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Rice root riposte to drought stress: Morphological and molecular apparatus

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Abstract

Rice crop is extensively grown in drought prone zones and remarkably vulnerable to drought stress. The multiple genetic control of drought tolerant traits would be a major impediment for the existing study, rendering breeding for drought tolerant rice cultivars a challenging endeavour. However, the primary organ to experience water deprivations is the root and are vital absorbents of water. A redesigned root system architecture in the form of deeper roots, increased root hairs with higher density and modified root growth angle probably adds drought tolerance behaviour. The most widely believed target trait for strengthening drought resistance is the tendency for deep root growth, but genetic variation has been revealed for a number of traits that may modulate drought response. To expedite the breeding process for stress-tolerant crops, it is fundamental for scientists to comprehend the regulatory mechanisms that drive root system resilience to extreme circumstances. Hence, this review assessment highlights newly discovered drought responsive genes, physiology and molecular pathways that determine the architecture of rice roots in relation with breeding.

Keywords: Drought stress, rice, root system architecture, growth

1. Introduction

Rice (*Oryza sativa* L.) is one of three foremost food crops, second supreme cereal (FAO, 2018) and the pivotal foundation of nutrients for the global human residents. Being a staple nourishment for more than 50 percent people on sphere, it plays a momentous role in enabling economic expansion and upholding national security (Chen *et al.*, 2022) [13]. The world human residents are anticipated to heighten ~10 billion by 2050, and additionally, rice production is projected to reach 852 million tons by 2035, up from 763 million tons in 2020. (Zhang *et al.*, 2018) [139]. Water deficit or scarcity poses a significant constraint, particularly affecting rice productivity in regions where rice is cultivated in rainfed environments. Within the Asian region, approximately 5 million hectares are dedicated to upland rice and 34 million hectares to lowland rice, both of which consistently face drought-induced stress, ultimately leading to reduced rice yields. (Barik *et al.*, 2018) [7]. Water deficit bothers the crop mainly at vegetative and reproductive developmental phases. Reproductive stage water dearth is most perilous as it grounds low crop harvest owing to higher portion of void grains in the panicles (Barik *et al.*, 2019) [7]. Additional tactics should be conditioned lessen the effects of stress, like generating drought-resistant plant cultivars and tweaking planting procedures. Researchers have a number of challenging tasks, including identifying the vital features causing stress resistance and breeding rice varieties with these qualities so that plants may flourish in harsh environments. One of the most crucial approaches for sustaining agricultural yields in water-limited provinces is the drought avoidance. Most routinely, root phenes that support the enhanced water uptake and conveyance to the shoot are accountable for drought avoidance. Progressive water restrictions will be well suited to cultivars having the ability to amend their roots to less moisture by retaining root depth and deep branching. Nevertheless, root traits have not been extensively used as breeding objectives in contrast to vegetative growth and yield, for the motive that phenotyping the root system under appropriate agronomic conditions is labour-intensive. Nowadays opportunity to correlate root phenes with absorption of water from dehydrated soil in cereals, has considerably expanded with the advancement of high-throughput phenotyping tools (Kadam *et al.*, 2017) [144]. Since roots are vital for procuring water, breeding approaches focused at averting drought must prioritise root architectural and anatomical aspects. As a result, endeavors to enhance yields during droughts also concentrate

on enhancing secondary characteristics such as root architecture.

2. Rice root system and architecture

Postembryonic and embryonic roots constitute root systems (Fig. 1). The majority of cereal plants, including rice, wheat, and barley, develop a compact fibrous root system consisting of crown roots and nodal adventitious roots (ARs). This stands in contrast to numerous dicot plants, which rely on a main root and lateral branching roots (Lin and Sauter, 2020; Coudert *et al.*, 2010) [66, 17]. Complete germination of rice seeds yields a sturdy durable embryonic radicle and as seedling progresses a four or five crown roots ascend from the nodes coleoptile (fig. 1A). These plantlet roots are crucial for examining and upholding a close eye on the soil moisture status (Sauter, 2013) [97]. At stem nodes during the post

seedling stage, AR primordia ultimately emerge to turn out to be the fully mature rice root system. ARs can be alienated into two categories: underground and above ground. Whether ARs are above ground or below rest on the ecotype and the habitat (Fig. 2). Lowland rice has a tendency to produce scarcer above-ground ARs and added underneath ARs. Through stem growth and the advent of ARs from above ground stem nodes, deepwater rice is modified to raise in locations with flexible aquatic heights. In order to boost the area that the root system explores, ARs also profile lateral roots (Fig. 1B). Large and small lateral roots of lateral ARs, which display various root lengths, can be characterised. As a result, the various root types impact the architecture of rice's root system and mutant genes affecting rice root are briefly reviewed by Rebouillat *et al.*, 2009 [91].

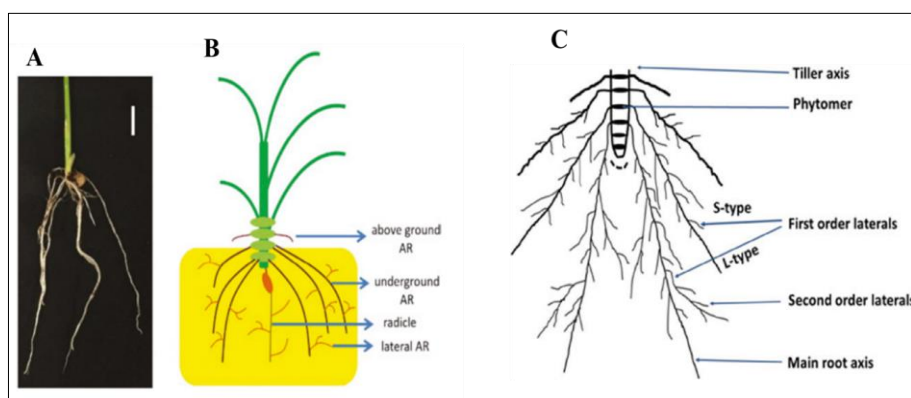


Fig 1: Root types and schematic root system architecture in rice plants. (A) Root system of a rice seedling. (B & C) Scheme of a mature rice root system in soil.

