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ABSTRACT

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ABSTRACT

The present scenario of climate change on agriculture in the form of groundwater depletion, flood, salinity, several new borne species of pathogens, and insect-pests, brings serious attention to developing rice varieties with higher resilience. As most of the above-ground plant parts are already explored to combat these situations, now the time came to improve the yield by reshaping the below-ground plant parts. Designing the root system architecture (RSA) in rice is one of the most imperative traits for such conditions, as modification in the root architecture in rice will be the best strategy to improve water uptake and nutrient acquisition. Many quantitative trait loci (QTLs) and genes playing the role for RSA have been recognized to improve the root parameters and the confirmed QTLs can be introgressed through marker-assisted backcross breeding to develop ideal genotypes. The recent advances in molecular plant breeding including genome editing, mutation study and genetic engineering has shown their potency in this direction. Even though most of the root architectural traits in rice are not documented properly, the present review will make comfortable to the future researchers on the aspects of molecular mechanisms involved in root traits development viz., genes functioning for root traits, their development, physiological role for moisture, and mineral-nutrient uptake under stressful environment.

Keywords: climate change, genome-wide association studies, genome editing, rice, root system architecture, QTLs.

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I. INTRODUCTION

Rice is considered to be the vital crop for billions and got ranked as the second-best significant cereal food in the world after wheat. This crop is being cultivated under various natural climatic conditions (Dokku *et al.*, 2013; Manna et al., 2025; Rasheed *et al.*, 2020). Conversely, the yield potentiality is hindered by several biotic and abiotic factors, including increasing water scarcity, flood, soil salinity and temperature fluctuation (Navea *et al.*, 2017). Asia is contributing maximum rice (90%) to the World's food security, while water scarcity affects around 50% of rice-cultivable land (Khan *et al.*, 2013; Shukla et al., 2024). The reason behind this is that it takes 3000 litres of water to yield one kilogramme of rice. Drought affects the crop at every stage of growth because of its shallow roots and thin cuticle, making it one of the most vulnerable plants (Figure-1), with a potential yield loss of 100% (Oladosu *et al.*, 2019). In the near future, rice could be subjected to more severe challenges, including drought, soil salinization, and a lack of readily available nutrients due to diminished fertilizer or moisture availability (Poot and Lambers, 2008; Shukla *et al.*, 2024). Roots are very essential for crop production and productivity because of their vital functions to the plant, including water uptake, nutrient gain and anchoring into the soil to withstand lodging (Yang *et al.*, 2019). The root system architecture (RSA) is the vital part towards overcoming the environmental complexity and ensuring an ideal response. They also have an impact on their surroundings by inducing physico-chemical and microbiological processes that affect essential factors such as nutrient bioavailability, organic matter cycling, soil mineral weathering, and water quality (Li *et al.*, 2025; Ma *et al.*, 2025). Most of the researchers are generally focused on the above-ground plant parts like leaf, stem, panicle and grain quality to achieve higher yield under stress. However, the root system scattering under ground is the main role performer to improve the above-ground parts. Therefore, more efforts are required to the ground to study the root architectural traits to enhance its capability to absorb sufficient moisture and mineral elements from the ground to boost the yield under diverse climatic conditions. The three-dimensional location of roots in the soil is referred to as a plant RSA, and this encompasses the morphology, topology, and distribution of roots (Li *et al.*, 2025). As a plant grows, its root system undergoes elongation, branching, and spacing changes, all of which affect RSA's ability to maintain its original shape. Root systems can show a high degree of developmental plasticity because of their ability to integrate environmental information into their growth programme (Novoplansky, 2002). In a dynamic, ever-changing environment, plants with root plasticity can adapt their root system's three-dimensional shape to maximise growth. An important part of root stability, as well as hormone biosynthesis and nutrition and water absorption, is the root system's design (Coudert et al. 2010). Specialized root architectures are effective in such conditions for a specific stress-prone environment (Poot and Lambers, 2008; Panda *et al.*, 2021). However, the molecular mechanisms of genes regulating root development and the physiological role (*e.g.*- nutrient uptake), root plasticity, plant-soil microbial interaction, high-throughput root phenotyping methods are not clearly understood. So it needs further analysis for proper understanding.

Root architecture, lateral root growth, and root symbiosis with host plants are all examples of how water and nutrient uptake rates can be changed to improve survival and production (Figure-1). Mutational analysis is a powerful technique for deciphering these processes and identifying genes that could be used to improve root function. The usage of numerous sorts of mutants will improve genetic studies on the detection of regulatory mechanisms. EST libraries and mutant protein/metabolite profiles, among other genomic and proteomic methods, add a new level to understanding root function (IAEA, 2006). Plant ecophysiology and genetics research should be combined to improve crop tolerance to adverse environments. Designing an optimum root system for a specific edaphic environment through gene mutation is ideal breeding without phenotypic selection (Uga, 2021; Li *et al.*, 2025). Therefore, this is highly essential to identify the unique QTLs or genes families or transcription factors accompanying yield attributing root traits in rice to design high-yielding cultivars. Keeping all the above facts in view, the present review illuminates the understanding of the genetic networks underlying in root-traits development and associated QTLs in rice and breeding innovation in the molecular era to develop an ideal climate resilient genotype thru root architectural trait modification.

II. DEVELOPMENT OF ROOTS IN RICE AND ITS GENETIC BASIS

Remarkable progress has been made to identify the genes or QTLs linked to the root traits in rice with the assistance of advanced molecular biology and biotechnology tools especially DNA sequencing technology. Most of the wild relatives of the cultivated crops have sufficient root systems to fight against drought by capturing water from a deeper layer. Therefore, genetic enhancement in the architecture of roots, regarded as an effective methodology to enhance the yield of crops. But, it is time-consuming and more laborious to select the below-ground parts (traits related to root) than aboveground traits. In rice including the wild species, a diverse variation for root characteristics has been observed. Different types of root traits in rice are illustrated in Figure-2 and listed in Table-1, which helps to withstand the plant under stress. The molecular mechanism involved in root improvement in rice has been discovered mostly based on QTL study and this was described by Champoux *et al.* (1995) for the first time. In rice, a number of QTLs have been found linked with root growth angle, length, thickness and volume, more or less which affect the RSA (Rebouillat *et al.*, 2009). A list of QTLs related to 29 root traits was summarized by Courtois *et al.* (2009) and many genes for root growth have been cloned in mutant genotypes with unusual root phenotypes (Li et al., 2025; Kong et al., 2024; Wu and Cheng, 2014). Yet, the hereditary mechanisms involved in these genes are understood poorly. Therefore, here, in brief we are discussing the genes/QTLs interrelated to quantitative variations of RSA in rice.

2.1. Genes controlling root Length and root number

Cell differentiation, expansion, and elasticity all contribute to root elongation. The investigation of mutant lines revealed the importance of quantitative trait loci (QTLs) underlying cell wall development, growth, and auxin signalling during root cell differentiation and elongation (Wang *et al.*, 2014). Two QTLs, QUICK ROOTING 1 (QRO1) and QRO2, were identified by Kitomi et al. (2018) as determinants of maximum root length. Transgenic rice overexpressing the *OsEXPA8* gene has managed to perform a variety of functions, including increasing crown root, seminal root, and lateral root length. Due to an increase in root and shoot vascular bundles, these also increase plant height, leaf size, and leaf number (Shin *et al.*, 2005). A low auxin concentration is most likely to blame for the short elongation zone. The far more important genomic regions containing QTLs for several traits (root length, root diameter, and root dry weight) were discovered on chromosomes number 1, 4, 9, 11, and 12 (Courtois *et al.*, 2003). Jonathan *et al.* (2015) discovered a QTL for total lateral root number; TLRN (*qTLRN-12*) flanked at 25.5 cM at the seedling stage (hydroponics system). The gene (*qLLRN-12*) which was discovered during the vegetative stage, controls lateral root number in rice.

2.2. Genes directing root growth angles

The environmental factors like temperature, light, water potential, and gravity are combined to control the root growth angle (Uga *et al.* 2015a). In rice, a few QTLs for the root gravitropism reaction have been identified (Manna *et al.*, 2025; Norton and Price, 2009), but the causal genes need to be identified. A significant QTL (DRO1), which plays a role in root development angle and gravitropism, was initially identified (Uga *et al.*, 2013a). Many other researchers have done extensive work on DRO series genes (*DRO2*, *DRO3*, *DRO4*, and *DRO5*) for growth angle root (Uga *et al.*, 2013b; Uga *et al.*, 2015b; Kitomi *et al.*, 2015). A variety "Kinandang Patong" is a prominent donor for this trait which was studied by the earlier researchers. This can be used as a contributing parent to tailor efficient rice genotypes.

2.3. Genes linked with other root related traits

The marker-assisted selection method was employed to fine-map a QTL (STELE TRANSVERSAL AREA 1; STA1) on chromosome 9 that influences root stele transversal area (Uga *et al*., 2010). Other genes, such as *qRT9* and *STA1*, are close to *DRO1* (16.31 Mb), and the phenotypic roots can be distinguished by the proximity of these associated QTLs. Root plasticity is characterized as the ability of a plant to change the phenotype of its roots in reaction to varying environments (O'Toole and Bland, 1987), and it is critical for plant adaptation. QTLs for soil-surface rooting were reported by Uga *et al*. (2012) from the RIL populations (Gemdjah Beton × Sasanishiki). The female parent has surface rooting, while the male parent is without. The result confirmed that the QTLs located on chromosomes number 3, 4, 6, and 7 (*qSOR*, with major effect).

III. DECIPHERING THE ROLE OF ROOT ASSOCIATED QTLS IN IMPROVED NUTRIENT AND WATER ACQUISITION

Modern agriculture system faced major challenges to improve nutrient acquisition properties of crop plants under dynamic environmental conditions. Thus, RSA is an important trait for genetic improvement of nutrient acquisition from nutrient deficient soils (Kong *et al.,* 2014). The upper and lower crown roots, which emerged from each node's upper and lower sections, respectively (Rebouillat *et al*., 2009). It's been observed that the crown roots closer to the ground are wider than those closer to the ceiling (Abe and Morita, 1994). The root system's vertical distribution is established by the relative growth inclination of the upper and lower crown roots. Roots are more likely to be dispersed in the topsoil when the root growth angle is shallow, and in the subsoil when the angle is steep. Each crown root can only grow so long, limiting the plant's ability to draw moisture and nutrients from the ground (Liu *et al*., 2023; Ma *et al*., 2025). Roots that are too short form compact root systems, whereas those that are too long produce vast root systems that are more resistant to lodging. A wide array of quantitative trait loci (QTLs) have been identified and characterized which significantly contribute to enhanced nutrient and water acquisition, especially under suboptimal or stress-prone environments (Table-2). These QTLs govern key root traits such as root length, root depth, root surface area, root hair density, root angle, and biomass allocation, which collectively determine the plant’s efficiency in accessing soil nutrients and water.

