Root System Architecture(RSA) and Drought Tolerance in Rice: Exploring Genetic Mechanisms and Genomic Approaches for Enhancing RSA

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ABSTRACT

Rice is a staple food crop for half of the world's population. Its production and productivity are significantly affected by various abiotic and biotic factors. In recent years, drought has become a critical environmental challenge exacerbated by climate change. Rice is highly vulnerable to water scarcity and leading to substantialreduction in crop yield during drought conditions. However, it has various adaptive mechanisms to cope with adverse environmental conditions. The main objective of this study the mechanisms underlying rice adaptations to water scarcity through Root System Architecture (RSA) and explore novel genomic approaches utilized to enhance RSA. It explores morphological, physiological, biochemical, and molecular mechanisms influencing RSA traits, underscoring the significance of deeper and well-distributed roots in alleviating water stress. Moreover, we discussed the role of key hormones, genes, Transcription Factors (TFs), metabolites, and key regulatory pathways governing RSA in rice. Genomics approaches such as multi-omics, genome-wide association studies (GWAS), Single nucleotide polymorphisms (SNPs), and CRISPR-Cas9 are being leveraged to improve RSA traits. Additionally, we attempt to presents some promising rice genotypes and cultivars from major rice-growing countries, which have enhanced RSA, significant drought tolerance and yield potential under water stress. Moreover, utilization of these knowledge offers wider understanding for breeding rice cultivars with improved RSA that are well adapted to water-scarce environments, thereby contributing to global food security amid climate challenges.

Keywords: Rice, Drought, RSA, DRO1, GWAS, CRISPR-Cas9

1. Introduction

Rice is globally a major food crop and a staple in most of Asian countries. It significantly contributes to people's nutrition and is cultivated across roughly 150 million hectares in about 100 countries. Over the last 50 years, rice demand and production have risen in African countries and other part of the world (Giri et al., 2021). With the global population projected to reach 9.9 billion by 2050, rice production must increase by at least 1% annually to fulfill the demand of growing population. However, environmental stresses (abiotic stresses drought, salinity, extreme temperatures, nutrient deficiencies, and heavy metal accumulation) are encountered as significant factors for substantial yield gaps. These abiotic challenges are expected to reduce global rice production by approximately 32%, resulting in an annual loss of three million tons. Moreover, drought is widespread, affecting about half of the world's arable land and significantly challenging sustainable rice production (Maghboli Balasjin et al., 2022; Normile, 2008; Panda et al., 2021; Ray et al., 2015; Singhal et al., 2016).

Additionally, climate change, global warming, and shifting precipitation patterns are intensifying drought and water stress, which poses significant challenges to rice production and productivity globally. Research findings suggest a rise in multi-year droughts across North America, South America, Asia, and Africa, occurring more often and at shorter intervals than in the past millennium (Wu et al., 2022). At present, drought stress impacts over 42 million hectares of rice fields, and with research projections indicating that by 2050, over half of the arable land could suffer from water scarcity (Jaldhani et al., 2021) and rise in temperature by 1.5–2.0 °C(Armstrong McKay et al., 2022). Drought is defined as a temporary weather phenomenon caused by prolonged precipitation deficiency compared to average conditions. It begins with reduced rainfall and can affect soil moisture, streams, and groundwater, depending on its duration and severity. As a recurring natural event, drought develops gradually, is complex to measure and manage, and has wide-reaching social and economic effects (Eriyagama et al., 2009). Rice is among the crops most sensitive to drought, with severe drought stress potentially causing up to 100% yield loss depending on the plant's growth stage. Two primary types of drought stress are recognized: terminal drought, resulting from a severe lack of water that can lead to plant death, and intermittent drought, where rainfall or irrigation shortages periodically disrupt plant growth but are typically non-lethal (Chengqi et al., 2024; Panda et al., 2021; Polania et al., 2017). Drought significantly hinders rice cultivation, affecting different growth stages and aspects such as morphological (germination, tiller count, grain yield per panicle, plant biomass, height, root structure), physiological (lowered photosynthesis, transpiration, stomatal conductance, water use efficiency, carbon isotope content, chlorophyll content, abscisic acid levels), biochemical (proline, sugar, antioxidants), and molecular levels (changes in gene expression encoding transcription factors and defense proteins) (Pandey & Shukla, 2015). Additionally, water scarcity notably affects rice growth and development, impacting above and underground parts. Roots are the main organs for sensing drought and play a crucial role in mitigating drought stress by increasing root density, root depth, and crown root ratio (Gupta et al., 2020; Kim et al., 2020). During drought stress plants modify roots into thicker and deeper, which facilitates access to water stored in deeper into the soil. At the same time, research reveals that during water scarcity, crops prioritize root growth by reallocating resources from the shoots to the roots (Yoshida & Hasegawa, 1982).

