Rice Genomics and Genetics 2025, Vol.16, No.3, 150-158
http://cropscipublisher.com/index.php/rgg

Review Article Open Access

Root System Architecture in Rice: A study of Genetic and Environmental Influences

Deshan Huang, Yuandong Hong, Haiying Huang
Hier Rice Research Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China
Corresponding email: haiying.huang@hitar.org

Rice Genomics and Genetics, 2025, Vol.16, No.3 doi: 10.5376/rgg.2025.16.0014
Received: 19 Apr., 2025
Accepted: 30 May, 2025
Published: 18 Jun., 2025

Preferred citation for this article:
Huang D.S., Hong Y.D., and Huang H.Y., 2025, Root system architecture in rice: a study of genetic and environmental influences, Rice Genomics and Genetics, 16(3): 150-158 (doi: 10.5376/rgg.2025.16.0014)

Abstract The root system architecture (RSA) of rice is a critical determinant of plant health, growth yield, and resilience to environmental stresses. This study explores the genetic and environmental factors influencing rice RSA, highlighting the importance of root traits such as length, number, density, and angle in nutrient and water uptake. Genetic studies have identified numerous quantitative trait loci (QTLs) and candidate genes, such as *PSTOL1* and *DRO1*, which play significant roles in improving RSA under various conditions. Advances in phenotyping technologies, including non-invasive imaging and high-throughput methods, have facilitated detailed studies of RSA, thereby promoting the development of rice varieties with optimized root systems. Environmental factors, such as drought and nutrient availability, also have significant impacts on RSA, necessitating adaptive strategies to enhance stress tolerance. This study emphasizes the potential of integrating genetic research with advanced phenotyping technologies, providing new strategies for breeding rice varieties with superior RSA, ultimately contributing to increased yield and resource-use efficiency.

Keywords Root system architecture (RSA); Quantitative trait loci (QTLs); Phenotyping technologies; Genetic variation; Environmental stress adaptation

1 Introduction

Root system architecture (RSA) is a critical determinant of plant fitness, crop performance, and grain yield in rice. RSA describes the spatial configuration of root tissues within the soil, which is essential for efficient nutrient and water uptake, anchorage, and interaction with the soil environment (Rogers and Benfey, 2015). The ability of rice plants to adapt to various abiotic stresses, such as drought and nutrient deficiencies, is largely influenced by the structure and functionality of their root systems (Ranjan et al., 2022). Given the increasing challenges posed by climate change and the need for sustainable agricultural practices, optimizing RSA in rice is pivotal for enhancing resource-use efficiency and ensuring food security (Dorlodot et al., 2007; Maqbool et al., 2022).

The development and plasticity of RSA in rice are governed by a complex interplay of genetic and environmental factors. Genetic influences include the identification and manipulation of quantitative trait loci (QTLs) and specific genes that regulate root traits such as root length, number, density, and angle (Panda et al., 2021; Karnatam et al., 2023). Advances in genomics and marker-assisted selection have facilitated the discovery of key genes like *PSTOL1*, *qSOR1*, and *DRO1*, which are associated with improved root growth and stress resilience (Khan et al., 2016). Environmental factors, including soil moisture, temperature, and nutrient availability, also play a significant role in shaping RSA. The ability of rice roots to exhibit plasticity in response to these environmental cues is crucial for maintaining plant health and productivity under varying conditions (Ye et al., 2018; Wedge et al., 2019).

This study aims to provide a comprehensive overview of the current understanding of RSA in rice, focusing on both genetic and environmental influences. The objectives are to Summarize the key genetic determinants of RSA in rice, including recent discoveries of QTLs and candidate genes. And discuss the impact of environmental factors on RSA and the adaptive mechanisms employed by rice plants. Highlight the potential applications of RSA research in rice breeding programs aimed at improving stress tolerance and resource-use efficiency.

2 Genetic Factors Influencing RSA in Rice

2.1 Major RSA-related Genes

Key genes such as Deeper Rooting 1 (*DRO1*) and Lateral Organ Boundaries Domain (LBD) genes play significant roles in root elongation and lateral root development. *DRO1* is particularly notable for its influence on root depth, which is crucial for water and nutrient acquisition in rice (Panda et al., 2021; Zhao et al., 2022). LBD genes are involved in the formation of lateral roots, contributing to the overall root system architecture (RSA) by enhancing root branching and increasing the root surface area for better resource uptake (Abdirad et al., 2022).

Root hair density and length are critical for nutrient absorption and soil interaction. Genes such as Xyloglucan Endotransglucosylase/Hydrolase (XTH) family members, specifically XTH19 and XTH23, have been identified to regulate lateral root development and root hair formation under stress conditions like salinity (Xu et al., 2020; Daryani et al., 2021). These genes are induced by environmental stressors and play a role in modifying root hair characteristics to adapt to changing soil conditions.