3.1. QTLs for Nitrogen uptake

The main form of nitrogen under aerobic condition to make available to plants is Nitrate, and is leached by precipitation into subsoil. Therefore, root system architecture greatly affects the acquisition of water and nutrients from soil (Gewin, 2010; Liu et al., 2023). The rice *QTL DEEPER ROOTING 1* (*DRO1*) has been identified from the RIL population derived from the cross between ‘IR 64’ (lowland cultivar nonfunctional allele of *DOR*, shallow roots) and ‘Kinandang Patong’ (upland cultivar with functional allele of *DRO1*); and reported on the chromosome number 9 (Uga *et al*., 2011) and has been cloned by Uga *et al*. (2013a). The yield performance of ‘IR64’ and *Dro1-NIL* was compared under upland field conditions with no drought, moderate drought, or severe drought (Uga *et al*., 2013a). Under moderate drought in comparison with no drought, the grain weight of ‘IR64’ decreased by nearly half, whereas that of *Dro1-NIL* was almost the same. Under severe drought, the grain weight of ‘IR64’ was very low, whereas that of *Dro1-NIL* was more than 30% of that with no drought. This study suggests that deep rooting induced by *DRO1* enhances drought avoidance, resulting in higher grain yield (Uga *et al*., 2013a). The *Dro1-NIL* showed about 10% higher grain yield than did ‘IR64’ irrespective of nitrogen treatment (Arai-Sanoh *et al*., 2014). Comparison among cultivars with different root and shoot morphologies has suggested that deep roots increase grain yield in paddy (Kawata *et al*., 1978; Morita *et al*., 1988). There was no significant difference between IR64 and *Dro1-NIL* in nitrogen content before heading, but nitrogen uptake was higher after heading in *Dro1-NIL* than in IR64. The results suggest that deep rooting induced by *DRO1* enhances nitrogen uptake from lower soil layers, resulting in better grain filling (Uga *et al.*, 2015a). The *QTL NITRATE TRANSPORTER 1.1* has the ability to transport for the first time a functional link between root development, auxin and nitrate availability in soil (Puiga *et al.*, 2012). Low nitrogen (N) availability, in contrast to P constraint, encouraged the elongation of primary and LRs in particular, whereas LR density remained substantially unaltered (Lopez-Bucio *et al.*, 2003; Liu *et al.*, 2023; Gruber *et al.*, 2013). Such RSA alterations are expected to boost the plant's ability to more efficiently forage the soil in quest of hardly available nutrients, or to collect N before it leaches out of the rooting zone, as part of the 'steep, cheap, and deep' root ideotype advocated for maize (Fu *et al.*, 2023; Lynch, 2013).

3.2. QTLs for Phosphorus uptake

Phosphorus (P) is a key inorganic plant nutrient that is required for cell growth and division in living organisms. P fertilizer application for crop development has expanded dramatically in recent decades, yet P-use efficiency has decreased to a low of 10-20% (Wissuwa *et al.*, 1998). Furthermore, much of the applied P has polluted the environment severely. The development of cultivars that are more resistant to P deprivation is thought to be a viable solution to this problem. Rice growth and development are severely hampered by phosphorus shortage. P deficiency can cause plant growth to be stunted, resulting in dark green leaves, reduced root formation, and reduced tillering (Dobermann and Fairhurst, 2000). Under P stress, high sterility, maturity delaying, and plant height reduction are all common. In P-deficient soils, root extension has been reported in a variety of plant species (He *et al.*, 2003; Shimizu *et al.*, 2004). Three primary ways for plants to adjust to low P-deficiency are root P-interception, P acquisition efficiency, and internal P-use efficiency (Ismail *et al.*, 2007). Under P deficit, changes in root architecture are considered an adaptation that improves phosphorus uptake (Lynch, 1995). Much evidence indicates that root hair development is also stimulated in response to (high/low) phosphate (Desnos *et al.*, 2008). Results found that the effect of low phosphate on RSA is opposite to that of low nitrate. Shallow and shorter root architecture with more branches is an ideal trait for immobile resource acquisition such as phosphorus, potassium, iron, and manganese in topsoil. The optimal RSA is also related to the plant's carbon status, air temperature, and planting density (Postma *et al.*, 2014) because the topsoil tends to hold less water but more immobile nutrients such as phosphorus than does the subsoil (Gewin, 2010). Breeders have focused their efforts on developing rice cultivars that are resistant to P deficiency. In practise, P-deficiency tolerance has been determined by directly measuring dry weight or grain yield in low-phosphorus soils (Fageria *et al.*, 1988), or indirectly evaluating relative tiller number and relative dry weight (Fageria *et al.*, 1988; Chaubey *et al.*, 1994). However, previous efforts to generate tolerant high yield varieties have been impeded by the complexity of the characteristics involved in P-deficiency tolerance and the lack of a screening criterion suitable for use in breeding programmes. Several plant features are complicated quantitative qualities in nature that are impacted by many genes and the environment (Li *et al.*, 2003). QTL analysis is a powerful method for understanding the genetic basis of complicated traits like P-deficiency tolerance. In rice, certain QTLs for characteristics linked to P-deficiency tolerance have been discovered (Wu and Ni, 2000; Shimizu *et al.*, 2004, 2008). Using a recombinant inbred line (RIL) population from the rice cross between IR20 and IR55178-3B-9-3 cultivated in P-deficiency and P-sufficiency nutritional solutions, mapped QTLs for relative tillering ability, relative shoot dry weight, and relative root dry weight. Wissuwa *et al.* (1998) used BC lines cultivated in P-deficient soil to map QTLs for P absorption, internal P-use efficiency, dry weight, and tiller number. On chromosomes 6 and 12, Wissuwa *et al.* (2001, 2002) identified two QTLs for P uptake. In addition, in the Kasalath Gimbozu population, a QTL for P deficiency-induced root elongation was mapped on chromosome 6 and fine mapped (Shimizu *et al.*, 2004; Shimizu *et al.*, 2008). Using molecular markers to discover genetic factors and incorporate them into a high yield variety is one efficient way to improve rice's adaptability to P deficit. Only a few publications have been published on QTLs for P uptake, P use efficiency, and P-related characteristics

(Ismail *et al.*, 2007). The bulk of P-deficiency tolerance genes have yet to be discovered. Furthermore, earlier studies mainly looked at additive QTL, ignoring epistatic effects and QTL-environment (Q × E) interaction effects. As a result, more research is needed to identify genes linked to resistance to P-deficiency and to decipher its complicated genetic architecture. Introgression lines can be used to find QTL, detect hidden genetic variation, evaluate genetic interaction, and provide valuable resources for map-based clone and marker assisted breeding. Under P-deficiency and P-sufficiency circumstances, a report on a set of 271 introgression lines (ILs) was used to assess seedling responses to low P availability and to discover QTLs for root characteristics, biomass, and plant height. P-deficiency inhibited plant height, total dry weight, shoot dry weight, and root number, whereas P-deficiency stress enhanced maximum root length (MRL) and root-shoot ratio (RS). P-deficiency tolerance may be influenced by the two QTL *qRN5* (influence root number) and *qRDW5* (influence root dry weight) which is consistently expressed to promote trait stability (Anis *et al.*, 2018). Twelve intervals were used to cluster QTLs for P-deficiency tolerance, and one QTL (*qRRS8*) showed pleiotropic effects on both P-deficiency and drought tolerance, suggesting that these QTLs could be employed in future marker-assisted breeding programmes (Li *et al.*, 2009). In rice, overexpression of *PHOSPHORUS-STARVATION TOLERANCE 1* (*PSTOL1*) enhanced grain yield and P acquisition increased in P-deficient soil through regulation of RSA (Gamuyao *et al.*, 2012). *Pup1* (*Phosphorous uptake1*) having *PSTOL1* is suitable in improving the phosphate uptake under rainfed/upland conditions in rice (Shin *et al.*, 2020) and *Pup1* was mapped on chromosome 12 of traditional rice variety Kasalath (*aus*-type) (Wissuwa *et al.*, 2002).

3.3. QTLs for heavy metal stress

Cadmium (Cd) is an extremely poisonous heavy metal that can kill living things. Rice grains containing an excessive amount of Cd pose a major concern to persons who eat rice as a staple food. Chronic exposure to Cd may result in a variety of health issues (Bertin and Averbeck, 2006; Clemens *et al*, 2013). It is critical to produce premier rice cultivars with minimal Cd accumulation, particularly indica types, which can accumulate more Cd than japonica varieties. Tang *et al.* (2017) used the CRISPR/Cas9 method to generate a novel indica rice line with minimal Cd accumulation by altering the metal transporter gene *NRAMP5*. Because this transporter is involved in Cd uptake at the root, mutations in this gene result in a significant drop in Cd concentration. The ninth exon of the gene is targeted by two sgRNAs. The root growth angle influences the efficiency of nitrogen, phosphorous absorption; it might also affect the uptake of other minerals such as heavy metals. In Cd-contaminated soil, the grain and straw Cd concentrations were significantly higher in 'IR64' than in *Dro1-NIL* (Uga *et al.*, 2015a). Hence, the plants with shallow rooting will capture Cd from top soil layer and the allele occurring shallow rooting is a potential genetic resource for phytoremediation under high Cd accumulation. From food safety point of view, the allele giving deep rooting could be a useful resource to avoid absorbing the bioavailable Cd from topsoil (Uga *et al.*, 2015a).

3.4. QTLs for water uptake under moisture stress

Approximately half of the world's rice production depends on rain water which is grown in aerobic upland and rainfed lowland systems and plants are frequently exposed to unpredictable stages of drought stress (Singh and Chinnusamy, 2008). The plant's root is the primary site to perceive drought stress and to initiate a signaling cascade at the molecular level. Hence, an ideal root architecture with extensive root system is desirable for water stress (drought) condition as they maximizing water capturing ability and supporting shoot growth under drought conditions (Gowda *et al.*, 2011; Khan *et al.*, 2013; Mai *et al.*, 2014; Agrawal *et al.*, 2016). Plants adopt diverse strategies like enhance their water uptake ability by developing their root system (by increasing root density, deep rooting, and root/shoot ratio); improve their water-storage ability in specific organs; reduce their water loss (by leaf rolling and rapid stomatal closure); and accelerate or decelerate the conversion from vegetative to reproductive stage to avoid complete abortion in severe drought conditions to deal efficiently with water stress. The mechanisms of interactions between root system architecture and drought stress in rice would have a noticeable impact on overcoming drought stress (Gowda *et al.*, 2011; Wu and Cheng, 2014). Early seedling vigor can cope with drought stress during the seedling stage, which is mostly determined by the environments of germination, genetic or inheritance pattern, and early seedling vigor (Zhang *et al.*, 2004; Qun *et al.*, 2007; Yang *et al.*, 2015). Sandhu *et al.* (2014) investigated the seedling vigor under drought stress conditions in rice, and a QTL analysis was performed using genotyping-by-sequencing (GBS) technique. A total of 162 recombinant inbred lines (RILs) of rice derived from the cross of two varieties, Milyang23 and Tong88-7, were subjected to seedling vigor evaluations which are grown under water stress condition for two weeks. A total of 6 main-effect QTLs (M-QTLs) and 21 epistatic QTLs (E-QTLs) associated with root morphological traits were identified on all chromosomes and information will be useful for molecular breeding of drought-tolerant rice with higher seedling vigor Sandhu *et al.* (2014). Though enhancement in seedling vigor is a promising strategy to overcome the negative effect on plant growth under drought conditions (Rebolledo *et al.*, 2013), the molecular basis for the seedling vigor under drought stress has not been fully explained. Root growth at soil depths below 30 cm may provide access to critical soil water reserves during drought in rainfed lowland rice. The lines evaluated by Henry *et al.* (2011) genotype Dular, which facilitate improvement in drought resistance in rice through dehydration avoidance and showed greater drought resistance associated with deep root growth and highest drought response index (less reduction in yield by drought stress). The QTL *qRFW9* reported by Price *et al.* (2002) for root fresh weight was detected only on chromosome 11 in rice and it might be a novel QTLs to develop molecular markers for breeding drought-tolerant rice varieties. To design new root ideotypes to adapt under diverse environmental stresses, amelioration of ideotype breeding with root trait QTLs through marker-assisted selection is a requirement (Coudert *et al.*, 2010). For this, updated understanding of the genetic mechanism associated with root system architecture, information on gene networks involved in root formation has been accumulated (Coudert *et al.*, 2010; Rebouillat *et al.*, 2009). The identified QTLs advancing the rice breeding technology by understanding molecular biology and with the help of DNA sequencing technology.