Rice consists of fibrous root system composed of primary, adventitious, and lateral roots the root system plays a crucial role in securing plants in the soil and facilitating the absorption of water and nutrients through a robust root system promoting healthy plant growth and enhancing yield under soil-related stresses (Kawata & Harada, 1975). Similarly, plant systems undergo dynamic physiological changes, signaling stress occurrence and triggering defense mechanisms to combat it. The research noted various alterations in physio-chemical properties during plant drought stress. Heightened drought stress escalates Reactive Oxygen Species (ROS) levels, causing oxidative stress. Similarly, a significant (>9%) decrease in chlorophyll content hampers photosynthetic efficiency. On the other hand, to cope with developed stress, plant defense systems boost various regulatory mechanisms and level of some plant hormones, such as proline content (>25%), total phenolic content (>19%), antioxidant potential (>7%), and epigenetic changes (>56%). These changes strengthen defense mechanisms against oxidative stress, enabling plants to thrive in drought conditions (S. Kumar et al., 2023). These overall phenotypic and genetic variations among rice varieties can be explored for deeper understanding of molecular mechanisms governing drought tolerance can serve as an important tool for developing drought-tolerant rice varieties and ensuring food security (Chengqi et al., 2024).

This paper offers a comprehensive review of the role of RSA in enhancing drought tolerance in rice, highlighting the associated genes, transcription factors, hormones, and regulatory pathways along with Promising rice cultivars and genotypes superior to drought tolerance. Additionally, it explores recent advancements in genomics for improving RSA traits in rice, focusing on drought adaptation. Furthermore, integrating phenotypic and genetic insights with advanced genomics approaches, such as multi-omics, metagenomics, CRISPR-Cas9, and genome-wide association studies (GWAS), is emphasized as a pivotal strategy for developing rice varieties optimized for drought-prone conditions.

2. Root System Architecture (RSA) and drought tolerance in rice

Drought stress is becoming a serious issue in crop cultivation. Therefore, it is essential to conduct various studies and innovate solutions to address this problem. Roots are vital plant organs required to absorb water and nutrients from the soil. Plants have various types of roots, including primary and lateral roots, as well as root hairs, which effectively absorb water and nutrients. The network of different root types in the soil is known as root system architecture (RSA) (Lynch, 1995). Root system architecture pertains to the 3D shape and spatial layout of roots in the soil. It includes the primary root, lateral roots, and adventitious roots (ARs). The root system's 3D layout is composed of root position, number, length, and growth angles (C. Lin & Sauter, 2020; Rogers & Benfey, 2015).

Among different crop species, numerous root characteristics and phenotypes were found significant for maintaining during stress conditions with deeper roots showing consistently beneficial performances. The significance of shallow root phenotypes like crown root growth and root anatomy in drought tolerance does not have enough justifiable evidence Designing an optimal root ideotype for rice in drought-prone areas is challenging due to the diversity of rice-growing environments and the variability in root responses to stress (Ahmadi et al., 2014). The study revealed that there are important components of both deep and shallow-root growth governing drought response. Moreover, the major observations from the research signify that a larger stele diameter was advantageous for crop productivity under drought stress (Siangliw et al., 2022). Roots with a small diameter and a high specific root length provide a larger surface area for moisture absorption, allowing plants to explore greater soil volume for water, and increasing the hydraulic conductance by reducing the apoplastic barrier for water entry into the xylem (Comas et al., 2012; Hernández et al., 2010).

Similarly, Plants adjust their physical and functional characteristics to cope with drought conditions. This adjustment involves changes in water movement through the soil by altering the structure of their root systems. Root systems can prolong the presence of soil water after rainfall, and sustain plants during water stress (Mair et al., 2022). Plants inhibit root growth to avoid undesirable circumstances like low phosphorus levels or high toxic metal concentrations. During drought stress plants reduced root length and density by increasing root diameter, root-shoot mass ratio, and root cortical aerenchyma. These flexible root system characteristics help plants sustain during stress conditions while facilitating growth and development (Teramoto et al., 2020).