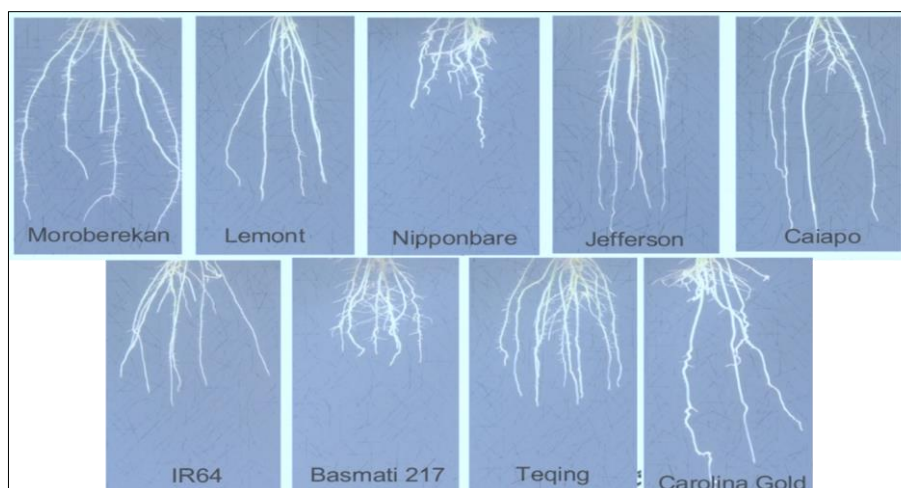


Fig 2: Diverse root system architecture of different rice cultivars

3. Root genetic improvement for enhancing tolerance to drought

Drought stands as one of the most crucial abiotic factors capable of impacting global rice productivity, posing a significant threat to the sustainability of rice production within rainfed agricultural systems. One of the goals of the water-saving agriculture initiatives is the development of rice cultivars that seems to be resistant to drought. Global food security may be significantly impacted by greater consideration of the rapport between rice root function and drought (Gowda *et al.*, 2011) [32]. Thus, rice drought tolerance mechanism encompasses acquiring more water from the soil. The key to

engineering superior rice varieties that are appropriate for water-saving farming systems will thus be strengthening root systems with deep roots and high water uptake core competencies. In addition, drought tolerance is primarily influenced by four root characteristics: root length, volume, thickness, and root growth angle (RGA; Uga *et al.* 2011) [118].

3.1 Rice drought mechanisms and strategies

Drought stress poses a significant agricultural threat by inducing abiotic stress that hampers plant growth and productivity, causing delays. This stress leads to reduced cell growth, elongation, and expansion, consequently retarding

overall plant development. Furthermore, drought stress disrupts the plant's antioxidant function by promoting the accumulation of reactive oxygen species (ROS). These ROS, triggered by drought, result in various responses at the morphological, biochemical, physiological, and molecular levels, driven by the up and down-regulation of genes and proteins (Fig. 4). The stress condition has been extensively studied through diverse functional genomics, proteomics, and metabolomics approaches, revealing numerous genes and proteins responsive to this stress.

Plants respond to drought stress through three distinct strategies: drought escape, drought avoidance, and drought tolerance. Drought avoidance refers to the plant's ability to maintain relatively high tissue water potential despite limited soil moisture. When faced with high evaporative demand and increasing soil water deficit, plants have two options to uphold sufficient water levels: they can either reduce water loss or extend the water supply. Rice varieties possessing enhanced root systems, increased ABA production, or other biochemical mechanisms to regulate water status fall into this category. These genotypes can mitigate the yield losses induced by drought (Kumar *et al.*, 2017) ^[57]. Drought avoidance is also facilitated by mechanisms that enhance water use efficiency (WUE) and minimize water loss.

Drought-resistant rice cultivars typically exhibit deep, coarse roots with high branching and soil infiltration capabilities, along with an improved root-to-shoot ratio (Wang *et al.*, 2006) ^[124].

4. Rice roots and component traits in response to water stress

Due to the lack of water in the plant, grain yield fades. A severe or extended drought damage or malfunctions the root system, which hinders or prevents the uptake of nutrients and water (Rogers and Benfey, 2015) ^[93]. Thus, a dynamic root system that offers drought resistance is a desirable component for the benefit of the plant and concerning agricultural growth. Considering roots are one of the indispensable drivers of water, their size, density, and rate of proliferation are crucial factors that encourage how plants retort to drought stress (Salehi-lisar *et al.*, 2016) ^[95]. In relation to plants with shallow roots, those with deep root systems and perennial phenotypic expression exhibited higher drought tolerance (Choudhary *et al.*, 2016; Atlin *et al.*, 2006; Fukai and Cooper 1995) ^[14, 5, 29]. Despite the aforementioned, preferring genotypes with a more developed root system will boost plant yield, as seen for instance in many rice seedlings.

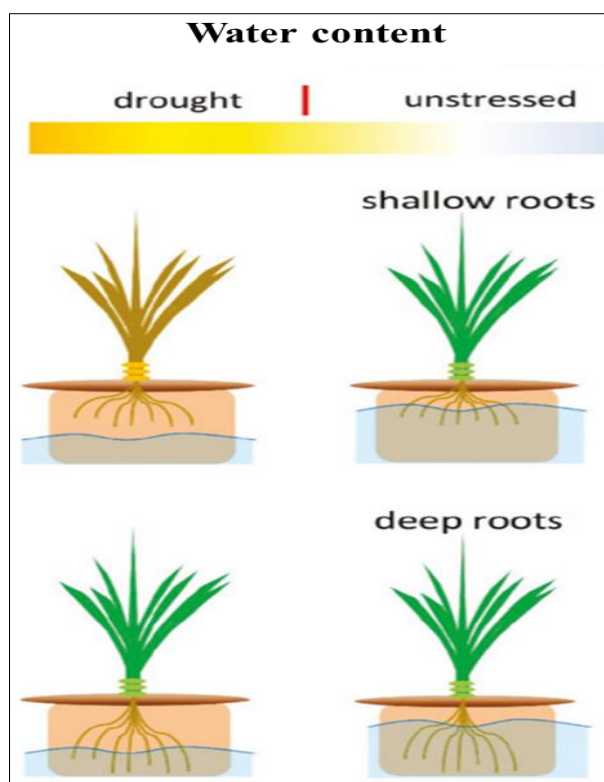


Fig 3: Scheme of a shallow and a deep root system in drought (Lin and Sauter, 2020) ^[66]

The dynamic root system architecture (RSA) approach enables plants to respond effectively to stressors such as drought. This adaptation involves the reconfiguration of root structures in response to the presence of drought, ensuring optimal resource utilization. For instance, in the case of rice introgression lines, there was a demonstration of increased adaptability in lateral root length, enhanced shoot mass, and denser growth under drought conditions when compared to the wild-type variety. This resilience in RSA was lacking in the wild-type variety (Kano-Nakata *et al.*, 2013) ^[50]. The

ability to conform to the varying environment is provided by RSA plasticity (Schneider and Lynch, 2020) ^[98], but it comes with a cost and it is questionable if RSA plasticity helps crops yield more under unfavourable situations. In comparison to IR64, Azucena displayed deeper root systems and a stronger root diameter, whereas IR64 exhibited less variability in root diameter. This link between root morphology and the metabolic costs of tissues was evidenced by the positive correlation observed between root respiration rates and parameters such as root diameter and the extent of live tissue

area. (Fonta *et al.*, 2022) [28].