Phytohormones such as auxins, cytokinins, and gibberellins are central to the regulation of RSA. Auxins are crucial for root initiation and elongation, influencing genes like AUX/IAA and PIN1b, which are involved in auxin transport and signaling (Abdirad et al., 2022; Zhao et al., 2022). Cytokinins regulate root growth by balancing cell division and differentiation, while gibberellins are involved in root elongation and lateral root formation. The interplay between these hormones creates a complex network that modulates root architecture in response to both intrinsic genetic factors and external environmental cues (Jung and McCouch, 2013; Sharma et al., 2021; Han, 2024).

2.2 Quantitative trait loci (QTLs) associated with RSA

Quantitative trait loci (QTL) mapping has been instrumental in identifying regions of the genome associated with RSA traits. Studies have mapped numerous QTLs related to root traits across different rice varieties, revealing significant genetic variation that can be exploited for breeding purposes (Xiong et al., 2021). For instance, QTLs like *qSOR1* and *PSTOL1* have been identified for their roles in surface rooting and early root growth, respectively, under various environmental conditions (Dorlodot et al., 2007; Panda et al., 2021).

Genome-wide association studies (GWAS) have provided deeper insights into the genetic basis of RSA by associating specific genetic markers with root traits across diverse rice populations. These studies have identified several candidate genes and QTLs that are conserved across different species, including rice, maize, and sorghum, highlighting the potential for cross-species genetic improvement (Wedger et al., 2019; Tripathi et al., 2020; Karnatam et al., 2023). GWAS has also facilitated the discovery of novel genes involved in root development, such as those related to drought adaptation and stress responses (Figure 1) (Abdirad et al., 2022).

2.3 Advances in molecular breeding for rsa improvement

Gene editing technologies like CRISPR-Cas9 have revolutionized the field of molecular breeding by enabling precise modifications of RSA-related genes. This technology has been used to edit genes such as *DRO1* and other key regulators of root development, allowing for the creation of rice varieties with optimized root systems for better resource use efficiency and stress tolerance (Panda et al., 2021; Zhao et al., 2022).

Marker-assisted selection (MAS) leverages genetic markers linked to desirable RSA traits to accelerate the breeding process. By using markers associated with QTLs for root traits, breeders can select for rice varieties with improved root architecture more efficiently. This approach has been successfully applied to incorporate traits like deep rooting and enhanced lateral root formation into new rice cultivars, thereby improving their adaptability to various environmental conditions (Dorlodot et al., 2007; Jung and McCouch, 2013; Zhang et al., 2021).

3 Environmental Factors Shaping RSA in Rice

3.1 Soil properties

Soil texture and compaction significantly influence the root system architecture (RSA) of rice. Different soil textures can alter the depth and spread of roots, impacting the plant's ability to access water and nutrients. For instance, X-ray computed tomography studies have shown that rice cultivars exhibit varying RSA plasticity in response to different soil textures (Chen et al., 2021; Gao et al., 2021). The cultivar Azucena displayed low RSA plasticity across various substrates, while Bala's root depth was notably affected by soil hardness, indicating a genotype-specific response to soil compaction. Understanding these interactions can help in breeding rice varieties with optimized RSA for specific soil conditions.