A critical area for research could be study and develop knowledge about root architecture and anatomy of crops, as roots play a vital role in absorbing water and nutrients from the soil. In simple terms, roots play an important role in absorbing water and nutrients from the soil. The characteristics of roots, both in terms of their physical appearance and function, influence the growth of the above-ground parts of the plant (shoots) and its overall productivity. The ability of a plant to access water depends on the root system's properties, structure, and networking in the soil. Therefore, enhancing the traits of roots can provide better absorption of soil water, and maintain crop productivity even when facing water scarcity. The root system architecture plays a crucial role in acquiring soil resources, with rice roots shows genetic diversity in terms of thickness and penetration ability (Kim et al., 2020). Compared to other cereal crops, rice has limited adaptation to water-scarce conditions, as it absorbs minimal soil water at depths of 60 cm. In dryland cultivation, where water scarcity is more common, selecting rice varieties with deeper roots could be an effective strategy to reduce drought impacts (Inthapan & Fukai, 1988). A study on 21 aerobic rice genotypes for drought tolerance revealed a significant positive association between grain yield and root length, root volume, root/shoot ratio, and root number. A higher root: shoot ratio offers resistance to drought and enhances crop adaptability in stress conditions. Genotypes with higher root: shoot ratios were identified as potential contributors to drought resistance breeding programs, offering the significance of this trait in selecting plants for the development of drought tolerance cultivars (Quadri et al., 2023). Overexpression of *RePRPs*forms water barriers, such as lignin and suberin, in the root vascular reducing water loss. The higher deposition of lignin and suberin in roots, coupled with decreased transpiration in shoots, helps decrease water loss in rice plants during drought. Furthermore, *RePRPs* overexpression decreases the root osmotic potential, leading to a more negative root cell osmotic pressure and enhancing water use efficiency (M.-C. Lin et al., 2023). Similarly, Rice root length, cortical cell file number, number of roots, and cell size play vital roles in water uptake ability among different root types for adaptation in dry conditions. Enhancing the root system architecture in drought-prone cultivation systems could be an important research area of genetic improvement for efficient water and nutrient utilization as well as rice yield stabilization (Dutta & Sarma, 2022).

3. Molecular Mechanisms of Drought Tolerance through RSA

3.1 Hormonal regulation of rice root system architecture

Hormonal regulation in rice root system architecture (RSA) is governed by genes, phytohormones, and root microbiota, impacting root type, tissue changes, and nutrient uptake efficiency shaping the structure of RSA. Rhizospheric microbes influence rice root development, encouraging natural soil microbes, which can improve sustainable plant growth, development, and yield (Verma et al., 2021). Moreover, root formation and root growth in rice are mediated by various plant growth hormones. Auxin and cytokinins are vital plant hormones in the development of root primordia. Recent findings and research reveal that ABA and GA also have a crucial role in root growth and development (C. Lin & Sauter, 2020). Cytokinin (CK) is produced in the root cap and promotes cytokinesis, sensitivity of the vascular cambium, vascular differentiation, and root apical dominance. On the other hand, auxin (indole-3-acetic acid, IAA) found in young shoot organs stimulates root development and induces vascular differentiation. Moreover, both hormones are involved in regulating root gravitropism (Aloni et al., 2006). Auxins, particularly IAA and Cytokinnins are the important components of a correlative system. Results showed that auxin application indicated a possible check in cytokinin production in the roots by basipolar auxin and its potential delivery to lateral buds. As a result, the increased delivery of cytokinins to the lateral buds stimulates a significant rise in IAA production and export. Therefore, there is a strong mutual interaction between auxin production in the shoots and cytokinin production in the roots, which may play a crucial role in regulating the balance between root and shoot growth (Bangerth et al., 2000). Similarly, the importance of auxin in root development is well known however, the molecular mechanisms governing such traits remain elusive. The characterization of mutant defective crown formation, crown rootless 1 (Crl1) showed that it encodes for positive regulation of crown and lateral roots. Moreover, its expression is directly mediated by ARF (AUXIN RESPONSE FACTOR) in the auxin signaling pathway (Inukai et al., 2005). The rice dominant mutant, root enhancer 1(ren1-D) suppresses plant height, develops a more robust rice root system, and increases crown root number. Multi-omics analysis reveals the activation of a cytokinin oxidase/dehydrogenase (CKX) family gene, *OsCKX4* which is expressed in the shoot base signals for the formation of crown roots by the integration between auxin and cytokinin (Gao et al., 2014).