IV. MOLECULAR APPROACHES TO REDESIGN THE UNDERGROUND HALF OF RICE

Roots are vital organs that help plants capture water and nutrients from the soil. The extent of the zone of the soil where water and nutrients can be obtained is determined by root system architecture (RSA). Because roots are front-line organs in the response to abiotic stresses such as drought, flooding, and salinity stress, it will be critical to improve belowground plant parts as well as aboveground plant parts as global climate change increases. However, because roots are hidden underground, conventional breeding focused on phenotypic selection makes it difficult to choose breeding lines with potential RSAs for abiotic stress adaptation. Design-oriented breeding of RSA without phenotypic selection is possible thanks to recent advancements in modelling, molecular biology and biotechnology (Holz *et al.*, 2024; Uga, 2021). Integrated breeding strategies for developing climate-resilient rice genotypes with improved yield and root traits are highlighted in Figure-3. Improved root systems are critical for greater water and nutrient uptake, especially in systems with limited water supply, such as aerobic farming (Kharb *et al.*, 2015; Meister *et al.*, 2014). Increased water extractions are linked to the ability of roots to vary their response developmentally and functionally, and it is usually recognised as a key component feature for yield and adaptation during variations in soil moisture (Catolos *et al.*, 2017; Phule *et al.*, 2019). The findings implies that plants' ability to acquire mineral elements is linked to their root systems' ability to investigate the soil. Mutants with root systems that better utilise the soil, acquire more mineral elements, and produce higher yields on depleted soils can be created (White *et al.*, 2009). Most root features for increasing yield in water-stressed situations are complicated in nature, making them difficult to incorporate into traditional breeding strategies (Jalil *et al.*, 2018; Sandhu *et al.*, 2019). Breeding for aerobic cultivars could be accelerated by finding Quantitative Trait Loci (QTL) related to features for aerobic adaptation using Marker-Assisted Selection (MAS). Therefore an hypothetical ideal root model is illustrated in Figure-4.

4.1. Mutation breeding to identify novel mutants

Using high-throughput genotyping, the populations are screened for mutations in genes of interest, and phenotypic changes are calculated (reverse genetics). Induced mutations for desirable features, such as root properties, provide a quick way to improve elite adapted germplasm for crop improvement. The creation of structured mutant populations for forward and reverse genetics aids mutant exploitation. These take advantage of the growing amount of sequence data available to confirm gene function. For model species like Arabidopsis, Medicago truncatula, *Lotus japonicus*, and rice, mutation grids or 'TILLING' populations have been produced, but agricultural plants like barley and wheat are also being developed (IAEA, 2006). As more sequencing data becomes available, this list will be expanded to include other species. Argentina (wheat), Australia (lupins), Belgium (annual plants), Brazil (wheat), China (soybean), China (wheat), Cuba (wheat), Germany (maize), Israel (annual food plants), Poland (barley), South Africa (*Vigna unguiculata* and *Vigna subterranean*), Turkey (barley and chickpea), United Kingdom (barley) are among the countries working on specific crops (IAEA, 2006). In comparison to control plants, overexpression of O. sativa *ROOT ARCHITECTURE ASSOCIATED 1* (*OsRAA1*) increases the quantity of crown and lateral roots (Ge *et al.* 2004). *OsRAA1* is an anaphase-promoting complex/cyclosome (APC/C)-targeted protein that stops the cell cycle from entering anaphase (Han *et al.* 2008). Although crown root initiation proceeds normally, a mutation in *rice CULLIN-ASSOCIATED AND NEDDYLATIONDISSOCIATED 1* (*OsCAND1*) causes a deficiency in the development of crown root primordia (Wang *et al.* 2011). In Arabidopsis thaliana, *CAND1* is a *SCFTIR1 E3* ubiquitin ligase involved in the degradation of *Aux/IAA* proteins in response to auxin (Chuang *et al.* 2004; Feng *et al.* 2004). *OsCAND1* is required for auxin signalling in the crown root meristem to maintain the G2/M cell cycle transition and, as a result, crown root emergence (Wang *et al.* 2011). The rice gene *AUXIN RESISTANT 1* (*OsAUX1*), which is evolutionarily related to the auxin influx carrier gene family *AUX1/LIKE AUX 1* (*LAX*), has T-DNA insertion mutations that lower the number of lateral roots (Zhao *et al.* 2015). The nal2 and nal3 double mutant (nal2/3) produces fewer lateral roots than the wild type due to mutations in two identical *OsWOX3A/OsNARROW SHEATH* (*OsNS*) genes on chromosomes 11 and 12, respectively (Cho *et al.* 2013). The decreased number of lateral root initiation in *nal2/3* appears to be due to a problem with endogenous IAA distribution mediated by changes in *OsPIN1* and *OsPIN2* expression (Cho *et al.* 2013).

4.2. Genetic engineering of root traits

Despite substantial limitations in our understanding of the genetic mechanisms that affect root system architecture in agricultural plants, multiple research have reported success in changing crop RSA features utilising various phenotyping methodologies and promoter and reporter expression. The bulk of these root-related genetic loci have not been addressed for transgenic manipulation thus far, and in a few cases, the impacts on RSA were accompanied by pleiotropic effects (Bian *et al.* 2012). Overexpression of transcription factors *OsNAC5/9* and *OsMYB2*, the receptor kinase *PSTOL1*, the G-protein coding Root Architecture Associated (*OsRAA1*), a cell wall extension gene *OsEXPA8*, and the identification of the *DRO1* allele for the deep root system have all been made in rice. There are several reports on RSA changes that boost nitrogen, phosphorus, and water utilisation efficiency, resulting in increased grain yield. Root characteristics are critical for enhancing grain yield, according to the findings. Deeper rooting QTL; *DRO1* (Uga *et al.* 2013b) and phosphorous uptake QTL; *PSTOL1* are two of the most extensively researched examples of where genes have been identified that bestow variations in root architecture (Gamuyao *et al.* 2012). Kinandang Patongan, a highland rice variety, was used to find the *DRO1* QTL. When roots develop longer and deeper, they are able to absorb more water from the deeper soil profile. The QTL, *DRO1* is a well-explained example of genetic alteration of root characteristics in rice, where root angle and rooting depth are targeted via breeding or transgenic techniques to achieve the steep-deep ideotype, as described by Uga *et al.* (2013b). The use of traditional breeding to introduce the *DRO1* allele and transgenic techniques to express the *DRO1* genomic fragment in IR64 gives evidence that steep-deep root architecture boosts yield under drought circumstances Uga *et al* (2013b). *PSTOL1* encodes a receptor-like kinase that has been demonstrated to increase root biomass and maps to a significant QTL for phosphorus shortage tolerance in rice (Gamuyao, *et al.* 2012). The finding of 23 differently regulated genes functionally related to root growth and stress responses came from transcriptional analysis of *PSTOL1* allele overexpression lines. The discovery of these QTLs emphasises the importance of root development and angle as features that influence drought tolerance and phosphorus shortage at the same time. Seo *et al.* (2008) found that *OsPT1* produced by a constitutive promoter in rice enhanced phosphorus concentrations in tissues over wild type, but the plants were shorter and had more tillers. Another phosphate transporter allele, *OsPT1.8*, was overexpressed in rice, and tissue phosphorus concentrations increased when plants were cultivated on high phosphorus levels, but not when levels were below 40 mg inorganic phosphorus/kg soil (Jia *et al.*, 2011).

4.3. Mapping of major effect QTLs for root architectural traits

Roots are important for crop yield maintenance, which is critical when plants are grown in soils with insufficient water or nutrients (Bengough *et al.*, 2011), and roots are one of the primary sites for stress signal perception, which triggers a cascade of gene expression responses in response to water deficit (Rabello *et al.*, 2008). Previous research has shown that plant growth is mostly dependent on the severity of the stress; a slight water deficit inhibits the growth of leaves and stems, but roots can continue to extend (Peng *et al.*, 2006). Furthermore, root architecture is an important characteristic for separating genotypic variants in rice responses to water shortages (Henry *et al.*, 2011). To increase rice varieties' adaptability to aerobic conditions, a better understanding of the underlying physiological and molecular mechanisms is required. Upland rice's long and deep root system, the ratio of root weight to shoot weight, and root penetration ability contribute considerably to drought tolerance, according to Price and Tomos (1997). Several of the QTL discovered for root length are consistent among mapping populations (Courtois *et al.*, 2009), and shared genomic areas for root thickness, root penetration, and stomatal behaviour have been identified across populations and even species (Zhang *et al.*, 2001). In lowland and irrigated rice, progress has been made in finding large effect QTL conferring drought tolerance (Price and Tomos, 1997; Serraj *et al.*, 2011). For both upland and lowland rice, many QTL for grain yield under drought stress have been identified (Bernier *et al.*, 2007; Venuprasad *et al.*, 2009). Sandhu *et al.* (2013) found 35 QTL related with 14 traits on chromosomes 1, 2, 5, 6, 8, 9, and 11 in the MASARB25 Pusa Basmati 1460 population and 14 QTL associated with nine traits on chromosomes 1, 2, 8, 9, 10, 11, and 12 in the HKR47 MAS26-derived population in their study. Three large-effect stable QTL for improved yield under aerobic settings, as well as QTL for various root-related features that are likely to boost water and nutrient intake under aerobic conditions, were discovered. Coexisting QTL for root and yield-attributing traits reveal a mechanism associated with better yield of promising lines under dry direct-seeded circumstances, indicating resource movement during grain filling (Sandhu *et al.*, 2013).

4.4. Speeding up QTL introgression thru marker-assisted backcross (MABC) breeding

Four QTLs for root characteristics were introduced into an upland rice cultivar using marker-assisted backcross breeding. The QTLs have previously been discovered in a different genetic background under experimental conditions. The introgressed lines and the recurrent parent were grown for 6 years in highland areas in Eastern India by resource-poor farmers, and yields were reported. Under generally favourable field conditions, the QTLs improved yield by 1 t.ha^{-1} when combined. Due to increased variation in soil-water availability in very low yielding conditions and resulting yield variability, the QTL effects were not identified in less favourable trials (Steele *et al.*, 2013). Introgressing QTL clusters into advanced backcross-derived lines and testcrosses resulted in an increase in grain yield, providing direct proof for the feasibility of boosting grain output by modifying root systems (Li *et al.*, 2015). *Deep Rooting 1* (*DRO1*), a significant locus influencing root development angle, was found in a bi-parental population of two rice lines with different drought tolerance by Uga *et al.* (2011). When *DRO1* was cloned and characterised, it was found to play a role in producing a steep root angle and, as a result, boosting drought tolerance and grain yield when introduced into the susceptible parent's genetic background (Uga *et al.*, 2013). Furthermore, using a specific allele of the *PHOSPHORUS STARVATION TOLERANCE 1* (*PSTOL1*) locus in rice or sorghum, a clear genetic relationship between root length and P acquisition as well as yield performance in phosphorus-deficient soil has been shown (Gamuyao *et al.*, 2012; Hufnagel *et al.*, 2014). Developing novel crop cultivars with improved root systems has the potential to improve resource use efficiency and plant adaptation to unstable climates when taken together. In the experimental population IR64 × Kinandang Patong, the locus *Deep Rooting 1* (*DRO1*) has been demonstrated to be a major factor for root angle (Uga *et al.*, 2013). Its orthologous gene in barley (MLOC 3895.5, 48.38 cM) was expected to be on Chr 5H (MLOC 3895.5, 48.38 cM) and mapped near an RSA QTL (*qRSA13*, Chr 5H, BOPA2 12 10899, 43.76 cM). *SCARECROW* (*SCR*) is a transcription factor that is expressed in the stele but moves out to govern endodermal development in Arabidopsis. It is activated by the transcription factor *SHORTROOT* (*SHR*), which is expressed in the stele but moves out to regulate endodermal differentiation (Cui *et al.*, 2007). Short roots are caused by mutations in either gene. *OsSCR1* and *OsSHR1* in rice have the same functional purpose as in Arabidopsis (Kamiya *et al.*, 2003; Cui *et al.*, 2007; Mai *et al.*, 2014).