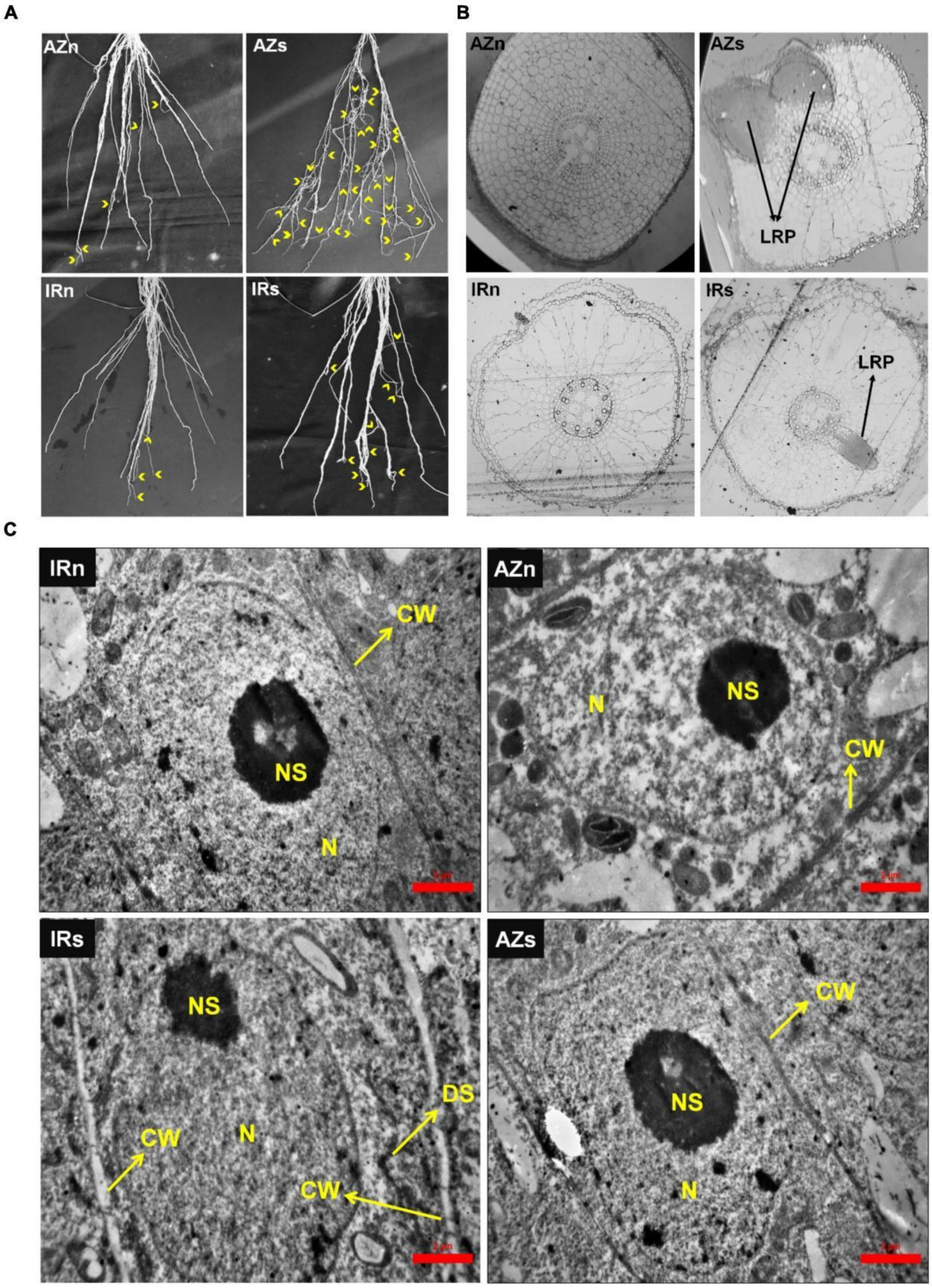

Figure 1 Lateral root expansion and structural and ultrastructural studies of Azucena and IR64 root tips in response to water stress (Adopted from Abdirad et al., 2022)

Image caption: (A) Lateral root expansion in Azucena and IR64 under normal and stress conditions; Yellow arrows indicate lateral roots. (B) Tissue structural studies of root (zone3) in both genotypes under normal and stress conditions shows the number of lateral root primordia. (C) Ultrastructural studies of root meristematic cells in both genotypes under normal and stress conditions shows cell wall thickening in IR64 in response to stress. IRn, IR64 genotype under normal condition; IRs, IR64 genotype under water-stress condition; AZn, Azucena genotype under normal condition; AZs, Azucena genotype under water-stress condition; Z1, Root Z1; Z2, Root Z2; Z3, Root Z3; CW, cell wall; N, nucleus; NS, nucleolus; DS, dictyosome; LRP, lateral root primordium (Adopted from Abdirad et al., 2022)

Nutrient availability, particularly nitrogen and phosphorus, plays a crucial role in modulating RSA. Efficient nutrient uptake is often linked to specific root traits such as root length, density, and branching patterns. For example, the presence of certain quantitative trait loci (QTLs) and transporters for nutrients has been identified as critical for developing an ideal RSA that enhances nutrient uptake efficiency (Liu et al., 2021). Marker-assisted selection and QTL cloning are being utilized to exploit these genetic variations, aiming to optimize RSA for better nutrient acquisition (Dorlodot et al., 2007).

3.2 Water availability

Drought stress triggers significant changes in RSA to enhance water uptake. Rice plants with a deep and branched root system are better equipped to access water from deeper soil layers. Studies have shown that drought-tolerant genotypes like Azucena enhance root growth and exploration under water stress, whereas drought-susceptible genotypes like IR64 may rely more on cell insulation and antioxidant systems to withstand stress (Teramoto et al., 2020; Ranjan et al., 2022). The identification of QTLs and genes associated with RSA under drought conditions has been pivotal in breeding drought-tolerant rice varieties (Maqbool et al., 2022).

Waterlogging conditions also necessitate specific RSA adaptations. Rice plants often develop aerenchyma, which are air-filled spaces in the root cortex, to facilitate oxygen transport to submerged roots. This adaptation helps in maintaining root function and overall plant health under hypoxic conditions. The genetic basis for these adaptations includes various QTLs and genes that regulate root growth and development in response to waterlogging (Rogers and Benfey, 2015; Panda et al., 2021).