3.2 Major Genes, TFs, Proteins governing drought tolerance through RSA in rice

Drought poses a significant threat to the growth, development, and grain yield of rice. Understanding genetic and molecular phenomena governing drought tolerance, genes, TFs, and regulatory pathways associated with this trait will provide deeper insights that can help develop innovative strategies and approaches to combat drought stress. Roots are critical for rice growth and development which, provide structural support, absorb water and nutrients, and respond to environmental stresses. The growth and development of rice roots are regulated by genetic and environmental factors, with plant hormones like auxin and cytokinin playing key roles. Advances in understanding the molecular mechanisms underlying root architecture and stress responses offer valuable insights for genetic improvements and the development of suitable crop varieties with enhanced drought stress(Meng et al., 2019; Park & Jeong, 2023)**.**

A deep and extensive root system can assist plants in mitigating water stress by enhancing their ability to acquire water and nutrients. The comprehensive transcriptome analysis of root tips to water stress in two rice genotypes: IR64(a high-yielding lowland shallow-rooted rice variety) and Azucena(mentioned in table 1) (a traditional deep-rooted upland variety) showed that Azucena adopted drought stress by promoting root exploration and growth for access to water, on the other hand, IR64 may primarily rely on cell insulation to endure stress and water retention. Meta-quantitative trait loci (QTL) analysis revealed 288 differentially expressed genes linked to root system architecture (RSA) under drought and normal conditions. Which, can be very useful resources for breeding purposes for improving root traits and drought tolerance in rice (Abdirad et al., 2022). Overexpression of *OsERF71* in rice roots under water stress conditions changes root structure, leading to larger aerenchyma and radial root growth. This root modification, commonly seen in drought-tolerant rice plants, is mediated by overexpression of *OsNAC5*, *OsNAC9*, and *OsNAC10*, for enhanced drought resistance. The *OsERF71*-induced root changes result from the combined overexpression of stress-inducible, cell wall-associated, and lignin biosynthesis genes that play a role in drought tolerance. So, *OsERF71*-mediated root modifications offer new insights and research areas for molecular mechanisms of drought tolerance (Lee et al., 2017). The overexpression of *OsNAC9*, a member of the rice NAC domain family, in rice crops by utilization of root-specific and constitutive promoters, resulted increase in the crop yield by 13%-32% under normal conditions. Field investigation conducted over two seasons revealed that *RCc3:OsNAC9* plants exhibited a significant increase in grain yields of 28%-72% in drought conditions, while *GOS2:OsNAC9* plants did not show significant changes in grain yield. Both transgenic lines of

OsNAC9 showed altered root architecture, characterized by enlarged stele and aerenchyma. Importantly, *RCc3:OsNAC9* roots had significantly larger aerenchyma compared to *GOS2:OsNAC9* roots, indicating enhanced resistance capacity under drought through alteration of root architecture and root phenotype (Redillas et al., 2012). Root-specific overexpression of *OsCCR10* in transgenic rice leads to higher grain yield under field drought conditions, highlighting the role of *OsCCR10*-mediated lignin biosynthesis in drought tolerance. The rice gene CINNAMOYL-CoA REDUCTASE 10 (OsCCR10) is directly activated by the transcription factor *OsNAC5*as shown in figure 1, Overexpression of *OsCCR10* in transgenic rice plants involved in H- and G-lignin biosynthesis enhances drought, salt and ABA tolerance, photosynthetic efficiency, and lignin content in roots (Bang et al., 2022). Expression of the HARDY (HRD) gene from Arabidopsis enhances water use efficiency in rice by enhancing photosynthetic assimilation and reducing transpiration. Low-water-consuming rice cultivars expressing the HRD gene increased shoot biomass under well-irrigated conditions and an adaptive increase in root biomass during drought stress. The HRD gene, an AP2/ERF-like transcription factor, was identified through the study of an Arabidopsis mutant(and-D), enhanced root strength, branching, and cortical cells. Moreover, expression of the HRD gene in rice also regulates drought resistance and salt tolerance (Karaba et al., 2007). Recent studies have indicated a correlation between root elongation and cell wall biosynthesis. The gene *OsGLU3* encodes a membrane-bound endo-1,4-β-glucanase, which performs a critical function in the elongation of rice roots. In the *Osglu3* mutant, the roots exhibited reduced length and decreased cellulose content in their cell walls. Furthermore, the silencing of the rice α-expansin gene OsEXPANSION 8 (OsEXPA8) which is predominantly located in roots and shoots resulted in a shorter primary root, fewer lateral roots, and decreased length of root hairs. This justifies that expensins are involved in root growth mediating cell wall loosening (Meng et al., 2019; Y. Wang et al., 2014; Zhang et al., 2012).