As moisture tends to persist in deeper soil layers, rice genotypes capable of extracting water from these depths often exhibit greater drought resistance (Arai Sanoh *et al.*, 2014) [4]. Factors such as having fewer nodal roots with smaller diameters, limited lateral root extension, steeper root growth angles (RGA), or reduced metabolic costs per unit length of root tissue can all contribute to the development of deeper root systems (Lynch, 2013) [72]. The alteration of root angles during early growth stages leads to the consistent development of a deep root architecture in rice, which subsequently aids in enhancing grain yield under drought conditions in later stages (Uga *et al.*, 2013) [119]. A well-known gene called *DROI* that inspires root development angle has been cloned and used in breeding efforts for enlightening drought tolerance (Uga *et al.*, 2013; Kitomi *et al.*, 2015) [119, 56]. The root growth angle also contributes in deeper rooting of rice plant. The average angle for drought-tolerant genotypes carrying the *DROI* gene ranged from 82.7° to 89.7° (Pandit *et al.*, 2020) [84]. The *MIZI* gene, also known as *MIZU KUSSEI 1*, plays a crucial role in hydrotropism, regulating root angles, *MIZU KUSSEI1* (*MIZ1* has also been found to interact with ABA signalling (Miao *et al.*, 2021 and Li *et al.*, 2022) [75, 63] and relate to root gravitropism (Li *et al.*, 2020) [62]. Furthermore, *MIZU KUSSEI1* (*MIZ1*) has been linked to ABA signaling (Miao *et al.*, 2021 and Li *et al.*, 2022) [75, 63] and associated with root gravitropism (Li *et al.*, 2020) [62]. The rice root-specific gene *OsMIZI* has been successfully cloned and characterized. In drought-tolerant rice lines, there was a significant upregulation of *OsMIZI* expression levels in the roots, whereas susceptible lines showed a decrease in expression (Kaur *et al.*, 2020) [51].

Root length density is closely linked to the plant's ability to penetrate soil and efficiently extract water from deeper soil layers (Kamoshita *et al.*, 2000; Siopongco *et al.*, 2005) [46, 103]. Given that rice possesses comparatively shorter nodal roots (in comparison to crops like maize or barley), the larger lateral roots play a pivotal role in the exploration of deeper soil layers. Under drought stress, increased lateral root development was hypothesized as a potentially beneficial (Henry *et al.*, 2012) [37]. Previous rice drought studies have documented the perks of larger lateral root length and density at depth by ministering water uptake from deep soils (Suralta *et al.*, 2015, 2018; Hazman and Brown, 2018) [109, 108, 35].

Root anatomical features, such as radial and axial water transport patterns, significantly influence the efficiency of water intake and distribution (Lynch *et al.*, 2014) [73]. Axial water conductance is particularly influenced by characteristics of the xylem channels, including their number, diameter, and area, while cortical characteristics and the presence of suberized cell layers can impact radial conductance. Upland rice, characterized by thicker roots and larger xylem channels, is associated with enhanced drought tolerance (Gowda *et al.*, 2011) [32].

In response to drought, Azucena demonstrated reduced theoretical axial hydraulic conductance in shallow roots and at the base of deep roots, while showing slightly higher conductance at the tips of deep roots. In contrast, IR64 exhibited lower plasticity in metaxylem phenotypes (Fonta *et al.*, 2022) [28]. Drought-tolerant rice cultivars showcased a higher count of xylem vessels with larger diameters compared to drought-susceptible cultivars (Abd Allah *et al.*, 2010) [1]. In the indica variety 'Mudgo', drought led to an increase in both

the number and diameter of xylem vessels, whereas NERICA4 (derived from *O. sativa* L. X *O. glaberrima* Steud.) exhibited a decrease in xylem vessel number but an increase in diameter with drought (de Bauw *et al.*, 2019) [22]. This emphasizes the significance of phenotypic variation along the root axis.

Although the average difference in late metaxylem vessel diameter and number between water-deficit and control treatments was only around -7% and -2% respectively, a diversity panel of indica rice genotypes displayed genetic variation for various anatomical traits, including late metaxylem vessel number and diameter, under water-deficient conditions (Kadam *et al.*, 2017) [44]. Previous studies have also noted metaxylem constriction at the base of nodal and lateral roots in rice (Vejchasarn *et al.*, 2016; Hazman and Brown, 2018) [123, 35]. In ensuring that growing tips of root tissues maintain sufficient water for growth, having lower axial hydraulic conductivity in the basal root regions could be a beneficial trait in rice.

Thicker roots play a direct role in drought avoidance by enhancing the ability to absorb water from soil layers. This is due to the larger xylem vessel radii and reduced axial resistance to water flow in roots with greater diameter (Yambao *et al.*, 1992) [130]. The accumulation of lignin around root cells modifies the architecture of the cell walls, enabling root growth even under drought conditions, thereby leading to root thickening (Yoshimura *et al.*, 2008) [134]. For instance, rice inbred lines like IR20 3 MGL-2, which exhibit long and thick roots, have demonstrated improved drought tolerance (Ekanayake *et al.*, 1985) [26]. These thicker roots are also associated with root length, penetration capacity, branching, and upland grain yield (Nguyen *et al.*, 1997; Li *et al.*, 2005; Clark *et al.*, 2008) [80, 64, 15]. A long and deep root system facilitates the extraction of water from deeper soil layers (Wasson *et al.*, 2012) [125].

However, having a deep-rooted phenotype in rice doesn't necessarily guarantee drought resistance. This is exemplified by certain upland rice varieties labeled as "deep rooting" that are still highly susceptible to stress, like Moroberekan (Henry, 2013) [36]. Additionally, the intrinsically disordered protein REPETITIVE PRO-RICH PROTEIN (RePRP) serves as a versatile stress modulator. It interacts with the cytoskeleton to regulate root development in response to water-deficit stress in rice (Hsiao *et al.*, 2020) [40].