3.3 Interaction with soil microbiota

Mycorrhizal fungi form symbiotic relationships with rice roots, significantly influencing RSA. These fungi enhance nutrient uptake, particularly phosphorus, by extending the root's absorptive surface area. The interaction between mycorrhizal fungi and rice roots can lead to changes in root branching and length, optimizing the plant’s ability to access soil nutrients (Rogers and Benfey, 2015). This symbiosis is crucial for improving nutrient use efficiency and overall plant health.

The rhizosphere, the soil region influenced by root exudates, hosts a diverse microbial community that interacts with rice roots. These microbial interactions can modulate RSA by influencing root growth patterns and nutrient uptake. For instance, certain beneficial microbes can promote root branching and elongation, enhancing the plant's ability to acquire nutrients and water (Rogers and Benfey 2015; Rogers et al., 2016). Understanding the dynamics of the rhizosphere microbial community and its impact on RSA is essential for developing sustainable agricultural practices.

4 Case Study

4.1 Criteria for selecting the case study

The selection of the case study focused on identifying a genetic pathway with significant influence on root system architecture (RSA) in rice, particularly under environmental stress conditions. The *DRO1* gene was chosen due to its well-documented role in enhancing drought tolerance by promoting deeper root growth, which is crucial for water uptake during periods of water scarcity. This gene has been extensively studied and validated in various research contexts, making it an ideal candidate for a detailed analysis (Panda et al., 2021).

4.2 Detailed analysis of a specific genetic pathway influencing RSA

The *DRO1* (Deeper Rooting 1) gene is a key genetic determinant of root depth in rice. It has been shown to significantly influence the angle of root growth, promoting deeper rooting systems that enhance the plant’s ability to access water from deeper soil layers. This trait is particularly beneficial under drought conditions, where surface water is limited (Daryani et al., 2021). The *DRO1* gene functions by modulating the gravitropic response of roots, thereby altering their growth direction and enabling the plant to maintain water uptake during periods of drought (Figure 2) (Panda et al., 2021).

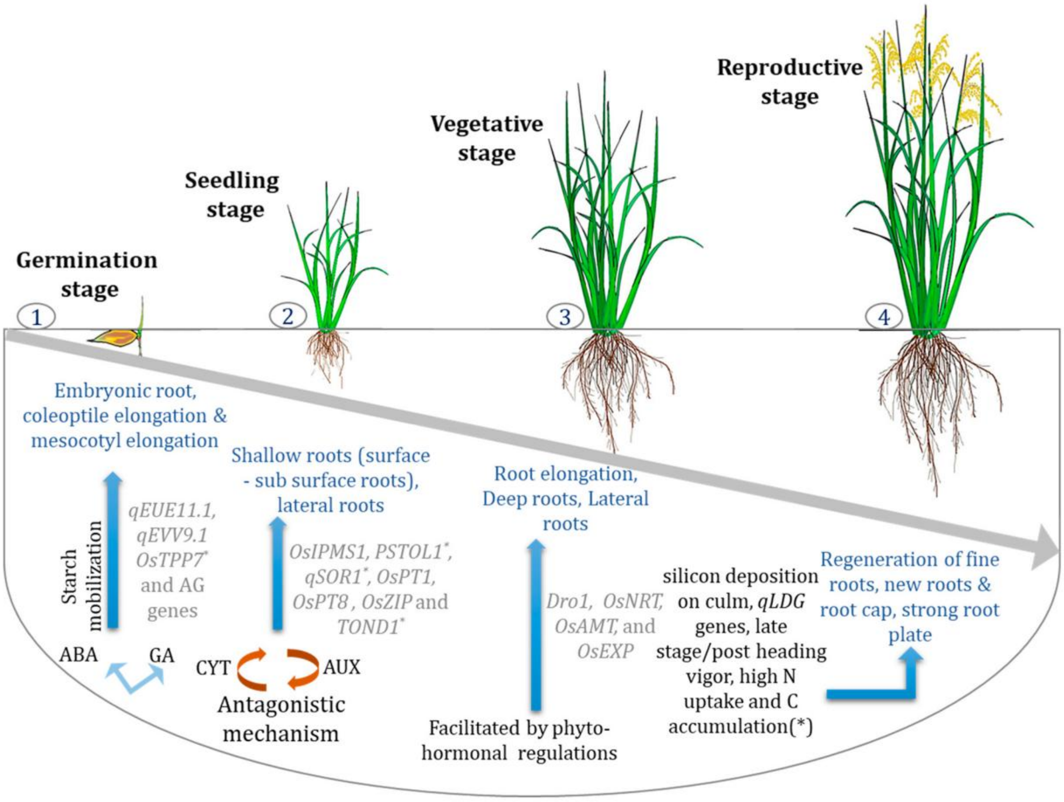

Figure 2 Ideal DSR root system with root-specific traits and genes/QTLs at different stages of growth. The varying growth stages have different requirements of root morphology and associated genes/QTLs (Adopted from Panda et al., 2021)

