABA. OsSHI1 promotes the production of auxin and brassinosteroids. It does this by activating OsYUCCA genes and the BR synthesis gene D11. At the same time, OsSHI1 induces OsNAC2, which suppresses ABA signaling. In this way, OsSHI1 helps balance root growth and drought resistance. This gene is directly regulated by OsARF19 from the auxin pathway, LIC from the BR pathway, and OsZIP26/86 from the ABA pathway (Duan et al., 2023). Under drought and salt stress, crown root development is also controlled by OsWOX11. OsWOX11 works together with the ethylene response factor OsERF3. They repress the expression of OsRR2, a type-A cytokinin response regulator. This weakens cytokinin signaling and shifts the balance toward auxin action. The wox11 mutant has much shorter root hairs. It also shows a weaker response to ethylene-induced crown root initiation when grown in compacted soil (Dabravolski and Isayenkov, 2025).

5 Root Development Genes in Root–Soil Interface Processes

5.1 Genetic regulation of root plasticity under heterogeneous soil environments

In this study, researchers worked on both traditional rice and improved rice. They tested 40 different rice genotypes. The main focus was on root traits. These included root dry weight, root length density, and the ratio of lateral roots. The roots were not tested in just one setting. Instead, the plants were grown under different conditions. These conditions included drought stress, re-watering after drought, low phosphorus supply, and different planting methods such as direct sowing and transplanting. The results were quite clear. Rice genotypes with high yield and stable yield usually had better root systems. When the environment became stressful, these plants still kept higher root dry weight and longer roots. In another experiment, researchers studied 274 rice germplasm resources. They measured 35 traits related to root shape and structure. These measurements were done under normal water conditions and also under water shortage. A large number of images were collected during the experiment. Around 45 000 root scanning images and 25 000 images of root base cross-sections were obtained. With these data, the researchers carried out genome-wide association studies (GWAS). Under normal water supply, 104 loci were linked to root traits. Under water stress, 106 loci were found. In addition, 76 loci were related to changes in root traits under different conditions (Kadam et al., 2017).

5.2 Influence of root development genes on root exudation and rhizosphere activity

The drought-tolerant rice variety Luodao 998 showed much less suppression of both main roots and lateral roots than the sensitive variety Nipponbare. When drought stress occurred, most organic acids in the root exudates of Luodao 998 increased. At the same time, the content of amino acids generally went down. In contrast, Nipponbare showed only a small increase in organic acids, and some amino acids were still released from the roots. Results from 16S rRNA amplicon sequencing indicated that drought stress did not cause obvious changes in the α-diversity of rhizosphere bacterial communities in either genotype. However, the β-diversity showed clear differences between the two varieties. Under drought conditions, Actinobacteria and several plant growth-promoting bacteria, such as Bacillus, were strongly enriched in the rhizosphere of Luodao 998 (Li et al., 2023). Mantel and Procrustes analyses further showed a strong relationship between the structure of bacterial communities and the metabolic profiles of root exudates. In particular, the abundance of dominant genera, including Streptomyces and Bacillus, was closely linked to the levels of certain organic acids and amino acids. In addition, ABA and JA, which act as signaling hormones in rice root exudates, were able to regulate the abundance of Streptomyces even when plants were not present.

5.3 Implications for nutrient mobilization and root–soil physicochemical interactions

When the genes related to root development change, they will directly affect the morphology and secretion mode of the roots. Once the root structure is altered, the environment between the roots and the soil will also change. The way nutrients move at the root-soil interface will change, and the physical and chemical conditions of the soil will also be affected. The ability of rice to absorb nutrients will be affected, and this effect will be more obvious when the soil is poor or under stress. Some genes can control the growth depth and angle of the roots, such as the QTL loci related to deep-rooted traits, which can increase the length of the roots in the deep soil, helping rice better absorb nitrate nitrogen and water from the deep soil. Some other genes will affect the number of crown roots, the density of lateral roots, and the formation of root hairs. These changes are beneficial for rice to absorb nutrients from the surface soil, especially elements such as phosphorus and potassium (Meng et al., 2019). Under different water conditions, some genes are related to the variability of root anatomical structure. These genes participate in the formation of cortical ventilation tissues and the deposition of pericycle sclerification. When the soil is in a flooded state, these structural changes can enhance the ability of the roots to transport oxygen downward. In drought conditions, they help the roots retain water and regulate the lateral movement of water in the roots.