5. Rice root morphology; *indica* v/s *japonica*

Morphological parameters are proven to be good indicators of water deficiency (Fig. 4) (Upadhyaya *et al.*, 2019; Anjum *et al.*, 2011; Zokaee-Khosroshahi *et al.*, 2014; Zaher-Ara *et al.*, 2016) [121, 3, 145]. Plant biomass showed a significant decrease in fresh and dry weight of root and shoot during dehydration (Dickin and Wright, 2008) [23]. Plasticity in root and shoot morphological traits is desirable for better drought stress adaptation in rice (Kadam *et al.*, 2017) [44] as they donate to grain yield stability. *Indica* and *japonica*, the two major rice varietal categories, with radically different root morphologies. Especially when compared to *japonica* types, *indica* varieties typically have smaller diameter roots with far more branching and smaller metaxylem vessels, while *japonica* varieties typically have bigger diameter roots with less branching and larger metaxylem vessels (Yoshida and Hasegawa, 1982; Gowda *et al.* 2011) [133, 32]. The high-yielding lowland cultivars, such IR64 (*indica* type), excel in sufficient scale

with access to water, fertilizers, and shallow soils. Despite their production potential is often inferior, upland varieties, such as Azucena (*Japonica* type), are frequently more resistant to abiotic stresses. Countless times, the relative drought tolerance of Azucena has been attributed to its large diameter, deep roots, which permit access to deep soil

moisture and foster penetration of hard soils. (Gowda *et al.*, 2011) [32]. Azucena is noted to act to dehydration by extending its root length density at depth (Henry *et al.*, 2011) [38], which is probably the result of both longer roots and deeper branching.

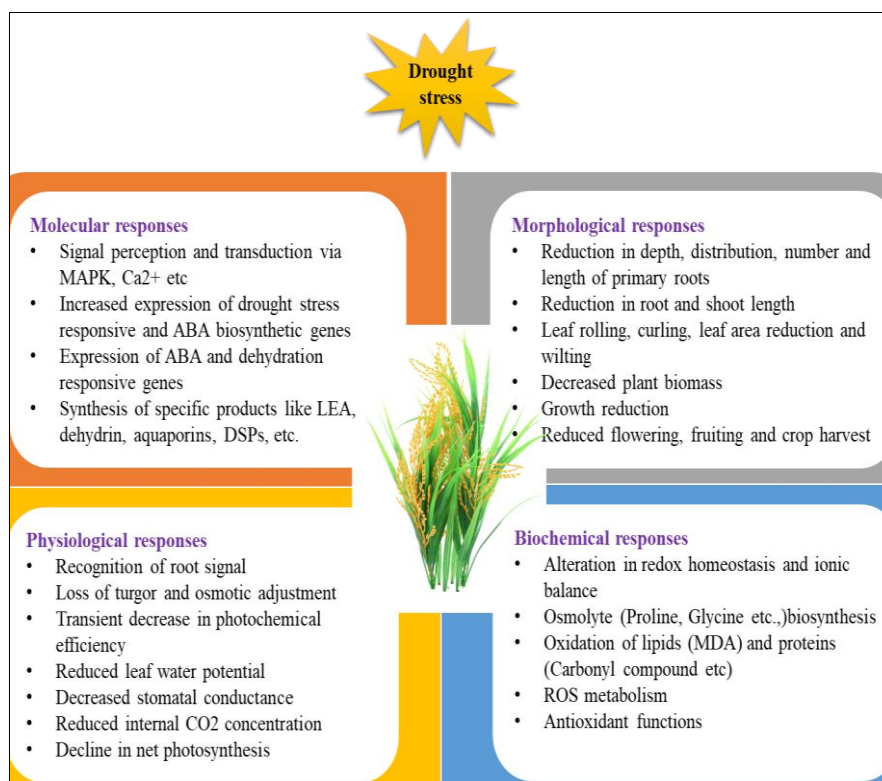


Fig 4: Drought stress induces various morphological, physiological, biochemical, and molecular responses in *Oryza sativa* L.

The notion that root versatility is advantageous for drought stress tolerance is substantiated by some findings in rice (Kano *et al.*, 2011; Henry *et al.*, 2012; Kadam *et al.*, 2015; Suralta *et al.*, 2018) [49, 37, 45]. The merits of root elasticity must be assessed in managed, higher input systems because they

might only apply to low-input agriculture systems. Based on their roots' physical attributes and capacity to draw water during crises, upland rice species were more tolerant to drought (Schneider and Lynch, 2020; Kisaakye *et al.*, 2022) [98, 54]

Table 1: Rice root traits and their functional characteristics that are most commonly characterized in root QTL mapping studies.

Root traits	Functional characteristics
Maximum root depth	Potential for absorption of soil moisture and nutrients in deeper soil layer
Root to shoot ratio	Assimilate allocation
Root volume	The ability to permeate a large volume of soil
Root number	Physical strength, potential for root system architecture
Root diameter	Potential for penetration ability, branching, hydraulic conductivity, regulates root length, surface area, increase water uptake under drought.
Deep root to shoot ratio	Vertical root growth, potential for absorption of soil moisture and nutrient in deeper soil layers
Root length/weight	density Rate of water and nutrient uptake
Root branching	Power of soil exploration (the major contribution to total root length)
Total root length/surface area	Total root system size: the size of contact with soil (Major determinant for water and nutrient uptake as an entire root system)
Specific root length	Degree of branching, density of root materials, porosity due to aerenchyma development
Hardpan penetration ability	Ability to penetrate subsurface hardpans
Fine roots	Extract water and nutrients from the soil
Root hairs	Assist in root contact with soil particles for uptake of water and nutrients as soil dries
Coarse roots	Support plants in soil, constitute root system architecture, control depth of root system and enhances plant's ability to grow in compact soil
Nodal roots	Harvest late season precipitation
Root angle	Helps in deeper root growth and affects the area from which roots capture water and nutrients
Root tissue density	Controls specific root length and specific surface area which increases plant's performance and carbon economy under water stress
Root length density at depth	Involved in efficient extraction of subsoil water

6. Phytohormones in supervising drought stress

Phytohormones, in precise Abscisic acid (ABA), are fundamental for integrating drought stress signals and modulating downstream stress reactions. Plants routinely alter endogenous ABA levels to deal to abiotic factors including cold, salt, and drought. Drought stress can also cause cytokinin (CK) levels to drop, thereby amplifies the shoot responses to ABA and triggers stomatal closure (Goicoechea *et al.*, 1997) [30]. These stress-related fluctuations in CKs and ABA amounts stimulate leaf senescence, which causes leaves to abscise and narrows water loss (Pospisilova *et al.*, 2005) [85].