3.3 Metabolites and their role in enhancing RSA and drought tolerance

Comparative metabolomics on root tips of rice cultivars IR64-a shallow rooting and Azucena-a deep rooting genotypes showed that allantoin, galactaric acid, gluconic acid, and glucose are major responsible metabolites governing root growth, root surface area, and extension of root length to access water. Moreover, differentially abundant metabolites (DAMs), biosynthesis of alkaloid-derivatives of the shikimate pathway, fatty acid biosynthesis, purine metabolism, TCA cycle, and amino acid biosynthesis were statistically significant pathways observed in drought-tolerant rice genotype Azucena (Ghorbanzadeh et al., 2023). Integrated transcriptomic, metabolomics, and proteomics analysis suggests that aromatic amino acids and soluble sugars significantly enhance rice tolerance to water scarcity (Dwivedi et al., 2023). An increased root-to-shoot (R/S) ratio resulting from alterations in sugar metabolism is pivotal for rice's drought resistance (Ma et al., 2024). N-feruloyl putrescine (drought-responsive metabolite) has a vital role in modifying root architecture under drought conditions. A transferase gene-linked variation in this metabolite was confirmed to enhance drought resistance in rice (Guo et al., 2024). Flavonoids (chalcones, flavonols, flavones, flavanols, anthocyanins, and proanthocyanins, or condensed tannins) are a group of secondary metabolites synthesized through the phenylpropanoid pathway. They play an important role in root development in rice, enabling adaptation to adverse stresses such as drought (Falcone Ferreyra et al., 2012; Winkel-Shirley, 2001; Y. Xu et al., 2019). Hydroxycinnamic acid and ferulic acid responsible for increasing osmotic potential and antioxidant capacity (AOC) are identified as key metabolites for drought tolerance in rice and they can be a good candidate to improve drought tolerance in rice (Ma et al., 2016). In wheat, citric and malic acids enhance root exudation processes and improve water and nutrient uptake through the rhizosphere under drought conditions (Hu et al., 2024). Aspartic and Glutamic Acid presence in roots In barley (*Hordeum vulgare*) correlates with improved grain yield under water scarcity, indicating their role in drought tolerance and stress adaptation (Krajewski et al., 2020). Similarly, putrescine, spermidine, and spermineaccumulated in alfalfa (*Medicago sativa*) response to drought stress aiding osmotic adjustment and stabilizing cellular structures to support root development under adverse conditions (K. Wang et al., 2024).

3.4 Major regulatory pathways enhancing RSA and drought tolerance

Integrated transcriptomic, metabolomics, and proteomics analysis revealed that auxiliary carbohydrate metabolism, glycolysis, and pentose phosphate pathway are major pathways governing drought tolerance in rice (Dwivedi et al., 2023).

RNA-seq transcriptome analysis in rice primary roots showed that phenylpropanoid biosynthesis, glutathione metabolism, and plant hormone signal transduction play crucial roles in primary root growth and development (Y. Xu et al., 2019). Comparative analysis of the root transcriptome profile of rice revealed that secondary metabolism, amino acid metabolism, hormone biosynthesis, and carbohydrate metabolism are key pathways governing drought tolerance in rice (Moumeni et al., 2011). Proteomics analysis on wheat roots revealed that proteins associated with cell wall biogenesis, carbohydrate metabolism, brassinosteroid biosynthesis, and transportation functioning in the growth and development of several RSA traits, thereby enhancing crop tolerance to water scarcity (Halder et al., 2022). Lignin synthesis via the phenylpropane pathway associated with drought resistance adaptation in upland and dry conditions (Y. Wang et al., 2024). Metabolic process and biosynthesis of secondary metabolites pathways are associated with the responses for abiotic responses including drought in rice (Azad et al., 2024).