6 Molecular Responses of Root Development Genes to Soil Stress

6.1 Transcriptional and epigenetic responses of root genes to drought stress

Phenotypic screening of 106 rice accessions under PEG-simulated drought conditions at 1, 3, and 7 days showed that the drought-tolerant variety Heena significantly outperformed the sensitive variety Kiran in root length, root hair number, secondary and adventitious root number, lignin deposition, and vessel area, and maintained higher relative water content and biomass under drought (Tiwari et al., 2020). The two varieties had 1033 and 936 specifically upregulated differentially expressed genes in their roots, respectively. Upregulated genes in Heena were enriched in hormone signaling (especially ABA, JA, and ethylene), typical stress-related genes (LEA, DREB), and numerous transcription factors (AP2/ERF, MYB, WRKY, bHLH), accompanied by enhanced photosynthesis and antioxidant pathways, while Kiran mainly showed oxidative stress and damage response pathways.

In Azucena, Z1 (meristematic/elongation phase) showed significant enrichment of cell cycle, cell division, root growth, and development-related genes under drought, while IR64 Z1 was enriched in oxidative stress response genes. Among the 375 strongly upregulated genes in Azucena Z1, 40 were clearly annotated as key genes for root structure and drought tolerance, including OsbHLH120 and OsNAC10 regulating root diameter, OsPHR3 for lateral root development, aquaporin PIP1;3/RWC3 for water avoidance, and OsMADS18, OsNLA1, etc., related to root length (Abdirad et al., 2022) (Figure 1).

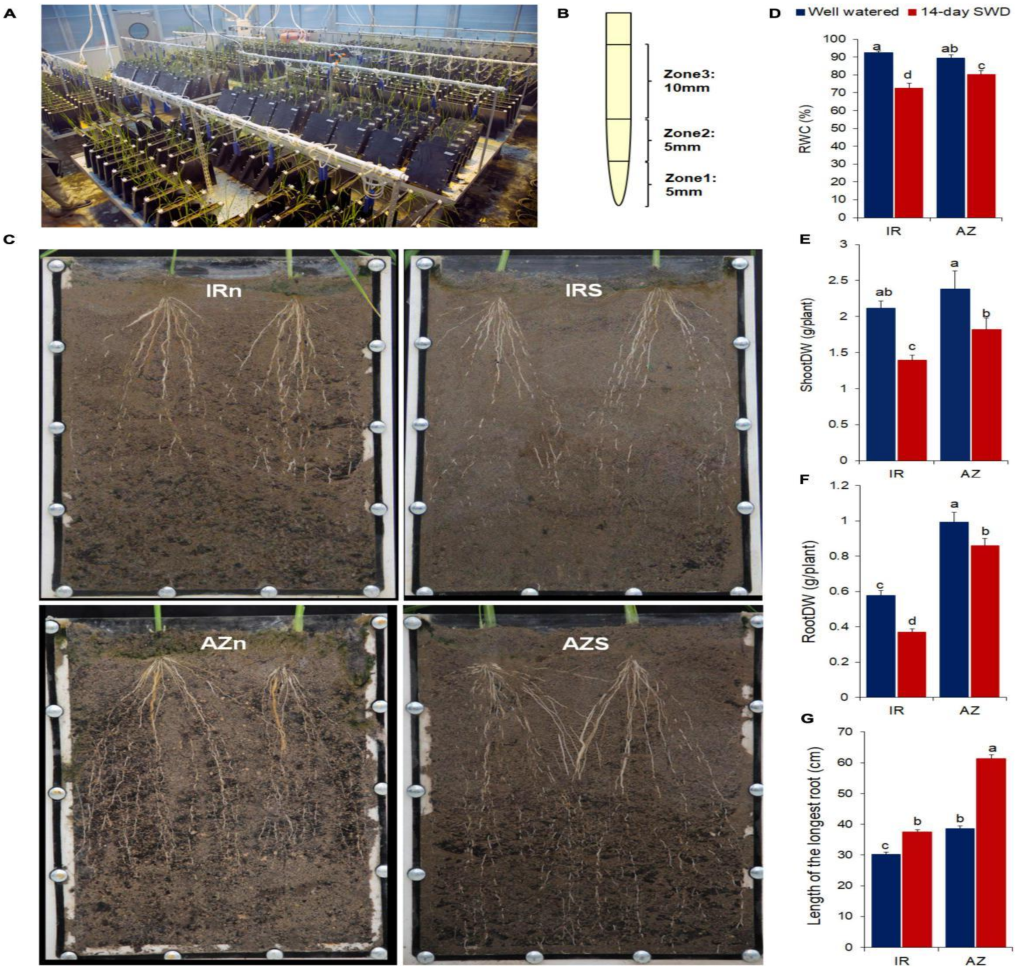

Figure 1 Root sampling and phenotypic responses of two contrasting rice genotypes, Azucena and IR64, to water stress (Adopted from Abdirad et al., 2022)