4.5. Genome-wide association study (GWAS) and Identification of Candidate Genes

The development of emerging high-throughput genomic technology will allow harnessing the genetic diversity (Varshney *et al.*, 2014) for several agro-morphological traits to improve the yield under dry-DSR through genomics-assisted breeding (Kang *et al.*, 2016). As the whole-genome sequence is available, high-density SNP arrays allow for the identification of genetic markers, quantitative trait loci, and significant relations between marker traits *via* GWAS (Zhu *et al.*, 2008). A GWAS study designed for a total of 39 traits was conducted on a complex mapping population. A total of ten substantial marker-trait associations (MTAs) were discovered, as well as 25 QTLs associated with 25 traits (Sandhu *et al.*, 2019). Subedi *et al.* (2019) discovered 15 MTAs that are associated with root hair, root length density, nodal root, and culm diameter. A positive association of grain yield was noticed, related to root-morphological traits, seedling establishment traits, grain yield attributing traits, and nutrient uptake traits, with phenotypic variance ranging from 8% to 84%. According to the findings of this study, several root phenotypical traits are related to grain yield under dry-DSR conditions were reported (Sandhu *et al.*, 2019). Liu *et al.* (2020) conducted a GWAS study with 208 numbers of accessions in rice to identify polymorphic markers (SNPs), that are expressively allied with mesocotyl length. Ten of the sixteen distinct loci corresponded to known quantitative trait loci (QTL) or genes, while the remaining six were potentially novel loci (Liu *et al.*, 2020).

4.6. Genome Editing: to identify the allelic variation

To meet food supply demands and support sustainable development, it is critical to reduce genetic erosion and improve the yield of modern rice cultivars. Hu *et al.* (2019) used the clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) genome editing technique to edit *Semi-Dwarf1* (*SD1*) and *Photosensitivity5* (*SE5*) in the elite landraces Kasalath and TTP (TeTePu), which contain many desirable agronomic traits such as low phosphorous tolerance (Gamuyao *et al* (Singh *et al.*, 2012). The results demonstrated that specific targeting of SD1 for gene editing in Kasalath or TTP produced in new lines with a semi-dwarf plant architecture, which is desirable in modern rice varieties, while retaining most of its progenitors' desired agronomic features (Hu *et al.*, 2019). Using gene editing on existing landraces, researchers can quickly boost genetic variety and create new kinds that meet current production needs. Plant development is negatively impacted by phosphorus deficiency. Phosphatic fertilisers could help to alleviate phosphorus deficiency, however rice varieties' low use efficiency of available phosphorus is a bottleneck that could have negative environmental repercussions. When breeding new rice varieties, it is critical to use landraces that possess genes for high phosphorus usage efficiency. Pup1 (also known as Pstol1), a key quantitative trait locus for phosphorus deficit tolerance, was discovered in Kasalath (Gamuyao *et al.*, 2012). Nipponbare does not have this gene. We conducted phenotypic analyses of Kasalath, sd1-3Kas, and sd1-5Kas in nutrient solution with low P (0.5 mg/L), CK (10 mg/L), and high P (25 mg/L) hydroponics solution over 18 days to see if the sd1 mutation in Kasalath affects phosphorus consumption efficiency. In comparison to Kasalath, the root lengths and surface area of sd1-3Kas and sd1-5Kas rose under low P, but decreased under CK and high-P concentration. These findings showed that in Kasalath mutants with low P, the sd1 mutation has no effect on PSTOL1 function (Hu *et al.*, 2019). *Semi-Dwarf1* (*SD1*) in the elite landraces Kasalath and TeTePu (TTP), which contain many desired agronomic traits such as tolerance to low phosphorous and broad-spectrum resistance to several diseases and insects, was edited using the clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated protein9 (Cas9) genome editing system. SD1 mutations result in shorter plants with improved lodging resistance (Hu *et al.*, 2019).

V. CONCLUDING REMARKS AND FUTURE OUTLOOK

Roots have been a neglected topic of research since they are difficult to examine because they are underground. Functional genomics and proteomics are providing powerful tools to help the scientific community examine root function and structure, ushering in a new age in root research. Roots information is directly relevant to agricultural/environmental issues including crop production with little environmental effect and crop production in low-input and stressed conditions. The Crop Root Research Consortium (CRRC) was formed in response to the recent spike in interest in roots. The CRRC’s purpose is to coordinate the research activities of an ever-increasing number of research groups working on root screening methodologies, molecular marker creation, root architecture modelling, genetic potential evaluation, environmental effect, and plant breeding. The CRRC platform aims to expand and facilitate information and material exchange, promote concerted development of new resources (populations/libraries), and foster collaboration through voluntary networking within thematic sub-consortia, as well as joint research proposal submission under bi-lateral or multilateral cooperation. Screening for features and finding genes/QTLs to improve the acquisition of N, P, Zn, and Mn, enhancing the uptake and efficient use of water, and minimising the entry of harmful components into the food chain are among the current root-related research efforts on rice. Knowledge of the genes that influence mineral acquisition can be used to develop genotypes of other common crops that can be used in extreme environments to improve their ability to grow on resource-poor soils, increase mineral accumulation for animal nutrition, and reduce toxic element accumulation. These results should improve population health by boosting nutritious content and minimising harmful substances in food ingested, as well as increasing the sustainability of agriculture on both a subsistence and industrial level. However, understanding and being able to manipulate components of signalling networks and transduction pathways that respond to translocated signals, both of which occur before physiological adjustment, would allow for intervention at a far earlier and more essential stage of the response. Such knowledge, as well as the genes that control signal flow, would be new and strong weapons in the arsenal of plant breeders. Recent advances in forward and reverse genetic approaches including; Next-generation mapping (NGM), MutMap, Targeting Targeting Induced Local Lesions in Genome (TILLING), Eco-TILLING, and Clustered Regularly Interspaced Short Palindromic Repeats mediated genome editing (CRISPR/Cas), have enabled successful demonstration and isolation of casual mutation sites, genes, or QTLs accompanying with the specific trait of importance. Improvement in the high-throughput root phenotypic screening method coupled with automated data analysis can resolve some major issues which are faced during manual root screening. The characterization of root traits and identification of QTL for rot related traits are not much successful with the biparental mapping populations (e.g. RILs) which show segregation in subsequent generations.

REFERENCE

1. Abe J, Morita S (1994) Growth direction of nodal roots in rice: its variation and contribution to root system formation. Plant Soil 165:333–337.
2. Agrawal L, Gupta S, Mishra SK, Pandey G, Kumar S, Chauhan PS, et al. 2016. Elucidation of complex nature of PEG induced drought-stress response in rice root using comparative proteomics approach. Front Plant Sci. 7: 1466.
3. Anis, G. B., Zhang, Y., Wang, H., Li, Z., Wu, W., Sun, L., ... & Cheng, S. (2018). Genomic regions analysis of seedling root traits and their regulation in responses to phosphorus deficiency tolerance in CSSL population of elite super hybrid rice. *International Journal of Molecular Sciences*, *19*(5), 1460.
4. Arai-Sanoh Y, Takai T, Yoshinaga S, Nakano H, Kojima M, Sakakibara H, Kondo M, Uga Y (2014) Deep rooting conferred by DEEPER ROOTING 1 enhances rice yield in paddy fields. Sci Rep 4:5563.
5. Bengough AG, McKenzie BM, Hallet PD, Valentine TA. (2011). Root elongation, water stress, and mechanical impedance: a review of limiting stresses and beneficial root tip traits. J Exp Bot, 62:59–68.
6. Bernier J., Kumar A., Venuprasad R., Spaner D., and Atlin, G.N. (2007). A large-effect QTL for grain yield under reproductive-stage drought stress in upland rice, Crop Sci., 47: 507-516 http://dx.doi.org/10.2135/cropsci2006.07.0495
7. Bertin G, Averbeck D. 2006. Cadmium: Cellular effects, modifications of biomolecules, modulation of DNA repair and genotoxic consequences. Biochimie, 88(11): 1549–1559.
8. Bian, H, Xie Y, Guo F, Han N, Ma S, Zeng Z, Wang J, Yang Y, Zhu M (2012) Distinctive expression patterns and roles of the miRNA393/TIR1 homolog module in regulating flag leaf inclination and primary and crown root growth in rice (Oryza sativa). New Phytol 196:149–161.
9. Catolos, M., Sandhu, N., Dixit, S., Shamsudin, N. A. A., Naredo, M. E. B., McNally, K. L., Henry, A., Diaz, M. G., & Kumar, A. (2017). Genetic loci governing grain yield and root development under variable rice cultivation conditions. Frontiers in Plant Science, 8, 1763. https://doi.org/10.3389/fpls.2017.01763
10. Champoux, M.C., G., Wang, S., Sarkarung, D.J., Mackill, J.C., O'Toole, N. Huang and S.R., McCouch, 1995. Locating genes associated with root morphology and drought avoidance in rice via linkage to molecular markers. Theor. Appl. Genet., 90: 969-981.
11. Chaubey, C.N., Senadhira, D., and Gregorio, G.B. (1994). Genetic analysis of tolerance for phosphorus deficiency in rice (Oryza sativa L.). Theor. Appl. Genet. 89: 313-317.
12. Cho SH, Yoo SC, Zhang H, Pandeya D, Koh HJ, Hwang JY, Kim GT, Paek NC (2013) The rice narrow leaf2 and narrow leaf3 loci encode WUSCHEL-related homeobox 3A (OsWOX3A) and function in leaf, spikelet, tiller and lateral root development. New Phytol 198:1071-1084.