4. Genomic approaches for improving root architecture in rice

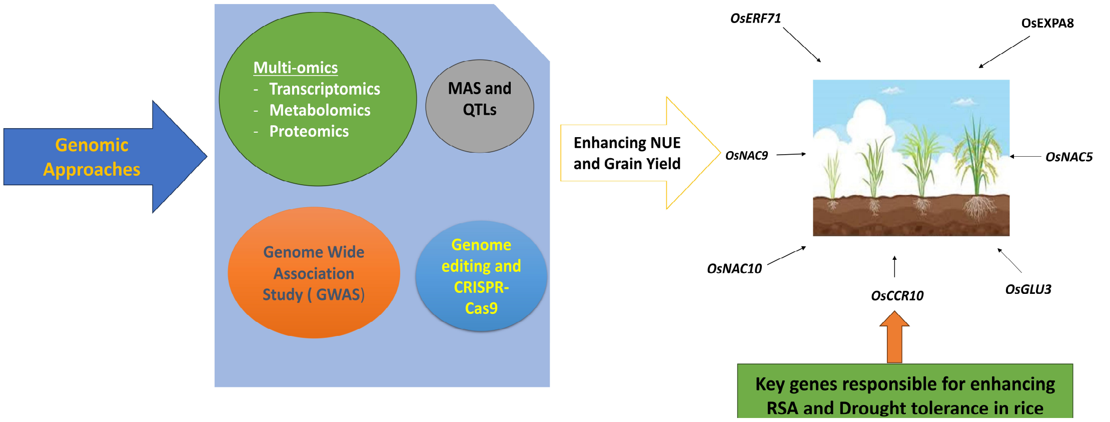

Figure 1: Key genes and genomic approaches utilized to improve RSA and drought tolerance in rice

4.1 Utilization of GWAS, SNPs, QTLsfor enhancing RSA and drought tolerance in rice

Introduction of the *DRO1* gene into a shallow-rooting rice cultivar through backcrossing enabled and enhanced deep rooting by improving root system architecture, leading to sustainable and high-yield performance under drought conditions compared to the original cultivar (Uga et al., 2013). A genome-wide association study (GWAS) identified 162 and 210 significant SNPs linked to root phenotypes in two seasons, leading to the discovery of 59 candidate genes associated with root development. The gene *OsRSL3* is located in a QTL region for median metaxylem diameter where, Four SNPs were identified, functioning in amino acid alterations and having significant correlation with the root phenotype. These candidate genes can be good genetic resources and offer valuable insights for enhancing root traits under drought conditions (Siangliw et al., 2022). GWAS study on root tips of Azucena and IR64 rice cultivars revealed that *NAC*, *AP2/ERF*, *AUX/IAA*, *EXPANSIN*, *WRKY*, and *MYB* are the major gene families responsible for RSA and drought tolerance in rice (Abdirad et al., 2022). Genomic approaches for breeding drought-tolerant crop varieties have significantly benefited from identifying quantitative trait loci (QTLs) associated with the regulation of root system architecture (RSA). Understanding specific QTLs for RSA traits will have a crucial role in the remodeling of root traits for improved drought stress adaptation(Ranjan et al., 2022).

4.2 Applications of Multi-omics, genome editing and CRISPR-Cas9 for improving RSA and drought tolerance in rice

Drought tolerance in plants is governed by many factors. A comprehensive understanding of fundamental biological and cellular mechanisms activated by crop plants during stress can be achieved through an umbrella of multi-omics technologies, such as transcriptomics, metabolomics, and proteomics. Moreover, traits like RSA can be enhanced by utilizing these approaches to develop drought-resilient crop varieties to combat changing and challenging climatic conditions (Yoshino et al., 2019; Zargar et al., 2022).