Image caption: (1) The germinating seed requires AG genes for germination: *qEUE11.1* and *qEVV9.1* for early high seedling vigor and *qSOR1* for better surface rooting. (2) From the nutrient perspective, the seedling stage would require *OsPT1* and *OsPT8* for P uptake, *OsZIP* genes for Zn uptake, and *TOND1* for nitrogen deficiency tolerance, supplemented with *PSTOL1* (a root growth enhancer). (3) The vegetative stage needs DRO genes that articulate the roots working in complementation with *SOR*, *OsNRT*, and *OsAMT* genes for nitrogen transport efficiency, expansin genes (such as *OsEXP*) for growth of root hair and increased root length, and most of the roots are ideally at a 45° angle with each other measured from the base. (4) The reproductive stage needs better anchorage and root spread, higher silicon deposition on culm supplemented with *qLDG* genes for lodging tolerance, higher nutrient and moisture uptake compensated with more fine roots, new roots and root cap development, high N uptake, and C accumulation. * The genes/QTLs for these attributes are yet to be identified (Adopted from Panda et al., 2021)

4.3 Integration of genetic and environmental insights from the case study

The integration of genetic and environmental insights reveals that the *DRO1* gene's influence on RSA is not only a genetic trait but also an adaptive response to environmental stress. Studies have shown that rice varieties with the *DRO1* gene exhibit improved drought tolerance due to their deeper root systems, which allow them to access water from deeper soil layers (Kim et al., 2020; Daryani et al., 2021). This genetic trait interacts with environmental factors, such as soil moisture levels, to optimize water uptake and maintain plant growth under adverse conditions. The ability of *DRO1* to enhance root depth and drought tolerance highlights the importance of considering both genetic and environmental factors in breeding programs aimed at improving crop resilience (Abdirad et al., 2022).

4.4 Implications for future research and breeding programs

The findings from the case study of the *DRO1* gene have significant implications for future research and breeding programs. The ability to manipulate root architecture through genetic pathways like *DRO1* offers a promising avenue for developing rice varieties with enhanced drought tolerance and resource-use efficiency. Future research should focus on identifying and characterizing additional genes and QTLs that influence RSA, as well as understanding their interactions with environmental factors (Abdirad et al., 2022). Breeding programs can leverage these insights to develop new rice cultivars with optimized root systems that are better equipped to withstand environmental stresses, thereby improving crop yield and stability in diverse growing conditions (Daryani et al., 2021).

5 Implications for Rice Yield and Resilience

5.1 Relationship between RSA and nutrient uptake efficiency

Root system architecture (RSA) plays a crucial role in nutrient uptake efficiency in rice. The spatial arrangement of roots within the soil directly influences the plant's ability to access essential nutrients. For instance, specific root traits such as root length, density, and angle are pivotal in determining the uptake of nutrients like nitrogen and phosphorus, which are critical for plant growth and yield (Shahzad and Amtmann, 2017). The genetic regulation of RSA involves various genes and quantitative trait loci (QTLs) that modulate these traits, thereby enhancing nutrient use efficiency. Advances in high-throughput phenotyping and genomic tools have facilitated the identification of these genetic components, enabling the development of rice varieties with optimized RSA for better nutrient acquisition (Maqbool et al., 2022).

5.2 RSA contributions to drought and stress tolerance

RSA significantly contributes to drought and stress tolerance in rice by enabling efficient water uptake and maintaining plant stability under adverse conditions. Deep and proliferative root systems are particularly beneficial in water-limited environments as they can access deeper soil moisture reserves (Rogers and Benfey, 2015; Ye et al., 2018). Genes such as *DRO1*, which control root growth angle, and other stress-responsive factors have been identified as key players in enhancing drought tolerance through RSA modifications (Panda et al., 2021). These genetic adaptations allow rice plants to avoid or mitigate the effects of abiotic stresses such as salinity and waterlogging, thereby improving resilience and yield under challenging environmental conditions (Kitomi et al., 2020).

5.3 Opportunities for enhancing RSA for future agricultural challenges

Enhancing RSA presents significant opportunities for addressing future agricultural challenges, particularly in the context of climate change and resource scarcity. By leveraging genetic diversity and advanced breeding techniques, it is possible to develop rice varieties with root systems tailored to specific environmental conditions and stressors (Dorlodot et al., 2007; Ye et al., 2018). Marker-assisted selection and QTL cloning are promising approaches for incorporating desirable RSA traits into new cultivars (Karnatam et al., 2023). Additionally, the integration of non-invasive root phenotyping technologies and spatiotemporal root simulation modeling can further refine our understanding of RSA and its impact on crop performance, paving the way for more resilient and high-yielding rice varieties (Jung and McCouch, 2013; Maqbool et al., 2022).