13. Chuang HW, Zhang W, Gray WM (2004) Arabidopsis ETA2, an apparent ortholog of the human cullin-interacting protein CAND1, is required for auxin responses mediated by the SCFTIR1 ubiquitin ligase. Plant Cell 16:1883-1897.
14. Clemens S, Aarts M G M, Thomine S, Verbruggen N. 2013. Plant science: The key to preventing slow cadmium poisoning. Trends Plant Sci, 18(2): 92–99.
15. Coudert Y, Pe´rin C, Courtois B, Khong NG, Gantet P (2010) Genetic control of root development in rice, the model cereal. Trends Plant Sci 15:219–226. doi:10.1016/j.tplants.2010.01.008
16. Courtois B, Ahmadi N, Khowaja F, Price AH, Rami J-F, Frouin J, Hamelin C, Ruiz M. 2009. Rice root genetic architecture: meta-analysis from a drought QTL database. Rice 2, 115–128.
17. Courtois, B., L., Shen, W., Petalcorin, S., Carandang, R., Mauleon and Z., Li, 2003. Locating QTLs controlling constitutive root traits in the rice population IAC 165 × Co39. Euphytica 134: 335-345.
18. Cui, H., Levesque, M. P., Vernoux, T., Jung, J. W., Paquette, A. J., Gallagher, K. L., et al. (2007). An evolutionarily conserved mechanism delimiting SHR movement defines a single layer of endodermis in plants. Science 316, 421–425. doi: 10.1126/science.1139531 Desnos, T. (2008) Root branching responses to phosphate and nitrate. Curr. Opin. Plant Biol. 11, 82–87
19. Dobermann, A., & Fairhurst, T. (2000). Manejo del nitrógeno en arroz. *Revista Informaciones Agronómicas*, *68*(58), 1-6.
20. Dokku, P., K.M., Das and G.J.N., Rao, 2013. Pyramiding of four resis‐ tance genes of bacterial blight in Tapaswini, an elite rice cultivar, through marker‐assisted selection. Euphytica, 192(1): 87-96.
21. Fageria, N.K., Morais, O.P., Baligar, V.C., and Wright, R.J. (1988). Response of rice cultivars to phosphorus supply on an oxisol. Fert. Res. 16: 195-206.
22. Feng S, Shen Y, Sullivan JA, Rubio V, Xiong Y, Sun TP, Deng XW (2004) Arabidopsis CAND1, an unmodified CUL1-interacting protein, is involved in multiple developmental pathways controlled by ubiquitin/proteasome-mediated protein degradation. Plant Cell 16:1870–1882
23. Fu Y, Zhong X, Lu C, Liang K, Pan J, Hu X, Hu R, Li M, Ye Q, Liu Y. Growth, nutrient uptake and transcriptome profiling of rice seedlings in response to mixed provision of ammonium- and nitrate-nitrogen. J Plant Physiol. 2023 May;284:153976. doi: 10.1016/j.jplph.2023.153976. Epub 2023 Mar 25. PMID: 37028191.
24. Gamuyao R, Chin JH, Pariasca-Tanaka J, Pesaresi P, Catausan S, Dalid C, Slamet-Loedin I, Tecson-Mendoza EM, Wissuwa M, Heuer S (2012) The protein kinase Pstol1 from traditional rice confers tolerance of phosphorus deficiency. Nature 488:535–539.
25. Ge L, Chen H, Jiang JF, Zhao Y, Xu ML, Xu YY, Tan KH, Xu ZH, Chong K (2004) Overexpression of OsRAA1 causes pleiotropic phenotypes in transgenic rice plants, including altered leaf, flower, and root development and root response to gravity. Plant Physiol 135:1502–1513.
26. Gewin V (2010) An underground revolution. Nature 466:552–553.
27. Gowda VRP, Henry A, Yamauchi A, Shashidhar H, Serraj R. 2011. Root biology and genetic improvement for drought avoidance in rice. Field Crops Research 122, 1–13.
28. Gruber BD, Giehl RFH, Friedel S, von Wirén N. 2013. Plasticity of the Arabidopsis root system under nutrient deficiencies. Plant Physiology 163, 161–179.
29. Han Y, Cao H, Jiang J, Xu Y, Du J, Wang X, Yuan M, Wang Z, Xu Z, Chong K (2008) Rice ROOT ARCHITECTURE ASSOCIATED1 binds the proteasome subunit RPT4 and is degraded in a D-box and proteasome-dependent manner. Plant Physiol 148:843–855.
30. He, Y., Lian, H., and Yan, X. (2003). Localized supply of phosphorus induces root morphological and architectural changes of rice in split and stratified soil cultures. Plant Soil 248: 247-256.
31. Henry A, Gowda VRP, Torres RO, McNally KL, Serraj R: Variation in root system architecture and drought response in rice (Oryza sativa): phenotyping of the OryzaSNP panel in rainfed lowland fields. Field Crops Res 2011, 120:205–214.

32. Holz, M., Zarebanadkouki, M., Benard, P., Hoffmann, M., & Dubbert, M. (2024). Root and rhizosphere traits for enhanced water and nutrients uptake efficiency in dynamic environments. *Frontiers in Plant Science*, *15*, 1383373.
33. Hu, X., Cui, Y., Dong, G., Feng, A., Wang, D., Zhao, C., ... & Qian, Q. (2019). Using CRISPR-Cas9 to generate semi-dwarf rice lines in elite landraces. *Scientific reports*, *9*(1), 1-7.
34. IAEA (2006). . Mutational analysis of root characters in food plants. Proceedings of a final research coordination meeting. P. 1-165.
35. Ismail, A.M., Heuer, S., Thomson, M.J., and Wissuwa, M. (2007). Genetic and genomic approaches to develop rice germplasm for problem soils. Plant Mol. Biol. 65: 547-570.
36. Jalil, M. A., Juraimi, A. S., Yusop, M. R., Hakim, M. A., & Uddin, M. K. (2018). Introgression of root trait genes for drought tolerance to a Malaysia rice variety by marker-assisted backcross breeding. International Journal of Agriculture and Biology, 20(1), 119–126. doi: 10.17957/ IJAB/15.0462
37. Jia, H.F. et al. (2011) The phosphate transporter gene OsPht1;8 is involved in phosphate homeostasis in Rice. Plant Physiol. 156, 1164–1175.
38. Jonathan, M.N., I., Yoshiaki, R., Roel, Suralta and Y., Akira, 2015. QTL associated with lateral root plasticity in response to soil moisture fluctuation stress in rice. Plant and Soil. 391: 63-75.
39. Kamiya, N., Itoh, J., Morikami, A., Nagato, Y., and Matsuoka, M. (2003). The SCARECROW gene's role in asymmetric cell divisions in rice plants. Plant J. 36, 45–54. doi: 10.1046/j.1365-313X.2003.01856.x
40. Kang, Y.J., T., Lee, J., Lee, S., Shim, H., Jeong, D., Satyawan, M.Y., Kim, and S.H., Lee, 2016. Translational genomics for plant breeding with the genome sequence explosion. Plant Biotechnol. J., 14(4): 1057-1069.
41. Kawata S, Soejima M, Yamazaki K (1978) The superficial root function and yield of hulled rice (in Japanese). Jpn J Crop Sci 47:617–628.
42. Khan, M.A., M., Iqbal, M., Akram, M., Ahmad, M.W., Hassan and M., Jamil, 2013. Recent advances in molecular tool development for drought tolerance breeding in cereal crops: a review. Zemdirbyste-Agri., 100: 325-334.
43. Kharb, A., Sandhu, N., Jain, S., & Jain, R. K. (2015). Linkage mapping of quantitative trait loci for traits promoting aerobic adaptation on chromosome 8 in indica rice (Oryza sativa L.). Rice Genomics and Genetics, 6(6), 1–5. doi: 10.5376/rgg.2015.06.0006
44. Kitomi, Y., Kanno, N., Kawai, S., Mizubayashi, T., & Fukuoka, S. (2015). QTLs underlying natural variation of root growth angle among rice cultivars with the same functional allele of DEEPER ROOTING 1. Rice, 8(1): 16. https://doi.org/10.1186/s12284-015-0049-2.
45. Kitomi, Y., N., Emari, K., Sawako, K., Noriko, A., Tsuyu, F., Shuichi, I., Kenji and Y., Uga, 2018. Fine Mapping of *QUICK ROOTING 1* and *2*, Quantitative Trait Loci Increasing Root Length in Rice. Genes Genome Genet., 8: 727-735.
46. Kong, X., Yu, S., Xiong, Y., Song, X., Nevescanin-Moreno, L., Wei, X., ... & Huang, G. (2024). Root hairs facilitate rice root penetration into compacted layers. *Current Biology*, *34*(10), 2039-2048.
47. Kong, Xiangpei, Maolin Zhang , Ive De Smet, and Zhaojun Ding. Designer crops: optimal root system architecture for nutrient acquisition. Trends in Biotechnology, December 2014, Vol. 32, No. 12: 597-598.
48. Li ZC, Mu P, Li CP, Zhang HL, Li ZK, Gao YM, Wang XK. 2005. QTL mapping of root traits in a doubled haploid population from a cross between upland and lowland japonica rice in three environments. Theoretical and Applied Genetics 110, 1244–1252.
49. Li, J., Xie, Y., Dai, A., Liu, L., & Li, Z. (2009). Root and shoot traits responses to phosphorus deficiency and QTL analysis at seedling stage using introgression lines of rice. *Journal of Genetics and Genomics*, *36*(3), 173-183.
50. Li, Y., Ren, M., Wu, Y. *et al.* A root system architecture regulator modulates OsPIN2 polar localization in rice. *Nat Commun* 16, 15 (2025). https://doi.org/10.1038/s41467-024-55324-5

51. Li, Z.K. (2003). QTL × environment interactions in rice. 1. Heading date and plant height. Theor. Appl. Genet. 108: 141-153.
52. Liu, H., Z., Junhui, L., Jiaolong, L., Xiang, L., Jindong, W., Yamei, Z., Quanzhi, and Y., Guoyou, 2020. Genome-Wide Association Study (GWAS) for Mesocotyl Elongation in Rice (*Oryza sativa* L.) under Multiple Culture Conditions. Genes. 11(49): 1-16.
53. Liu, L., Cui, K., Qi, X., Wu, Y., Huang, J., & Peng, S. (2023). Varietal responses of root characteristics to low nitrogen application explain the differing nitrogen uptake and grain yield in two rice varieties. *Frontiers in Plant Science*, *14*, 1244281.
54. Lopez-Bucio J, Cruz-Ramirez A, Herrera-Estrella L. 2003. The role of nutrient availability in regulating root architecture. Current Opinion in Plant Biology 6, 280–287.
55. Ma, S., Lu, J., Ren, T., Liu, S., Cong, R., Lu, Z., ... & Li, X. (2025). Integrated soil-crop system management improves rice N uptake and yield by reducing iron plaque formation. *Field Crops Research*, *322*, 109722.
56. Mai, C. D., Phung, N. T. P., To, H. T. M., Gonin, M., Hoang, G. T., Nguyen, K. L., et al. (2014). Genes controlling root development in rice. Rice 7:30. doi: 10.1186/s12284-014-0030-5
57. Manna, M., Rengasamy, B., & Sinha, A. K. (2025). Nutrient and water availability influence rice physiology, root architecture and ionomic balance via auxin signalling. *Plant, Cell & Environment*, *48*(4), 2691-2705.
58. Meister, R., Rajani, M. S., Ruzicka, D., & Schachtman, D. P. (2014). Challenges of modifying root traits in crops for agriculture. Trends in Plant Science, 19(12), 779–788. https://doi.org/10.1016/j.tplants.2014.08.005
59. Morita S, Suga T, Yamazaki K (1988) The relationship between root length density and yield in rice plants (in Japanese). Jpn J Crop Sci 57:438–443.
60. Navea, I.P., M.S., Dwiyanti, J., Park, B., Kim, S., Lee, Huang, X., H.J., Koh and J.H., Chin, 2017. Identification of quantitative trait loci for panicle length and yield related traits under different water and P application conditions in tropical region in rice (*Oryza sativa* L.). Euphytica. 213: 37.
61. Norton, G.J. and A.H., Price, 2009. Mapping of quantitative trait loci for seminal root morphology and gravitropic response in rice. Euphytica. 166: 229-237.
62. Novoplansky, A. (2002). Developmental plasticity in plants: implications of non-cognitive behavior. *Evolutionary Ecology*, *16*(3), 177-188.
63. Oladosu, Y.; Rafii, M.Y.; Samuel, C.; Fatai, A.; Magaji, U.; Kareem, I.; Kamarudin, Z.S.; Muhammad, I.; Kolapo, K. Drought Resistance in Rice from Conventional to Molecular Breeding: A Review. Int. J. Mol. Sci. 2019, 20, 3519.
64. Panda, S.; Majhi, P.K.; Anandan, A.; Mahender, A.; Veludandi, S.; Bastia, D.; Guttala, S.B.; Singh, S.K.; Saha, S.; Ali, J. Proofing Direct-Seeded Rice with Better Root Plasticity and Architecture. Int. J. Mol. Sci. 2021, 22, 6058. https://doi.org/ 10.3390/ijms22116058
65. Peng S, Bouman BAM, Visperas RM, Castaneda A, Nie L, Park HK: Comparison between aerobic and flooded rice in the tropics: agronomic performance in an eight-season experiment. Field Crops Res (2006), 96:252–259.
66. Phule, A. S., Barbadikar, K. M., Maganti, S. M., Seguttuvel, P., Subrahmanyam, D., Prasad Babu, M. B. B., & Kumar, P. A. (2019). RNA-seq reveals the involvement of key genes for aerobic adaptation in rice. Scientific Reports, 9(1), 5235. https://doi.org/10.1038/s41598-019-41703-2
67. Poot, P. and H., Lambers, 2008. Shallow-soil endemics: adaptive advantages and constraints of a specialized root-system morphology. New Phytol. 178: 371-381.
68. Postma, J.A. et al. (2014) The optimal lateral root branching density for maize depends on nitrogen and phosphorus availability. Plant Physiol. 166, 590–602.
69. Price AH, Tomos AD (1997) Genetic dissection of root growth in rice. II Mapping quantitative trait loci using molecular markers. Theor Appl Genet 95:143–152.