6.2 Molecular mechanisms underlying root adaptation to salinity stress

The germination and seedling growth experiments of the salt-tolerant variety "Sea Rice 86" (SR86) and the sensitive variety P559 under 100 mM NaCl conditions showed that SR86 maintained bud growth and enhanced root elongation at moderate salt levels, while the root system of P559 was significantly inhibited. The number of differentially expressed genes (DEGs) in SR86 in the roots was much higher than that in P559 (1829 vs. 480); SR86 was enriched in transmembrane ion transport, hormone signaling, and oxidative stress regulation pathways, while P559 mainly activated ABA-related and oxidative stress pathways (Jin et al., 2025). Both genotypes showed an increase in GA3 and GA4 under salt stress, but IAA in the roots of SR86 was significantly increased and JA was decreased, while IAA and JA in the roots of P559 remained basically unchanged.

The expression of vacuolar protein transport-related gene *OsVPS16* was significantly inhibited under salt stress, and the T-DNA insertion mutant vps16 hardly expressed this gene. In the presence of 150 mM NaCl, vps16 exhibited longer main roots, higher survival rates, and lower Na^+/K^+ ratios compared to the wild type DJ. The determination of Na^+ and K^+ contents in the roots indicated that vps16 plants reduced Na^+ transport to the stems and leaves while maintaining higher K^+ levels, accompanied by a decrease in MDA content and an increase in SOD and POD activities (Liu et al., 2025). Under salt stress, there were 1236 DEGs common between vps16 and DJ, with functional enrichment in serine/threonine protein kinase activity, Ca^{2+} signaling, and MAPK signaling pathways. Key upregulated factors included OsSRK1, OsCDPK21, and OsNAC45, etc. Under continuous salt treatment, both salt-tolerant CSR28 and sensitive IR28 significantly accumulated osmotic regulatory substances (various amino acids and sugars), while most organic acids decreased, but the accumulation of osmotic regulators in CSR28 was greater (Lelekami et al., 2025a). The activities of proline, inositol, CAT, and SOD were highly correlated with their encoding genes OsP5CS2, OsIMP, OsNCA1a, and OsSOD-Fe, while H_2O_2 content was correlated with the expression of GLO (ethylmalonyl-CoA oxidase) (Lelekami et al., 2025b). Under salt stress, a total of 249 lipid components were differentially accumulated in the roots, with phospholipids (PA, PC, PS) and sphingolipids (Cer, CerP, Hex1Cer, SPH) significantly increasing, while triglycerides decreased (Xue et al., 2024).

6.3 Gene–environment interactions shaping stress-adaptive root architecture

Cell cycle genes in the meristematic zone reduce DNA synthesis to inhibit growth under conditions of excess water (flooding or paddy fields), but maintain or enhance it under drought/water deficit conditions. In the root cortex and pericycle tissues, genes related to auxin signaling, circadian clock, and small RNA regulation are highly sensitive to extreme changes in water availability, regulating lateral root initiation and cortical aerenchyma formation (Reynoso et al., 2022). Local varieties containing different OsWRKY53 alleles showed differential Na^+ efflux and xylem retrieval capabilities in salt field trials, thereby affecting root-stem Na^+ distribution and plant growth (Yu et al., 2023). Under salt stress, the expression curve of OsWRKY53 shows a time- and dose-dependent negative correlation with OsMKK10.2 and OsHKT1;5, and root Na^+ flux measurements directly correlate this transcriptional difference with the measured Na^+ efflux rate.

7 Conclusions and Future Perspectives

The PSTOL1 locus enhances yield under low phosphorus conditions by promoting early root growth and phosphorus uptake, highlighting the close coupling between root development and nutrient efficiency. The multi-omics studies on drought and salt stress revealed the molecular response network consisting of root tip zone-specific transcriptional responses, epigenetic mark remodeling such as 5mC/5hmC, and reconfiguration of membrane lipids and cell wall components.

Most candidate genes have been analyzed under nutrient solution or single stress conditions. Long-term data is still lacking regarding their comprehensive effects on water/ion flux at the root-soil interface, soil structure (aggregates, porosity), rhizosphere redox state, and microbial communities under realistic field conditions with multiple stresses (drought × high temperature × nutrient deficiency × salt/secondary hardpan).

In the future, rice root molecular biology, combined with CRISPR/Cas, precise insertion, and multi-gene editing technologies, will be used to superimpose deep roots, shallow roots, aeration, root hair/root diameter, and specific secretory metabolic modules within the same genetic background. High-throughput field root phenotyping platforms and soil sensing networks will then be used to test their comprehensive contributions to nutrient use efficiency, yield stability, methane emissions, and soil health under realistic agricultural field conditions.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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