6 Future Directions

6.1 Emerging tools and technologies for RSA research

The advancement of tools and technologies is pivotal for enhancing our understanding of root system architecture (RSA) in rice. High-throughput sequencing and transcriptome analysis have significantly progressed, enabling the identification and characterization of numerous genes involved in root development (Yoshino et al., 2019). However, the phenotyping of roots remains a challenge due to their hidden nature. Recent developments in non-invasive imaging techniques, such as X-ray CT and MRI, have allowed for more accurate and detailed observation of root systems (Maqbool et al., 2022). Additionally, computer vision applications have facilitated high-throughput phenotyping, making it possible to analyze RSA traits on a large scale. These technologies, combined with forward genetics approaches, can help identify sequence variations in genes that underpin desirable RSA traits, thus aiding in the development of rice varieties with optimized root systems.

6.2 Integrating RSA with systems biology approaches

Integrating RSA research with systems biology approaches offers a comprehensive understanding of the genetic and molecular mechanisms underlying root development. Multi-omics approaches, including genomics, transcriptomics, and phenomics, provide a holistic view of the factors influencing RSA (Yoshino et al., 2019). For instance, the integration of genome-wide association studies (GWAS) with QTL mapping has led to the identification of meta-QTLs and candidate genes associated with RSA traits (Daryani et al., 2021). These integrated datasets can be used to develop climate-resilient rice varieties by targeting specific genes and pathways involved in root development and stress responses. Moreover, the use of Bayesian networks and machine learning models can improve the prediction of RSA traits from genotypic data, facilitating the selection of superior genotypes for breeding programs (Sharma et al., 2021).

6.3 Breeding strategies for optimal RSA in diverse agroecosystems

Breeding strategies aimed at optimizing RSA must consider the diverse agroecosystems in which rice is cultivated. Identifying and utilizing natural alleles of key genes, such as *DRO1* and its homologs, can help develop rice varieties with root systems adapted to specific environmental conditions, such as saline or drought-prone soils (Kitomi et al., 2020). Marker-assisted selection and QTL cloning are essential tools for incorporating desirable RSA traits into breeding programs (Dorlodot et al., 2007). Additionally, understanding the genetic flexibility and evolutionary mechanisms of RSA in different rice strains, including weedy rice, can provide insights into developing competitive and resilient root systems (Wedger et al., 2019; Piacentini et al., 2023). By focusing on the genetic and phenotypic diversity of RSA traits, breeders can create rice varieties that optimize water and nutrient uptake, enhance stress tolerance, and ultimately improve yield in various agroecosystems (Panda et al., 2021; Abdirad et al., 2022).

7 Conclusion

The study of root system architecture (RSA) in rice highlights the significant role of RSA in enhancing resource-use efficiency and grain yield, particularly under stress conditions such as drought and nutrient deficiency. Key genetic factors influencing RSA include quantitative trait loci (QTLs) and specific genes like *PSTOL1*, *qSOR1*, and *DRO1*, which have been identified and validated for their roles in root growth and stress adaptation. Environmental factors also play a crucial role, with RSA traits such as root length, density, and branching being critical for nutrient and water uptake under varying soil conditions. Advances in phenotyping technologies, including non-invasive imaging and high-throughput genotyping, have facilitated the detailed study of RSA, enabling the identification of genetic variations and the development of rice varieties with optimized root traits.

The interplay between genetic and environmental factors in shaping RSA is complex and multifaceted. Genetic factors provide the foundational blueprint for root development, while environmental conditions modulate the expression and effectiveness of these genetic traits. For instance, genes like OsVST1 and various QTLs have been shown to influence root growth patterns, which are further modified by soil moisture, nutrient availability, and other environmental stresses. This synergy between genetics and environment underscores the importance of a holistic approach in RSA research, where both intrinsic genetic potential and extrinsic environmental influences are considered to develop resilient and high-yielding rice varieties.

Future research in RSA should focus on integrating advanced genomic tools with environmental modeling to predict and enhance root traits that contribute to sustainable rice production. The use of genome-wide association studies (GWAS) and meta-QTL analysis can help identify key genetic regions associated with desirable RSA traits, which can then be targeted for breeding programs. Additionally, the development of high-throughput phenotyping platforms and non-invasive imaging techniques will be crucial in accurately assessing root traits in diverse environmental conditions. By leveraging these technological advancements, researchers can develop rice varieties with optimized RSA that are better equipped to cope with climate change and resource limitations, ultimately contributing to global food security and sustainable agriculture.

Acknowledgments

The authors sincerely thank Dr. Chen for carefully reviewing the initial draft of the manuscript and providing detailed revision suggestions. The author also extends deep gratitude to the two anonymous peer reviewers for their valuable comments and suggestions on the initial draft of this study.