Mutation of the OsPIN1b gene leads to changes in root system architecture, such as decreased primary root growth, fewer adventitious roots, and a curly root phenotype. Disruption of OsPIN1b also affected IAA balance and played a role in regulating root gravitropism, with light and nutrient signals influencing root phenotype in various conditions. Therefore, CRISPR/Cas9 may be the most practical way and compatible technology for disrupting the OsPIN1b gene and enhancing root system architecture in rice (K. Xu et al., 2023). Transgenic rice plants expressing OsCKX4, controlled by the root-specific promoter RCc3, showed promising effects on root development without affecting their shoots. Results suggested that this could be a valuable tool in breeding and engineering rice roots (Gao et al., 2014). CRISPR/Cas9 gene-editing system can be utilized to modify the OsRAA1 gene, which plays a critical role in rice root development, improving the root architecture and enhance their ability to withstand drought stress. This can be valuable assets for developing drought-resistant rice varieties, which can be vital for combating climate change issues ensuring food security (Arpita et al., 2024). Utilization of CRISPR/Cas9 to target the CAROTENOID CLEAVAGE DIOXYGENASE 7 (CCD7) gene, which is involved in strigolactone biosynthesis, represents a promising approach to enhance plant architecture and root system structure offers potential adaptive strategies and enhance crop resilience to drought stress and sustainable crop production (Butt et al., 2018).

Table 1: Promising Rice cultivars and genotypes from major rice-producing countries with enhanced RSA and drought tolerance

S.N.	Country	Cultivar or genotypes	Characteristics	References
1.	China	IAC1246	Deep roots, higher osmotic adjustment and antioxidant capacity, and photosynthesis rate	(Ma et al., 2016)
2.	China	Hanyou 3015	Water-saving rice, early maturation and high yield	(Mengchen et al., 2024)
3.	China	Chuanguyou208 and Deyou 4727	Larger root length, higher number of roots, higher activities of anti-oxidants like Peroxidase (POD) and superoxide dismutase (SOD)	(X. Wang et al., 2019)
4.	Nepal	NR 119, Chaite 5 and Chaite 4	Higher mean productivity and lower yield loss in water scarcity	(Kandel et al., 2022)
5.	Nepal	Sukha Dhan 1-6 and Radha-4	Drought tolerance, high Stress tolerance index (STI) and low Stress susceptibility index (SSI)	(Adhikari et al., 2019)
6.	India	Jhitpiti, Angurguchcha, E-1702 and Elayachi	Low drought susceptibility and stable yield under irrigated, rainfed and terminal stage drought (TSD) conditions	(Rawte et al., 2021)
7.	India	SahbhagiDhan	Drought Tolerance, long and deep roots	(Basu et al., 2017)
8.	India	DRR DHAN 42	High yield under drought stress conditions at reproductive and grain filling stages.	(A. Kumar et al., 2023)
9.	India	DRR DHAN 44	Early maturing; drought tolerant, high yielding	(A. Kumar et al., 2023)
10.	Iran	Azucena	Drought-tolerant and deep-rooting genotype	(Abdirad et al., 2022)
11.	Bangladesh	BRRI dhan56, BRRI Dhan 66 and	Drought tolerance	(A. Kumar et al., 2023; Nayak et

		BRRI dhan71		al., 2022)
12.	Pakistan	Pokkoli, Vehari, Nonabokra, Kalomonk, PK10683, and Basmati 375	Drought tolerance	(Abbas et al., 2024)

5. Conclusions andFuture Prospects

RSA is crucial for water uptake and drought tolerance in rice, longer, deeper, and thicker roots play a crucial role in enhancing drought resilience. Advances and innovations in transcriptomics, metabolomics, and proteomics have identified many genes and pathways (e.g., OsNAC9, OsERF71) governing RSA traits amidst water scarcity. Moreover, Genome-editing tools like CRISPR-Cas9 and GWAS have facilitated precision breeding, leading to the development of drought-tolerant rice varieties. For instance, drought-tolerant genotypes and cultivars, such as ‘Azucena’ and ‘SahbhagiDhan,’ exhibit improved RSA and yield stability, making them highly suitable for drought-prone areas.

Collaborative research and the broader technology dissemination of promising rice varieties will offer a wider understanding of these technologies. This will encourage widespread adoption, leading to improved crop production and productivity. Additionally, integrated omics, GWAS, SNPs, Metagenomics approaches offer a deeper understanding of particular traits for crop development. So, further utilization big omics data, key genes, metabolites and various molecular pathways governing drought tolerance via enhancing RSA leads to the development of drought-resilient rice varieties for sustainable rice production and food security.

Disclaimer (Artificial intelligence)

Author(s) hereby declares that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

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