70. Price AH, Townend J, Jones MP, Audebert A, Courtois B. 2002. Mapping QTLs associated with drought avoidance in upland rice grown in the Philippines and West Africa. Plant Mol. Biol. 48: 683-695.
71. Puiga, J., Germain, P., Emmanuel Guiderdonib and Pascal Ganteta. 2012. Regulation of Shoot and Root Development through Mutual Signaling. Molecular Plant 5 (5): 974–983.
72. Qun S, Wang JH, Sun BQ. 2007. Advances on seed vigor physiological and genetic mechanisms. Agric. Sci. China 6: 1060-1066.
73. Rabello AR, Guimaraes CM, Rangel PHN, Silva FR, Seixas D, Souza E, Brasileiro ACM, Spehar CR, Ferreira ME, Mehta M: Identification of drought responsive genes in roots of upland rice (Oryza sativa L). BMC Genomics 2008, 9:485–491.
74. Rasheed, A., U.H., Muhammad, A., Muhammad, B., Maria, F., Sheng, W., Ziming, L., Huijie, 2020. A critical review on the improvement of drought stress tolerance in rice (*Oryza sativa* L.). Notulae Botanicae Horti Agrobotanici Cluj-Napoca. 48(4): 1756-1788.
75. Rebolledo MC, Luquet D, Courtois B, Henry A, Soulié JC, Rouan L, et al. 2013. Can early vigour occur in combination with drought tolerance and efficient water use in rice genotypes? Funct. Plant Biol. 40: 582-594.
76. Rebouillat J, Dievart A, Verdeil JL, Escoute J, Giese G, Breitler JC, Gantet P, Espeout S, Guiderdoni E, Pe´rin C (2009) Molecular genetics of rice root development. Rice 2:15–34.
77. Sandhu N, Singh A, Dixit S, Cruz MTS, Maturan PC, Jain RK, et al. 2014. Identification and mapping of stable QTL with main and epistasis effect on rice grain yield under upland drought stress. BMC Genet. 15: 63.
78. Sandhu N., Jain S., Kumar A., Mehla B.S., and Jain R., 2013, Genetic variation, linkage mapping of QTL and correlation studies for yield, root, and agronomic traits for aerobic adaptation, BMC Genet., 14: 104-119 http://dx.doi.org/10.1186/1471-2156-14-104
79. Sandhu, N., R.S., Sushil, V.K., Singh, P., Sinha, K., Santosh, S.P., Singh, G., Surya Kant, P., Madhav, Y., Ram Baran, K.V., Rajeev and K., Arvind, 2019. Deciphering the genetic basis of root morphology, nutrient uptake, yield, and yield-related traits in rice under dry direct-seeded cultivation systems. Scientific Reports. 9(1): 1-16.
80. Seo, H. M., Jung, Y., Song, S., Kim, Y., Kwon, T., Kim, D. H., ... & Nam, J. (2008). Increased expression of OsPT1, a high-affinity phosphate transporter, enhances phosphate acquisition in rice. *Biotechnology Letters*, *30*(10), 1833-1838.
81. Serraj R, McNally KL, Slamet-Loedin I, Kohli A, Haefele SM, Atlin G, Kumar A: Drought resistance improvement in rice: an integrated genetic and resource management strategy. Plant Prod Sci 2011, 14:1–14.
82. Shimizu, A., Kato, K., Komatsu, A., Motomura, K., and Ikehashi, H. (2008). Genetic analysis of root elongation induced by phosphorus deficiency in rice (Oryza sativa L.): Fine QTL mapping and multivariate analysis of related traits. Theor. Appl. Genet. 117: 987-996.
83. Shimizu, A., Yanagihara, S., Kawasaki, S., and Ikehashi, H. (2004). Phosphorus deficiency-induced root elongation and its QTL in rice (Oryza sativa L.). Theor. Appl. Genet. 109: 1361-1368.
84. Shin, J.H., D.H., Jeong, M.C., Park and G., An, 2005. Characterization and transcriptional expression of the α-expansin gene family in rice. Mol. Cells., 20: 210-218.
85. Shin, N. H., Han, J. H., Jang, S., Song, K., Koh, H. J., Lee, J. H., ... & Chin, J. H. (2020). Early vigor of a pyramiding line containing two quantitative trait loci, phosphorus uptake 1 (Pup1) and anaerobic germination 1 (ag1) in rice (O. sativa L.). *Agriculture*, *10*(10), 453.
86. Shukla, A. K., Singh, R. R., Mishra, T., Tripathi, K. M., Mishra, S., & Kumar, D. (2024). Optimizing nutrient uptake in rice crops through integrated organic manure application: A comprehensive analysis of grain and straw composition. *Asian J. Soil Sci. Plant Nutr*, *10*(1), 167-174.
87. Singh AK, Chinnusamy V. 2008. Enhancing rice productivity in water stressed environments: perspectives for genetic improvement and management. p. 233-257. In: R. Serraj, J. Bennett, B.

Hardy (eds.). Drought frontiers in rice: crop improvement for increased rainfed production. International Rice Research Institute, Manila, Philippines.

88. Singh, A. et al. Molecular breeding for the development of multiple disease resistance in Basmati rice. AoB PLANTS 2012, pls029 (2012).
89. Steele, K. A., Price, A. H., Witcombe, J. R., Shrestha, R., Singh, B. N., Gibbons, J. M., & Virk, D. S. (2013). QTLs associated with root traits increase yield in upland rice when transferred through marker-assisted selection. *Theoretical and applied genetics*, *126*(1), 101-108.
90. Subedi, S.R., S., Nitika, K.S., Vikas, S., Pallavi, K., Santosh, S.P., Singh, G., Surya Kant, P., Madhav, Y., Ram Baran, K.V., Rajeev and K., Arvind, 2019. Genome-wide association study reveals significant genomic regions for improving yield, adaptability of rice under dry direct seeded cultivation condition. BMC Genomics, 20: 471
91. Tang L, Mao B G, Li Y K, Lv Q M, Zhang L P, Chen C Y, He H J, Wang W P, Zeng X F, Shao Y, Pan Y L, Hu Y Y, Peng Y, Fu X Q, Li H Q, Xia S T, Zhao B R. 2017. Knockout of OsNramp5 using the CRISPR/Cas9 system produces low Cd-accumulating indica rice without compromising yield. Sci Rep, 7: 14438.
92. Uga Y, Hanzawa E, Nagai S, Sasaki K, Yano M, Sato T (2012) Identification of qSOR1, a major rice QTL involved in soil-surface rooting in paddy fields. Theor Appl Genet 124:75–86.
93. Uga Y, Kitomi Y, Ishikawa S, Yano M (2015a) Genetic improvement for root growth angle to enhance crop production. Breed Sci 65:111–119.
94. Uga Y, Okuno K, Yano M (2011) Dro1, a major QTL involved in deep rooting of rice under upland field conditions. J Exp Bot 62:2485–2494. doi:10.1093/jxb/erq429
95. Uga Y, Sugimoto K, Ogawa S, Rane J, Ishitani M, Hara N, Kitomi Y, Inukai Y, Ono K, Kanno N, Inoue H, Takehisa H, Motoyama R, Nagamura Y, Wu J, Matsumoto T, Takai T, Okuno K, Yano M (2013a) Control of root system architecture by DEEPER ROOTING 1 increases rice yield under drought conditions. Nat Genet 45:1097–1102.
96. Uga Y, Yamamoto E, Kanno N, Kawai S, Mizubayashi T, Fukuoka S (2013b) A major QTL controlling deep rooting on rice chromosome 4. Sci Rep 3:3040.
97. Uga, Y. (2021). Challenges to design-oriented breeding of root system architecture adapted to climate change. *Breeding science*, *71*(1): 3-12.
98. Uga, Y., Kitomi, Y., Yamamoto, E., Kanno, N., Kawai, S., Mizubayashi, T., & Fukuoka, S. (2015b). A QTL for root growth angle on rice chromosome 7 is involved in the genetic pathway of DEEPER ROOTING 1. Rice, 8(1): 8. https://doi.org/ 10.1186/s12284-015-0044-7
99. Uga, Y., Okuno, K. and Yano, M. (2010). Fine mapping of Sta1, a quantitative trait locus determining stele transversal area, on rice chromosome 9. Mol. Breed., 26: 533-538.
100. Varshney, R.K., R., Terauchi and S.R., McCouch, 2014. Harvesting the promising fruits of genomics: applying genome sequencing technologies to crop breeding. PLoS Biol., 12(6): p.e1001883.
101. Venuprasad, R., Dalid, C. O., Del Valle, M., Bool, M. E., Zhao, D., Espiritu, M., Sta Cruz, M. T., Amante, M., Kumar, A., & Atlin, G. N. (2009). Identification and characterization of large-effect quantitative trait loci (QTL) for grain yield under lowland drought stress in rice using bulk-segregant analysis (BSA). Theoretical and Applied Genetics, 120(1), 177–190. https://doi.org/10.1007/s00122-009-1168-1
102. Wang XF, He FF, Ma XX, Mao CZ, Hodgman C, Lu CG, Wu P (2011) OsCAND1 is required for crown root emergence in rice. Mol Plant 4:289–299.
103. Wang, S., Y., Xu, Z., Li, S., Zhang, J.M., Lim, K.O., Lee, C., Li, Q., Qian, A., de Jiang, and Y., Qi, 2014. *OsMOGS* is required for N-glycan formation and auxin-mediated root development in rice (*Oryza sativa* L.). Plant J., 78: 632-645.
104. White, P. J., Bengough, A. G., Bingham, I. J., George, T. S., Karley, A. J., & Valentine, T. A. (2009). Induced mutations affecting root architecture and mineral acquisition in barley. Induced plant

mutations in the genomics era. Food and Agriculture Organization of the United Nations, Rome, 338-340.