At physiological doses, auxin drives stomata to open and may modify the way in which ABA regulates stomatal aperture (Tanaka *et al.*, 2006) [112]. For instance, a mutation in the putative auxin influx carrier gene *OsAUX1* led to a decreased number of lateral roots, while its overexpression had the contradictory effects. By suppressing the root apical dominance imposed on by cytokinins, auxins facilitate the creation of new roots. In one instance, 31 *Aux/IAA* genes were uncovered in rice under drought stress, and *OsIAA6* was clarified to be one of these genes (Jung *et al.*, 2015) [43]. Auxin and abscisic acid in duo were claimed to diminish the roots' resistance to water flow. In order to minimize loss, plants may respond to water stress by increasing root auxin concentration and decreasing leaf auxin concentration, or auxin signalling. There are four *PIN1* genes and one *PIN2* gene that turns out as auxin efflux transporters in the rice genome. *OsPIN1* is crucial for tillering and auxin-dependent adventitious root emergence. Similar to *AtPIN1*, *OsPIN1* exemplifies vascular tissues and root primordial expression (Xu *et al.*, 2015) [126]. Similarly, *OsPIN3t* takes part in auxin polar transport and response to drought stress. While suppression of *OsPIN3t* resulted in malformed crown roots at the seedling stage and its overexpression amplified drought tolerance (Zhang *et al.*, 2012) [140]. Enhanced drought tolerance has been achieved through the overexpression of auxin efflux carrier genes like *OsGH3.2* (Du *et al.*, 2012) [25] and *OsGH3.13* (Zhang *et al.*, 2009) [141], as well as the auxin/IAA gene *OsIAA6* (Ljung *et al.*, 2013) [70], which targets the auxin receptor TIR1. Similarly, overexpression of YUC genes in rice results in the generation of multiple adventitious roots (Yamamoto *et al.*, 2007) [129]. This suggests that inducing the YUC gene under drought stress triggers auxin production, leading to an increased number of roots. This adaptation assists rice plants in coping with challenging environments. Given the significance of a robust root system in drought resistance, auxins play a supportive yet pivotal role in this process.

Furthermore, it has been demonstrated that elevated ethylene levels during drought stress inhibit processes like photosynthesis, shoot/leaf expansion, and root growth and development (Rajala and Peltonen-Sainio, 2001; Sharp, 2002) [89, 99].

7. Fungi in drought stress tolerance

The mycorrhizal assembly of fungus with the host plant increases drought resistance by partaking in physiological and molecular progression. One of the most significant soil bacteria, arbuscular mycorrhizal fungi (AMF), work as symbionts with plant roots (Brundrett *et al.*, 2018) [10]. External hyphae expand in size in the soil and develop highly branching mycelia, where water can be absorbed from deeper

soil layers, which is subsequently transported to cortical tissues, where it joins water transport through apoplastic routes (Simard *et al.*, 2015) [101]. Arbuscular mycorrhizas in rice increased the number of lateral roots through either a potentially involved AMF signalling mechanism or by altering the nutrient status of the plant (Vallino *et al.*, 2014) [122]. Plant adaptation to osmotic stress may be greatly aided by this AMF interaction and root architecture response.

8. Genomics of drought tolerance

8.1 Quantitative Trait Loci (QTL) mapping

Numerous researchers have identified a variety of QTLs associated with root morphology traits in rice (as summarized in Table 2). To date, there have been reports of 675 root QTLs and over 85 genes related to 29 distinct root parameters in rice (<https://snp-seek.irri.org/>). Additionally, 102 QTLs have been linked to root length. While several QTLs have been recognized for their significant roles in governing root growth and development in rice, many of them remain to be cloned (Coudert *et al.*, 2010; Meng *et al.*, 2019) [17, 74].

In situations of nutrient deficiency, Obara *et al.* (2010) [82] identified a QTL for root length and determined that the QTL *qRL6.1* enhanced root length under varying NH₄⁺ levels, contributing to rice yield in molecular breeding programs. Uga *et al.* (2011) [118] emphasized the importance of the *Dro1* gene in promoting the development of deep root systems, a crucial strategy for enhancing rice's drought resistance. Notably, there are three significant QTLs for root growth angle (RGA) in rice (Uga *et al.*, 2011, 2013, 2015) [118, 119, 115], with DRO1 remaining the most prominent. This QTL has been meticulously mapped, and the underlying gene—an early auxin responsive factor—has been cloned into the IR64 variety (which has shallow roots) and the Kinandang Patong (KP) variety (which has deep roots). Furthermore, two other QTLs, DRO2 (Uga *et al.*, 2013) [118] and DRO3 (Uga *et al.*, 2015) [115], have been found to interact with *DRO1*, functioning in tandem. In subsequent research, a QTL controlling root volume in rice, qFSR4, was precisely mapped to a 38-kb region on chromosome 4. The candidate gene for this QTL is believed to be Narrow leaf 1 (Nal1) (Ding *et al.*, 2011) [24]. Additionally, Stal1, a QTL governing the transverse area of the stele in rice roots, was fine-mapped to chromosome 9 (Uga *et al.*, 2010) [117].

8.1.1 Deeper rooting 1

The creation of a deep roots system allows access to water moisture stores, an avoidance strategy, that allows rice plants to endure under drought stress. A breeding population created by crossing the widely cultivated shallow-rooted IR64 rice with the deep-rooted Kinandang Patong landrace, which exhibited yield stability under drought, yielded the *DEEPER ROOTING 1* (*DRO1*) QTL. The *DRO1* allele from Kinandang Patong, referred to as *DRO1-kp*, stimulates elongation of cells at the root tip, initiating downward growth. Conversely, a single 1-bp deletion within exon 4 of the IR64 *DRO1* gene results in a premature stop codon, leading to the production of a truncated protein and a reduced root angle response to gravity (Uga *et al.*, 2011; 2013) [118-119].

The introduction of *DRO1-kp* into IR64 leads to the development of a deep-rooted phenotype, which outperforms the recipient parent, especially in prolonged or severe water crises, in terms of both yield and drought avoidance. Therefore, *DRO1* is implicated in promoting extensive root

growth and an expanded root angle, enhancing gravitropism. Beyond rice, recent research has identified and examined *DRO1* homologs in various plant families, including *Arabidopsis* and *Prunus*. There is evidence suggesting that these homologs also contribute to deeper rooting and lateral root angle enhancement (Guseman *et al.*, 2017) [34].