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.

References

Abdirad S., Ghaffari M., Majd A., Irian S., Soleymaniniya A., Daryani P., Koobaz P., Shobbar Z., Farsad L., Yazdanpanah P., Sadri A., Mirzaei M., Ghorbanzadeh Z., Kazemi M., Hadidi N., Haynes P., and Salekdeh G., 2022, Genome-wide expression analysis of root tips in contrasting rice genotypes revealed novel candidate genes for water stress adaptation, Frontiers in Plant Science, 13: 792079.
https://doi.org/10.3389/fpls.2022.792079

Chen M., Zhang S., Liu L., Wu L., and Ding L., 2021, Combined organic amendments and mineral fertilizer application increase rice yield by improving soil structure, P availability and root growth in saline-alkaline soil, Soil and Tillage Research, 212: 105060.
https://doi.org/10.1016/j.still.2021.105060

Dorlodot S., Forster B., Pagès L., Price A., Tuberosa R., and Draye X., 2007, Root system architecture: opportunities and constraints for genetic improvement of crops, Trends in Plant Science, 12(10): 474-481.
https://doi.org/10.1016/J.TPLANTS.2007.08.012

Daryani P., Ramandi H., Dezhsetan S., Mansuri R., Salekdeh G., and Shobbar Z., 2021, Pinpointing genomic regions associated with root system architecture in rice through an integrative meta-analysis approach, Theoretical and Applied Genetics, 135: 81-106.
https://doi.org/10.1007/s00122-021-03953-5

Gao M.Y., Chen X.W., Huang W.X., Wu L., and Li H., 2021, Cell wall modification induced by an arbuscular mycorrhizal fungus enhanced cadmium fixation in rice root, Journal of Hazardous Materials, 416: 125894.
https://doi.org/10.1016/j.jhazmat.2021.125894

Han L.Z., 2024, Harnessing the power of PGPR: unraveling the molecular interactions between beneficial bacteria and crop roots, Molecular Soil Biology, 15(1): 8-16.
https://doi.org/10.5376/msb.2024.15.0002

Rogers E., and Benfey P., 2015, Regulation of plant root system architecture: implications for crop advancement, Current Opinion in Biotechnology, 32: 93-98.
https://doi.org/10.1016/j.copbio.2014.11.015

Jung J., and McCouch S., 2013, Getting to the roots of it: genetic and hormonal control of root architecture, Frontiers in Plant Science, 4: 186.
https://doi.org/10.3389/fpls.2013.00186

Karnatam K., Chhabra G., Saini D., Singh R., Kaur G., Praba U., Kumar P., Goyal S., Sharma P., Ranjan R., Sandhu S., Kumar R., and Vikal Y., 2023, Genome-wide meta-analysis of QTLs associated with root traits and implications for maize breeding, International Journal of Molecular Sciences, 24(7): 6135.
https://doi.org/10.3390/ijms24076135

Khan M., Gemenet D., and Villordon A., 2016, Root system architecture and abiotic stress tolerance: current knowledge in root and tuber crops, Frontiers in Plant Science, 7: 1584.
https://doi.org/10.3389/fpls.2016.01584

Kitomi Y., Hanzawa E., Kuya N., Inoue H., Hara N., Kawai S., Kanno N., Endo M., Sugimoto K., Yamazaki T., Sakamoto S., Sentoku N., Wu J., Kanno H., Mitsuda N., Toriyama K., Sato T., and Uga Y., 2020, Root angle modifications by the *DRO1* homolog improve rice yields in saline paddy fields, Proceedings of the National Academy of Sciences of the United States of America, 117: 21242-21250.
https://doi.org/10.1073/pnas.2005911117

Kim Y, Yong S.C., Lee E, Tripathi P., and Kim K.H., 2020, Root response to drought stress in rice (*Oryza sativa* L.), International Journal of Molecular Sciences, 21(4): 1513.
https://doi.org/10.3390/ijms21041513

Liu Q., Liang Z., Feng D., Jiang S., Wang Y., Du Z., Li R., Hu G., Zhang P., Ma Y., 2021, Transcriptional landscape of rice roots at the single-cell resolution, Molecular Plant, 14(3): 384-394.
https://doi.org/10.1016/j.molp.2020.12.014

Maqbool S., Hassan M., Xia X., York L., Rasheed A., and He Z., 2022, Root system architecture in cereals: progress, challenges, and perspective, The Plant Journal, 110(1): 23-42.
https://doi.org/10.1111/tpj.15669

Panda S., Majhi P., Anandan A., Mahender A., Veludandi S., Bastia D., Guttala S., Singh S., Saha S., and Ali J., 2021, Proofing direct-seeded rice with better root plasticity and architecture, International Journal of Molecular Sciences, 22(11): 6058.
https://doi.org/10.3390/ijms22116058