105. Wissuwa, M., and Ae, N. (2001). Further characterization of two QTLs that increase phosphorus uptake of rice (Oryza sativa L.) under phosphorus deficiency. Plant Soil 237: 275-286.
106. Wissuwa, M., Wegner, J., Ae, N., & Yano, M. (2002). Substitution mapping of Pup1: a major QTL increasing phosphorus uptake of rice from a phosphorus-deficient soil. *Theoretical and Applied Genetics*, *105*(6), 890-897.
107. Wissuwa, M., Yano, M., and Ae, N. (1998). Mapping of QTLs for phosphorus-deficiency tolerance in rice (Oryza sativa L.). Theor. Appl. Genet. 97: 777-783. Dobermann, A., and Fairhurst, T. (2000). Phosphorus deficiency. In Rice: Nutrient Disorders and Nutrient Management. (Manila, The Philippines: International Rice Research Institute), pp. 60-71.
108. Wu, P., and Ni, J.J. (2000). Detection of the quantitative trait loci with AFLP and RFLP markers for phosphorus uptake and use efficiency in rice. J. Integr. Plant Biol. 42: 229-233.
109. Wu, W. and Cheng, S (2014) Root genetic research, an opportunity and challenge to rice improvement. Field Crops Res 165:111–124.
110. Wu, W. and S., Cheng, 2014. Root genetic research, an opportunity and challenge to rice improvement. Field Crops Res., 165: 111-124.
111. Yang P, Chen CL, Zou GX, Peng ZQ, Wu YS, Huang YP, et al. 2015. Research progress in relevant theories of increasing breeding level of direct-seeding rice. Acta Agriculturae Jiangxi 27: 33-35.
112. Yang, J., S, Kai, L., Dongxiu, L., Lixin, L, Yongzhu, H., Ming, Y., Guili, L., Hong, W., Hui, C., Zhiqiang and G., Tao, 2019. Identification of stable QTLs and candidate genes involved in anaerobic germination tolerance in rice via high-density genetic mapping and RNA-Seq. BMC Genomics., 20(355): 1-15.
113. Zhang ZH, Qu XS, Wan S, Chen LH, Zhu YG. 2004. Comparison of QTL controlling seedling vigour under different temperature conditions using recombinant inbred lines in rice (Oryza sativa). Annal. Bot. 95: 423-429.
114. Zhang, J., Zheng, H. G., Aarti, A., Pantuwan, G., Nguyen, T. T., Tripathy, J. N., Sarial, A. K., Robin, S., Babu, R. C., Nguyen, B. D., Sarkarung, S., Blum, A., & Nguyen, H. T. (2001). Locating genomic regions associated with components of drought resistance in rice: Comparative mapping within and across species. Theoretical and Applied Genetics, 103(1), 19–29. https://doi.org/10.1007/s001220000534
115. Zhao Y, Cheng S, Song Y, Huang Y, Zhou S, Liu X, Zhou DX (2015) The interaction between rice ERF3 and WOX11 promotes crown root development by regulating gene expression involved in cytokinin signaling. Plant Cell 27:2469–2483.
116. Zhu, L.H., D.B., Zhong, J.L., Xu, S.B., Yu and Z.K., Li, 2008. Differential expression of lodging resistance related QTLs in rice (*Oryza sativa* L.). Plant Sci., 175: 898-905.

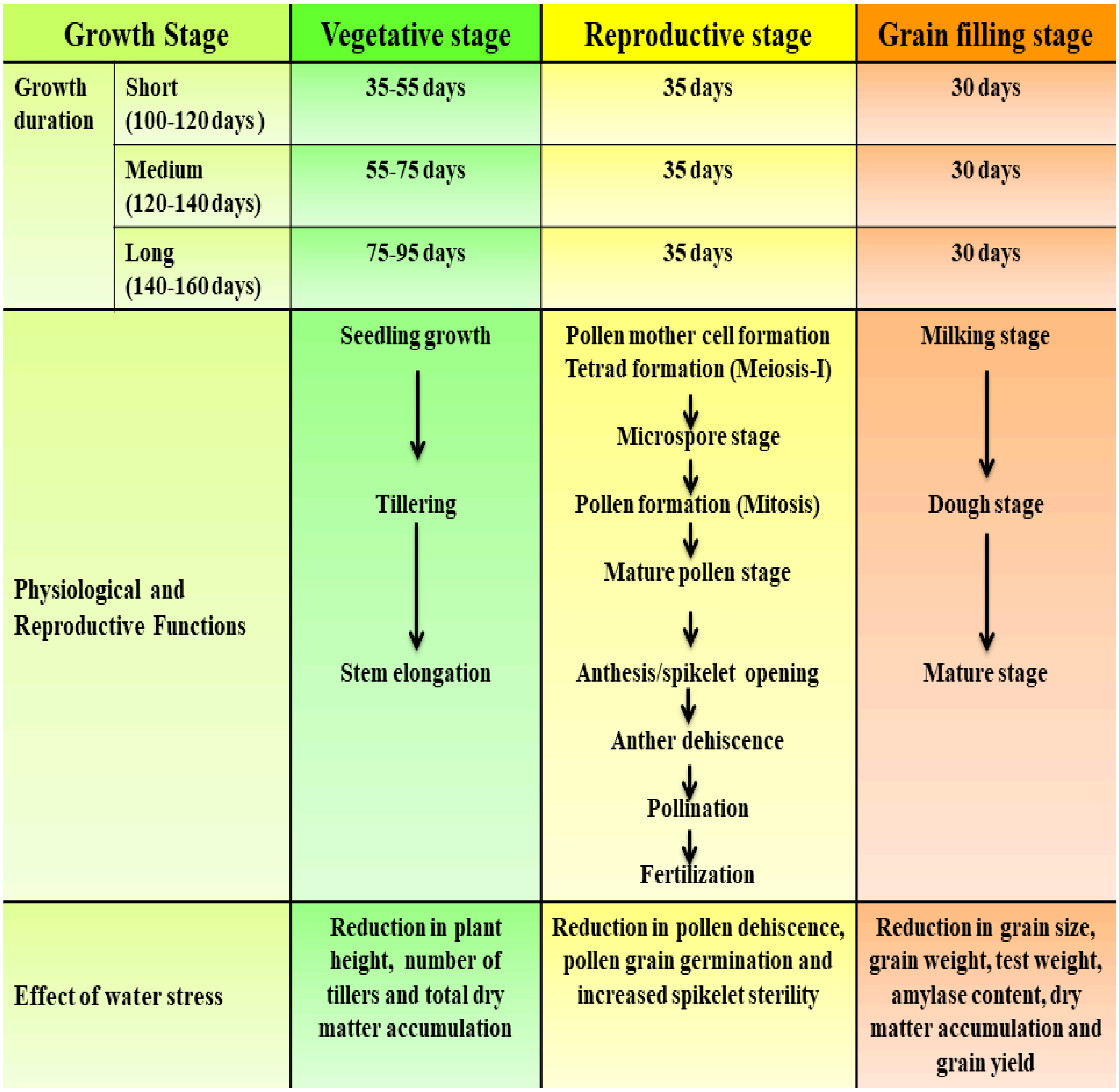
Table-1: Genes/QTLs controlling root traits development in Rice

Sl. No.	Root Traits	Genes/ QTLs	Position on Chromosome	Reference
1.	Root Length	*QRO1*	1	Kitomi *et al.* (2018)
		QRO2	2	
		OsEXPA8	8	Shin *et al.* (2005)
		$qRL_{8.1}$	8	Qu *et al.* (2008)
		$qRL_{8.2}$	8	Qu *et al.* (2008) Sandhu *et al.* (2013)
		$qRL_{9.1}$	9	Qu *et al.* (2008)
2.	Root number	*qTLRN-12*	12	Jonathan *et al.* (2015)
		qLLRN-12	12	

		qRN5	5	Anis *et al.* (2018)
3.	Root growth angles	*DRO1*	9	Uga *et al.* (2013a)
		DRO2	4	Uga *et al.* (2013b); Uga *et al.* (2015); Kitomi *et al.* (2015)
		DRO3	7	
		DRO4	2	
		DRO5	5	
4.	Root hair density	*qRHD*$_{1.1}$	1	Sandhu *et al.* (2015)
		qRHD$_{5.1}$	5	
5.	Root hair length	*qRHL*$_{1.1}$	1	Sandhu *et al.* (2015)
6.	Root volume	*qRV*$_{2.1}$	2	Bernier *et al.* (2007)
7.	Root lodging resistance	*SCM3*		Ma and Yamaji, (2006)
8.	Root stele	*STA1*	10	Uga *et al.* (2010)

Table-2: QTLs linked with improved Nutrient and Water Acquisition

Sl. No.	Nutrient and Water Acquisition	Genes/QTLs	Position on Chromosome	Reference
1.	Nitrogen uptake	*DRO1*	9	Uga *et al.* (2011); Uga *et al.* (2013a); Arai-Sanoh *et al.* (2014)
		NRT$_{1.1}$	1	Puiga *et al.* (2012)
2.	Phosphorous uptake	*qRN5*	5	Anis *et al.* (2018)
		qRDW5	5	
		qRRS8	5	Li *et al.* (2009)
		PSTOL1	12	Gamuyao *et al.* (2012) Shin *et al.* (2020)
		Pup1	12	Shin *et al.* (2020) Wissuwa *et al.* (2002)
3.	Heavy metal tolerance	*NRAMP5,* *OsLCD1*	7	Tang *et al.* (2017)
		Dro1-NIL	-	Uga *et al.* (2015a)
4.	Water uptake	*qRFW9*	11	Price *et al.* (2002)
		DRO1	9	Uga *et al.* (2013a)



Growth Stage		Vegetative stage	Reproductive stage	Grain filling stage
Growth duration	Short (100-120 days)	35-55 days	35 days	30 days
	Medium (120-140 days)	55-75 days	35 days	30 days
	Long (140-160 days)	75-95 days	35 days	30 days
Physiological and Reproductive Functions		Seedling growth ↓ Tillering ↓ Stem elongation	Pollen mother cell formation Tetrad formation (Meiosis-I) ↓ Microspore stage ↓ Pollen formation (Mitosis) ↓ Mature pollen stage ↓ Anthesis/spikelet opening ↓ Anther dehiscence ↓ Pollination ↓ Fertilization	Milking stage ↓ Dough stage ↓ Mature stage
Effect of water stress		Reduction in plant height, number of tillers and total dry matter accumulation	Reduction in pollen dehiscence, pollen grain germination and increased spikelet sterility	Reduction in grain size, grain weight, test weight, amylase content, dry matter accumulation and grain yield

Figure-1: An illustration for effect of water stress on different growth stages of rice.