8.1.2 Soil Surface Rooting 1 (SOR1)

He second cloned QTL responsible for root growth angle in crops is named Quantitative trait locus for *SOIL SURFACE ROOTING 1* (*qSOR1*), found on chromosome 7. This QTL was identified through the analysis of a mapping population generated by crossing "Gemdjah Beton," a lowland rice variety exhibiting soil surface rooting (SOR), with "Sasa nishiki," a lowland rice variety lacking SOR. Interestingly, a Near Isogenic Line (NIL) of "Sasanishiki" carrying a non-functional allele of *qSOR1* from "Gemdjah Beton" exhibited SOR in both upland and paddy areas. This NIL contributed to

reducing yield loss by alleviating stress typically found in saline paddy fields.

Through homology searches based on the amino acid sequence of *qSOR1*, rice *DRO1* was found to be the closest relative to rice *qSOR1* (Kitomi *et al.*, 2020) [55]. Additionally, the *Dro2* located on chromosome 4 and *Dro3* located on chromosome 7 have also been mapped in relation to root growth angle (Uga *et al.*, 2013b; Kitomi *et al.*, 2015) [120, 56].

8.1.3 Tillering angle control 1 (TAC1)

"Tiller Angle Control 1" (*TAC1*), a gene in rice responsible for regulating tiller angle (Yu *et al.*, 2007) [135], shares a significant resemblance to the *DRO1* family in various domain sequences (Nakamura *et al.*, 2019) [79]. These findings suggest a broader implication, indicating that a substantial gene family of *DRO1* homologs is associated with the control of shoot and/or root gravitropism in monocot plants (Uga, 2021) [113].

Table 2: Summary of QTL identified for root related traits in rice under water deficit condition

Parents	Population type	Marker	Traits	references
CO39 × Moroberekan	RIL	RFLP	RP, RN	Ray <i>et al.</i> , 1996 [90]
IR64 × Azucena	DH	RFLP	Root architecture	Yadav <i>et al.</i> , 1997 [127]
IR58821 × IR52561	RIL	AFLP, RFLP	RT, RL, RN, RP	Ali <i>et al.</i> , 2000 [2]
Bala × Aucena	RIL	RFLP, AFLP	RP	Price <i>et al.</i> , 2000 [87]
IR58821 × IR52561	RIL	RFLP, AFLP	RT	Kamoshita, A. <i>et al.</i> , 2002 [47]
Bala × Aucena	RIL	RFLP, AFLP, SSR	RDW, RT, RL, RN	Price <i>et al.</i> , 2002 [86]
IAC165 × Co39	RIL	RFLP, SSR	RL, RT, RDW	Courtois <i>et al.</i> , 2003 [20]
IRAT109 X Yuefu	DH	SSR, RFLP	RT, RN, RL, RFW, RDW	Mu <i>et al.</i> , 2003 [78]
IAC65 × Co39	RIL	RFLP	RL, RT	Babu <i>et al.</i> , 2003 [6]
IR1552 × Azucena	RIL	RFLP, AFLP, SSR	RL, RN	Zheng <i>et al.</i> , 2003 [142]
Yuefu × IRAT109	DH	SSR, RFLP	RT, RN, RL, RDW	Li <i>et al.</i> , 2005 [64]
Akihikari × IRAT109	BC	SSR	RDW, RL	Hori <i>et al.</i> , 2006 [39]
IR64 × Azucena	BC	SSR, RFLP	RL, RT	Steele <i>et al.</i> , 2006 [105]
ZenShan 97B × IRAT109	RIL	SSR	RDR, RL	Yue <i>et al.</i> , 2006 [137]
Otomemochi × Yumenohatamochi	RIL	SSR	RDW, RL, RN	Ikeda <i>et al.</i> , 2007 [41]
IRAT109 × Yuefu	RIL	SSR	RT	Liu <i>et al.</i> , 2008 [68]
Yuefu × IRAT109			RT, RN, RL	Qu <i>et al.</i> , 2008 [88]
Kinandang Patong × IR64	F ₂	SSR, STS	RT	Uga <i>et al.</i> , 2008 [116]
IR64 × Azucena	DH	RFLP, SSR	RL	Zheng <i>et al.</i> , 2008 [143]
Yuefu × IRAT109	BC	SSR	RT	Li <i>et al.</i> , 2011 [60]
Yuefu × IRAT109	F ₂	SSR	RT	
IR64 × INRC10192	RIL	SSR	RDW	Srividya <i>et al.</i> , 2011 [104]
IR64 × INRC10192	RIL	SSR, STS	RDR	Uga <i>et al.</i> , 2011 [118]
CT9993 × IR20	BC	SSR	RT	Suji <i>et al.</i> , 2012 [107]
Bala X Azucena				
Kinandang Patong × ARC5955	F ₂	SSR, SNP	RDR	Uga <i>et al.</i> , 2013a [119]
Kinandang Patong × Pinulupot1	F ₂	SSR, SNP	RDR	
Kinandang Patong × Tupa729	F ₂	SSR, SNP	RDR	
IR64 × Dro1-NIL	BC	SSR	RDR	Uga <i>et al.</i> , 2013b [120]
Kinandang Patong × Momiroman	F ₂	SSR, SNP	RDR	Kitomi <i>et al.</i> , 2015 [56]
Kinandang Patong × Yumeaoba	F ₂	SSR, SNP	RDR	
Kinandang Patong × Tachisugata	F ₂	SSR, SNP	RDR	
Yuefu × IRAT109	F ₂	SSR	RT, RL	Li <i>et al.</i> , 2015 [59]
Zhenshan 97B × IRAT109	RIL	SNP	RDR	Lou <i>et al.</i> , 2015 [71]
Nipponbare × Kasalath	F ₂	SSR, RFLP, AFLP	RN	Niones <i>et al.</i> , 2015 [81]
Kinandang Patong × IR64	F ₂	SSR, SNP	RDR	Uga <i>et al.</i> , 2015 [115]
KaliAus × AUS276	BC	SNP	RDW, RL	Sandhu <i>et al.</i> , 2016 [96]
IR64 × Dular	RIL	SSR	RL, RDW, RN, RDR	Catalos <i>et al.</i> , 2017 [111]
N-22 × Cocodrie RIL	RIL	SNP	RDW, RL	Bhattarai <i>et al.</i> , 2018 [9]
IR55419 × Super Basmati	F ₂	SSR	RDW, RL	Sabar <i>et al.</i> , 2019 [94]
M-203 × M-206	RIL	SNP	RDW, RL	Yun <i>et al.</i> , 2019 [138]

Note – RDW-root dry weight, RFW- Root fresh weight, RL-root length, RDR -ratio of deep rooting, RN-root number, RP_ Root penetration, RT- root thickness, RIL-recombinant inbred lines, DH-double haploids, SNP- Single nucleotide polymorphism, BC-backcross.