Ranjan A., Sinha R., Singla-Pareek S., Pareek A., and Singh A., 2022, Shaping the root system architecture in plants for adaptation to drought stress, Physiologia Plantarum, 174(2): e13651.
https://doi.org/10.1111/ppl.13651

Rogers E., Monaenkova D., Mijar M., Nori A., Goldman D., and Benfey P., 2016, X-ray computed tomography reveals the response of root system architecture to soil texture1, Plant Physiology, 171(3): 2028-2040.
https://doi.org/10.1104/pp.16.00397

Piacentini D., Della Rovere F., Lanni F., Cittadini M., Palombi M., Fattorini L., Cecchetti V., Altamura M.M., and Falasca G., 2023, Brassinosteroids interact with nitric oxide in the response of rice root systems to arsenic stress, Environmental and Experimental Botany, 209: 105287.
https://doi.org/10.1016/j.envexpbot.2023.105287

Shahzad Z., and Amtmann A., 2017, Food for thought: how nutrients regulate root system architecture, Current Opinion in Plant Biology, 39: 80-87.
https://doi.org/10.1016/j.pbi.2017.06.008

Sharma M., Singh D., Saksena H., Sharma M., Tiwari A., Awasthi P., Botta H., Shukla B., and Laxmi A., 2021, Understanding the intricate web of phytohormone signalling in modulating root system architecture, International Journal of Molecular Sciences, 22(11): 5508.
https://doi.org/10.3390/ijms22115508

Sharma S., Pinson S., Gealy D., and Edwards J., 2021, Genomic prediction and QTL mapping of root system architecture and above-ground agronomic traits in rice (*Oryza sativa* L.) with a multitrait index and Bayesian networks, G3, 11(10): jkab178.
https://doi.org/10.1093/G3JOURNAL/JKAB178

Teramoto S., Takayasu S., Kitomi Y., Arai-Sanoh Y., Tanabata T., and Uga Y., 2020, High-throughput three-dimensional visualization of root system architecture of rice using X-ray computed tomography, Plant Methods, 16: 1-14.
https://doi.org/10.1186/s13007-020-00612-6

Tripathi D.K., Rai P., Guerriero G., Sharma S., Corpas F.J., and Singh V.P., 2021, Silicon induces adventitious root formation in rice under arsenate stress with involvement of nitric oxide and indole-3-acetic acid, Journal of Experimental Botany, 72(12): 4457-4471.
https://doi.org/10.1093/jxb/eraa488

Wedger M., Topp C., and Olsen K., 2019, Convergent evolution of root system architecture in two independently evolved lineages of weedy rice, The New Phytologist, 223(2): 1031-1042.
https://doi.org/10.1111/nph.15791

Xiong Q., Hu J., Wei H., Zhang H., and Zhu J., 2021, Relationship between plant roots, rhizosphere microorganisms, and nitrogen and its special focus on rice, Agriculture, 11(3): 234.
https://doi.org/10.3390/agriculture11030234

Xu P., Fang S., Chen H., and Cai W., 2020, The Brassinosteroid (BR) responsive Xyloglucan Endotransglucosylase/Hydrolase 19 (*XTH19*) and *XTH23* genes are involved in lateral root development under salt stress in Arabidopsis, The Plant Journal, 104(1): 59-75.
https://doi.org/10.1111/tpj.14905

Ye H., Roorkiwal M., Valliyodan B., Zhou L., Chen P., Varshney R., and Nguyen H., 2018, Genetic diversity of root system architecture in response to drought stress in grain legumes, Journal of Experimental Botany, 69: 3267-3277.
https://doi.org/10.1093/jxb/ery082

Yoshino K., Numajiri Y., Teramoto S., Kawachi N., Tanabata T., Tanaka T., Hayashi T., Kawakatsu T., and Uga Y., 2019, Towards a deeper integrated multi-omics approach in the root system to develop climate-resilient rice, Molecular Breeding, 39: 165.
https://doi.org/10.1007/s11032-019-1058-4

Zhao J., Jiang L., Bai H., Dai Y., Li K., Li S., Wang X., Wu L., Fu Q., Yang Y., Dong Q., Yu S., Wang M., Liu H., Peng Z., Zhu H., Zhang X., He X., Lei Y., Liang Y., Guo L., Zhang H., Yu D., Liu Y., Huang H., Liu C., Peng S., and Du Y.. 2022, Characteristics of members of IGT family genes in controlling rice root system architecture and tiller development, Frontiers in Plant Science, 13: 961658.
https://doi.org/10.3389/fpls.2022.961658

Zhang T.Q., Chen Y., Liu Y., Lin W.H., and Wang J.W., 2021, Single-cell transcriptome atlas and chromatin accessibility landscape reveal differentiation trajectories in the rice root, Nature Communications, 12(1): 2053.
https://doi.org/10.1038/s41467-021-22352-4