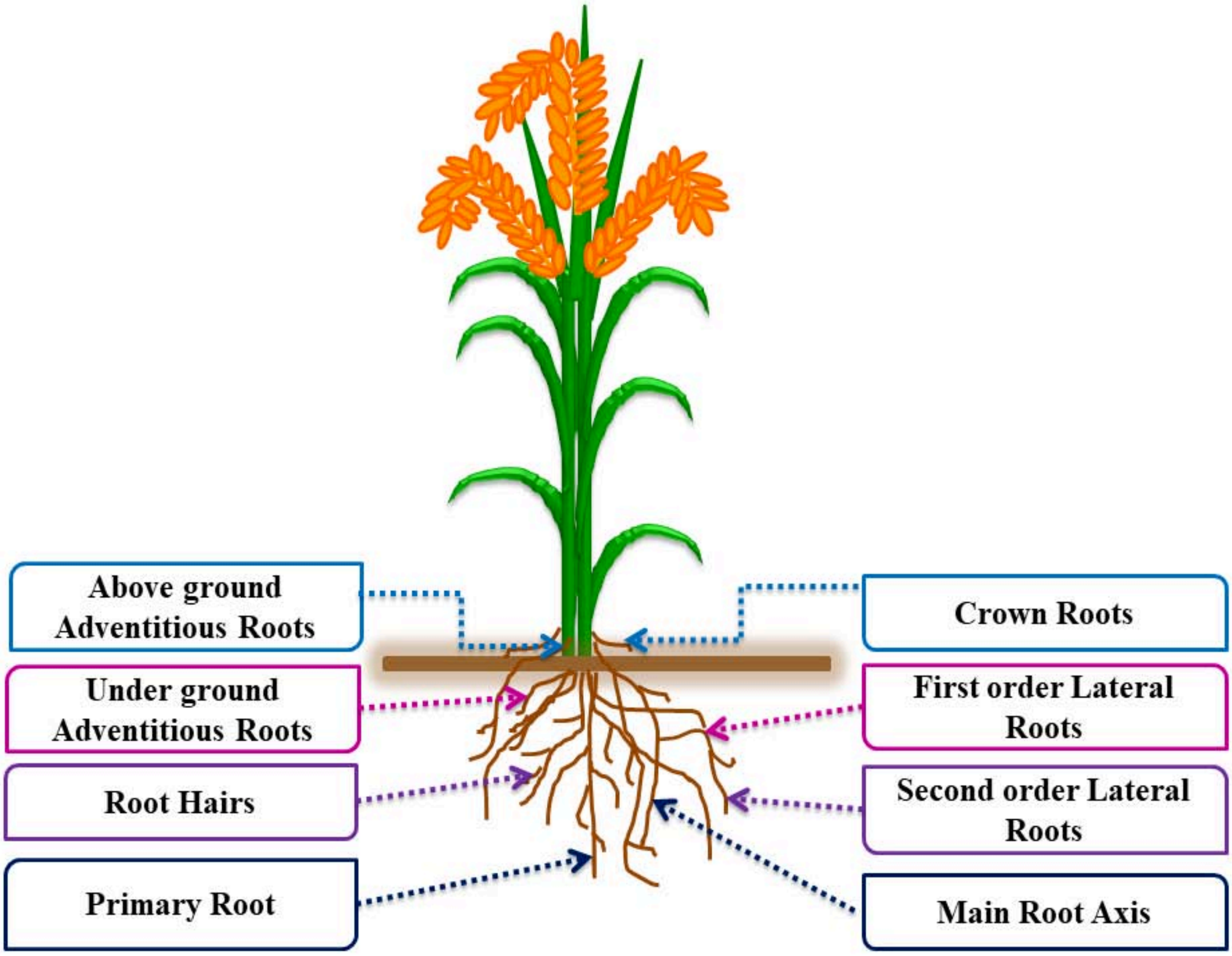


Figure-2: Structural Organization of the Rice Root System Showing Key Root Types and Their Hierarchies

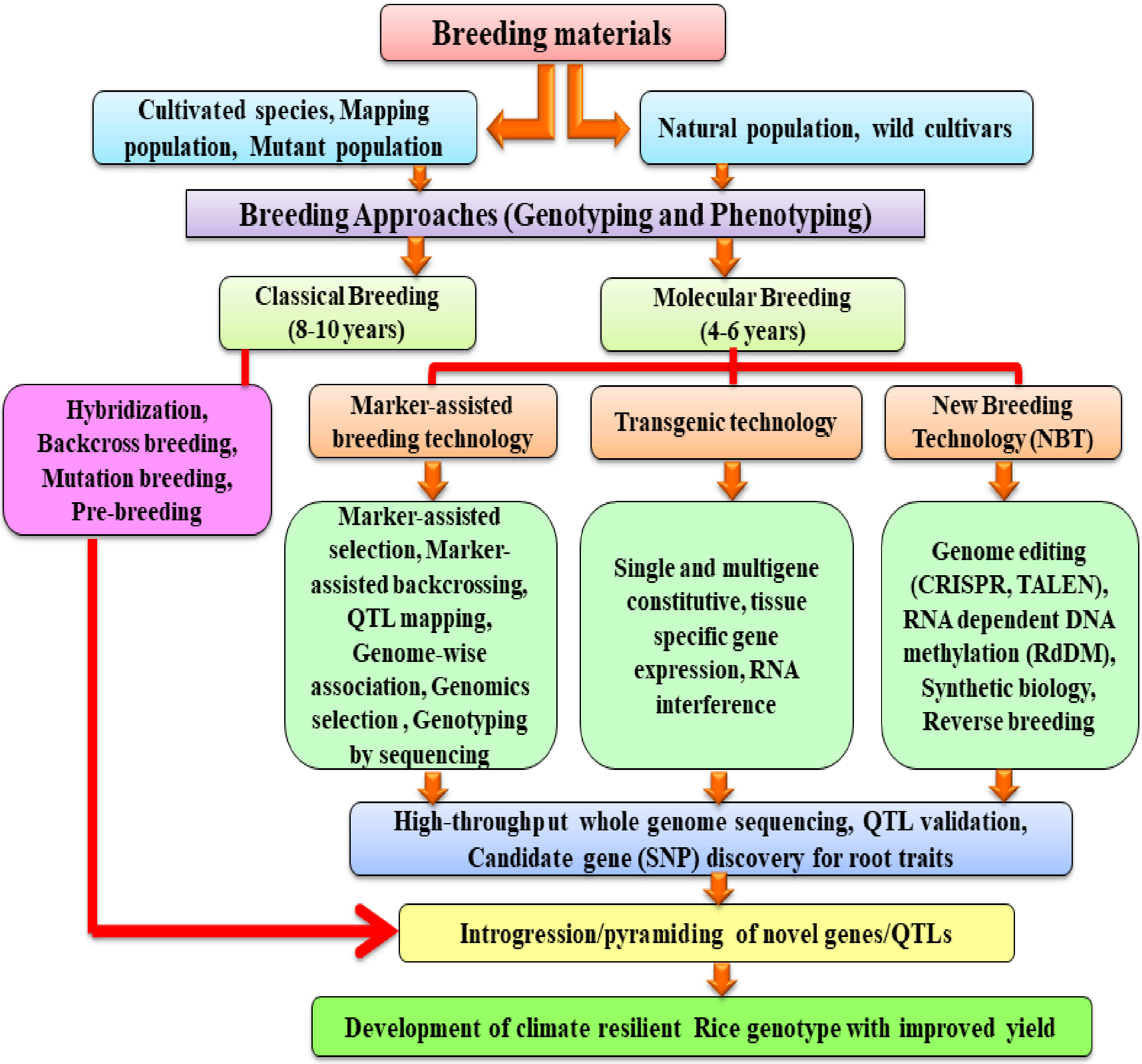


Figure-3: Integrated Breeding Strategies for Developing Climate-Resilient Rice Genotypes with Improved Yield and Root Traits

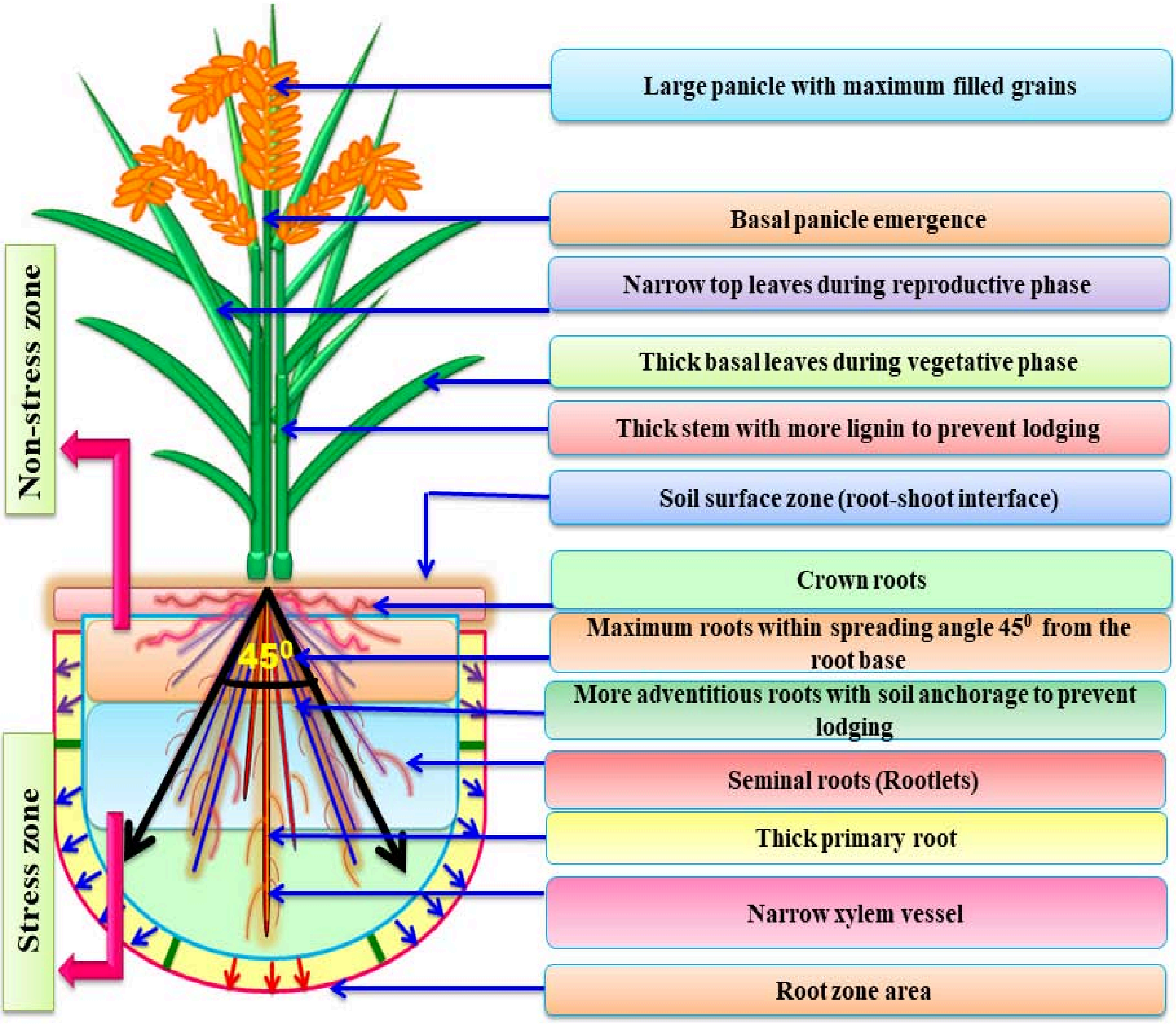


Figure-4: A hypothetical root ideotype for rice with improved dimorphic vigorous root system to optimize soil anchorage, water absorption and nutrient acquisition.

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