8.2 Allele mining

The Deeper Rooting 1 (DRO1) gene located on chromosome 9 plays a role in enhancing the root growth angle (RGA). To investigate this gene further, a study involving twenty-four significant Indian highland and lowland genotypes, including those carrying the "yield under drought" (DTY) QTL, conducted allele mining of DRO1. This process utilized four pairs of overlapping primers to sequence a 3058 bp segment of the gene (Singh *et al.*, 2021) [102]. The results revealed a total of 216 single nucleotide polymorphisms (SNPs) in the entire gene and 52 SNPs in the coding region (756 bp). Interestingly, the occurrence of transversions was found to be 3.6 times more frequent than transitions in the gene, and 2.5 times more common in the coding sequence (CDS). This information on structural variants within the DRO1 gene can be of significant value to breeders, particularly in the context of ongoing breeding efforts aimed at improving drought tolerance in rice.

8.3 Genome-wide association mapping

In recent times, the application of genome-wide association study (GWAS) has gained widespread use as an effective tool to uncover the genetic basis of various traits. This approach has enabled researchers to establish connections between traits and their underlying genetics. Numerous GWAS studies have been conducted to investigate root traits in rice as well as other crops. In a study involving a panel of 167 japonica rice accessions, root-related traits during the seedling stage were investigated using a hydroponic growth method (Courtois *et al.*, 2013) [19]. Across 21 different root traits, a total of 413 suggestive relationships were identified, which included 143 significant associations. Remarkably, eleven of these associations were found to be collocated with previously known root-related genes such as DRO1, WOX11, and OsPID (Li *et al.*, 2017) [61].

Additionally, an evaluation was carried out on an aus panel consisting of around 220 genotypes. This evaluation focused on component traits associated with deep root growth, including angle, elongation, and branching. Interestingly, the number of nodal roots categorized as 'large-diameter' exhibited a positive correlation with deep root growth. Furthermore, this particular trait displayed the highest number of collocated genome-wide association study (GWAS) peaks with grain yield under drought conditions (Liao *et al.*, 2022) [65].

8.4 Marker-assisted backcrossing (MABC)

Only a few publications on the use of MABC to develop the most suitable lines or varieties for drought tolerance are known, irrespective of the fact that MABC has been used extensively for introducing resistance to biotic stress (Mir *et al.*, 2012; Gupta *et al.* 2010) [76, 33]. For instance, the superior rice cultivars IR64 and Kalinga III have been utilized MABC to introgress root trait QTLs (Shen *et al.*, 2001; Steele *et al.*, 2006) [100, 105]. A variety designated as "Birska Vikas Dhan 111 (PY 84)" was created utilizing these MABC products and introduced in the Indian state of Jharkhand (Steele *et al.*, 2007) [106]. In this scenario, multiple QTLs were transferred *via* MABC to enhance root growth in dry climates.

8.5 Transcriptomics

Formulating critical target traits for drought resistance can be facilitated by integrating knowledge about genes governing

growth, development, adaptive processes, and genes that exhibit differential expression during drought stress. These differentially expressed genes have the potential to serve as candidate genes for allele mining and further characterization. Additionally, an understanding of the genes and signaling pathways involved in the morphological and anatomical development of rice roots, particularly in crown root initiation during drought stress, has been documented (Coudert *et al.*, 2011; Rebouillat *et al.*, 2009) [16, 91]. Exploring tissue-specific gene expression in rice roots under drought stress, Yang *et al.* (2004) [131] identified 66 transcripts that demonstrated altered expression. Notably, four of these transcripts were located within the QTL regions associated with root development under water-deficit conditions. In another study, Wang *et al.* (2006) [124] observed distinct patterns of gene expression in the leaves and roots of upland rice and lowland rice varieties. This collective information contributes to the identification and understanding of key genetic elements and pathways that influence root development and response to drought stress in rice.

8.5.1 Transcription factors

Multiple transcription factors that improve plant survival in drought-prone environments have been investigated and reported by many researchers.

8.5.1.1 DREB

The transcription factor *AtDREB1A*, or its equivalent *OsDREB1A* (*Dehydration-Responsive Element Binding* gene), when introduced into transgenic rice, exhibited heightened resistance to simulated drought conditions (Yamaguchi-Shinozaki and Shinozaki, 2005) [128].

8.5.1.2 bHLH

It was determined that the transcription factor *OsbHLH120* (*Basic helix-loop-helix*) is encoded by the QTL *qRT9*, which regulates root thickness and length. The drought-response hormone abscisic acid (ABA), polyethylene glycol, and salt all significantly increased the expression of *OsbHLH120*, revealing a relationship with drought avoidance.

8.5.1.3 NAC transcription factor

Rice genes belonging to the *NAC* domain family have garnered significant attention due to their diverse roles in facilitating the root system's adaptation to drought stress (Ooka *et al.*, 2003) [83]. Transgenic rice lines carrying the *OsNAC045* transcription factor exhibited improved survival rates after exposure to salt and drought stress, attributed to the enhanced growth of lateral roots (Zheng *et al.*, 2009) [144]. Through the utilization of root-specific promoters, rice plants that overexpressed *OsNAC10*, *OsNAC9*, and *OsNAC5* demonstrated notable enhancements in root thickness and exhibited greater drought tolerance during the reproductive phase (Jeon *et al.*, 2013; Redillas *et al.*, 2012) [42, 92]. To summarize, *NAC* genes play a key role in increasing both the length and diameter of roots, consequently reshaping root structure and contributing to the development of drought resistance in rice.

8.5.1.4 Other transcription factors

Novel transcription factors within transformed rice plants have highlighted their capacity for enhanced drought resistance. When introduced into rice, the homeodomain-

leucine zipper transcription factor derived from the Arabidopsis *EDT1/HDG11* gene has been shown to heighten the plant's drought resilience. This improvement in drought resistance has been attributed to the presence of a robust root system in these plants (Yu *et al.*, 2013) [136]. In transgenic rice lines containing genes that promote drought tolerance, such as *BRX* (*BREVIS RADIX*-like homologous genes; Liu *et al.*, 2010a) [67], *OsVPI* (H⁺ pyrophosphatase in tonoplasts), and *OsNHX1* (Na⁺/H⁺ exchangers; Liu *et al.*, 2010b) [69], root development exhibited enhancement. Overexpression of *OsERF71*, either globally within the plant or specifically in the roots, yielded a drought-resistant phenotype during the vegetative growth stage (Lee *et al.*, 2016) [58]. Additionally, the rice root-specific pathogenesis-related protein RSOsPR10 was found to elevate drought resistance by enhancing root

mass (Takeuchi *et al.*, 2016) [111]. These findings underscore the pivotal role of specific transcription factors and genes in fortifying rice plants against the impacts of drought (Takeuchi *et al.*, 2016) [111].

8.6 Micro RNAs in drought stress administration in rice

Small non-coding regulatory RNAs called micro RNAs (miRNAs) control gene expression by directing the cleavage of target mRNA or by inhibiting translation. The single member of the *miR169* family, *miR169g*, was significantly upregulated in rice when subjected to drought stress, and the induction of *miR169g* was more pronounced in roots than in shoots. Sequence study showed that *miR169g* may be directly regulated by transcription factors that bind to DREs, whereas *miR393* was briefly activated.

Table 3: Drought Stress induced miRNAs and its function in *Oryza sativa* L.

miRNA	Target gene	Plant species studied	Functions	References
<i>osamiR166e-3p</i>	Alkaline neutral invertase	<i>O. sativa</i> L.	Root development, carbohydrate metabolic process, cellular amino acid metabolic process	Cheah <i>et al.</i> , (2015) [12]
<i>osamiR169r-3p</i>	UDP-glucose 4-epimerase	<i>O. sativa</i> L.	Root development, response to stress, carbohydrate metabolic process, cell wall biogenesis	Cheah <i>et al.</i> , (2015) [12]

8.7 Transgenics

Through genetic engineering, the genetic basis of drought tolerance elements has been validated by modifying gene constructs to endorse specific identified genes in rice plants. These validated elements can serve as models for developing cultivars with heightened drought tolerance. As an illustration, when transgenic plants overexpress the Arabidopsis ortholog of *DROUGHT STRESS RESPONSE-1* (*OsDSR-1*) and are cultivated in media containing abscisic acid (ABA), they exhibit significantly shorter lateral roots (LRs). This observation suggests that *OsDSR-1*, which encodes a putative calcium-binding protein, might act as a positive regulator during the ABA-mediated inhibition of LR development. This approach showcases how genetic engineering can provide insights into the role of specific genes in drought responses and contribute to the development of more drought-tolerant rice cultivars (Yin *et al.*, 2011) [132].

8.8 Comparative genomics and meta-analysis of QTLs

Comparative genomics of genes and QTLs associated with drought tolerance is being advanced through the application of bioinformatics and systems biology tools (Swamy *et al.*, 2013) [110]. This approach streamlines the process of allele mining and aids in understanding the shared mechanisms of drought tolerance across related crops. The validation of markers linked to major-effect QTLs on a panel of drought-tolerant lines is aimed at ensuring their presence across a wider range of genotypes.

In the pursuit of meta-QTLs for root characteristics under drought conditions, initial QTLs were significantly condensed into a smaller number of consistent meta-QTLs (MQTLs), with corresponding confidence intervals becoming narrower (Courtois *et al.*, 2009) [18]. A total of 61 stable MQTLs have been identified, spanning various genetic backgrounds and contexts for root architectural features (Kahani *et al.*, 2021) [52]. These regions have the potential to serve as essential tools for marker-assisted selection (MAS), fine mapping, and functional analysis.

One notable instance is the identification of three meta-QTLs covering a 35 cM region on chromosome 9, displaying

extensive root QTL activity (Khowaja *et al.*, 2009) [53]. In rice genome-wide association studies (GWAS), 50 MQTLs were found to align with SNP peak sites associated with root morphological traits. Among these MQTLs, numerous genes related to root system architecture (RSA) and drought tolerance were discovered. These included genes involved in auxin biosynthesis or signaling (e.g., *YUCCA*, *WOX*, *AUX/IAA*, *ARF*), root angle (*DRO1*-related genes), lateral root development (e.g., *DSR*, *WRKY*), root diameter (e.g., *OsNAC5*), plant cell wall (e.g., *EXPA*), and lignification (e.g., *C4H*, *PAL*, *PRX*, and *CAD*). This comprehensive analysis provides valuable insights into the genetic underpinnings of root traits associated with drought tolerance in rice (Daryani *et al.*, 2022) [21].

9. Conclusion and Perspectives

This article primarily engrossed on swotting on together classic and current research exertions concerning rice root response to moisture insufficiency. The significance of understanding root responses to drought stress has gained prominence in the context of ongoing global warming, prompting exploration through various approaches and methodologies. While much emphasis in drought resistance research has been placed on above-ground traits, there remains a significant gap in understanding below-ground traits, largely due to the challenges associated with phenotyping. Given the crucial roles that root elasticity and architecture play in growth, stomata regulation under drought conditions, and maintaining optimal yield, it is imperative to dedicate attention to these aspects in drought resistance studies. The comprehensive analysis of root traits and metabolic processes is still relevant for analyzing drought tolerance and designing breeding strategies for specific crops.

Significant progress in cytology, biochemistry, and molecular biology has accelerated the exploration of the molecular pathways underlying rice root responses to water stress. Numerous relevant genes and proteins have been identified and updated, leading to the discovery of multiple major regulatory pathways. The adoption of "omics" techniques, including genomics, transcriptomics, proteomics,

metabolomics, and phenomics, provides robust avenues for identifying critical root components essential for plant development and fitness, especially under conditions of increasingly severe drought stress. These approaches offer powerful tools for unraveling the intricate mechanisms governing rice root responses to water stress and hold promise for advancing crop improvement strategies in the face of changing environmental conditions.

Many biological processes participate in the responsiveness of roots to drought stress. Furthermore, the majority of recent research has concentrated on the effects of a single stress factor on roots, regardless of the fact that in actual field scenarios, roots may be challenged to multiple stresses, counting those caused by water, nutrients, and microbes. And therefore, how to monitor and behave to varied sources of stress as well as whether or if there are any commonalities in the way of reaction to different sources of stress that can be pooled for analysis, continue to be crucial issues in empirical investigations. With the incorporation of new technologies, it is foreseen that rice drought resistance will expand in the near future. Advanced breeding practices are also predicted to yield a number of new germplasm and genotypes that are more resistant to water restrictions and future climate change. Thus, to harness roots and dehydration avoidance characteristics to develop drought-resistant rice, a trait-based paradigm with a exhaustive knowledge of the target environment, including temporal and spatial heterogeneity, is a potential route.

10. References

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