Controlling The Root System Architecture In Rice: Impact of Genes, Phytohormones And Root Microbiota

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Abstract

Background

In order to feed expanding population, new crop varieties were generated which significantly contribute to world food security. However, the growth of these improved plants varieties relied primarily on synthetic fertilizers, which negatively affect the environment as well as human health. Plants adapt to adverse environmental changes by adopting root systems through architectural changes at the root-type and tissue-specific changes and nutrient uptake efficiency.

Scope

Plants adapt and operate distinct pathways at various stages of development in order to optimally establish their root systems, such as change in the expression profile of genes, changes in phytohormone level and microbiome induced Root System Architecture (RSA) modification. Many scientific studies have been carried out to understand plant response to microbial colonization and how microbes involved in RSA improvement through phytohormone level and transcriptomic changes.

Conclusion

In this review, we spotlight the impact of genes, phytohormones and root microbiota on RSA and provide specific, critical new insights that have been resulted from recent studies on rice root as a model. First, we discuss new insights into the genetic regulation of RSA. Next, hormonal regulation of root architecture and the impact of phytohormones in crown root and root branching is discussed. Finally, we discussed the impact of root microbiota in RSA modification and summarized the current knowledge about the biochemical and central molecular mechanisms involved.

Introduction

The world's population is projected to reach up to 9 billion by the middle of the twenty-first century (DESA, 2019). Rice is a widely eaten cereal grain that feeds nearly half of the world's population (GRiSP, 2013). The crop yield should increase up to 40% by 2025 on existing agricultural soils under favourable and unfavourable soil and environmental conditions to feed the expanding world's population. Roots are the plant's primary organ responsible for resource uptake, anchorage and formation of the rhizosphere zone (Chen et al., 2019). In order to increase crop productivity, root system improvement may play a significant role. Different Root System Architecture (RSA) ideotypes are identified after extensive studies; these ideotypes are tailored to different soil mineral nutrient balance and water status (Duque and Villordon, 2019).

Cultivated rice varieties considerably differ in their RSA. Rice has a relatively complex root system, consisting of the embryonic primary root and seminal roots with post-embryo adventitious roots (Kitomi et al., 2018). Primary and seminal roots have vital functions throughout the seedling stage, while

adventitious roots form the mature plant's functional root system (Steffens and Rasmussen, 2016). Several wild rice varieties have evolved root systems that can adapt to various environmental stresses. For example, the plants develop a deeper root system during water deficit conditions for obtaining water from the subsoil portion to prevent drought stress (Lynch and Wojciechowski, 2015). In addition to water uptake, a deep root system would be favourable for the rapid acquisition of nitrogen from the subsoil because dissolved nitrogen moves downward owing to gravity (Plett et al., 2020). In general, thicker, branched, and deeper roots with a high root relationship to shooting magnitude increase rice resistance to drought (Klein et al., 2020).

Root development is an intricate process in plants comprised of constitutive, adaptive, and regulatory mechanisms and correlations with the upper plant parts, including shoot, leaf, flowers and seed etc. Earlier research has shown that several factors can alter the root system through a complex network that may involve genetic and environmental factors. Several microbes also affect root development and RSA by altering hormonal, genetic and regulatory mechanisms (Valette et al., 2020). Thus, it is also crucial to discover hormonal and genetic determinants governing root development. In the current review, we focus on the genetic, hormonal and microbial effect on root development and modification of RSA in rice and its correlation with sustainable development.

Rice Root System

Rice roots have a thick fibrous root system, produced by postembryonic adventitious roots (nodal roots or crown roots) that emerge from the stem (Wang et al., 2020). The root apical meristem (RAM) differentiates at the time of embryogenesis to initiate the radical, the first root to emerge during germination, which further proceeds by generating embryonic crown roots (CRs) that took shape from the coleoptiles' node. The consecutive postembryonic nodal roots or crown roots are differentiated from the nodal region of stem and tillers. The bifurcation of the radical and crown roots may result in broad lateral roots and small lateral roots. Large lateral roots show positive geotropism and indeterminate growth. On the other hand, small lateral roots are short in length, ageotropic and show determinate growth. Moreover, large lateral roots occur infrequently and may carry expandable large or small lateral roots until around the fifth branching order. Simultaneously, small lateral roots are more in number and never develop higher orders of branching.

Crown roots differentiate from the stem and radial ground meristem, having similar characteristic features to root pericycle (Mai et al., 2014). Pericycle and endodermal cells of root proliferate to differentiate lateral roots by an auxin-regulated mechanism (Jing and Strader, 2019). From the centre to the periphery, rice root radial structure encompasses the stele (phloem and xylem vessels), pericycle, endoderm, cortex, aerenchyma, sclerenchyma, exodermis, and epidermis (Figure 1). This radial structure reflects rice root's capacity to grow in aerobic and anaerobic (flooding) environment (Maurel and Nacry, 2020). Notably, the aerenchyma helps in gas exchange with shoot in anaerobic condition (Pedersen et al., 2020).

RSA modulation in rice

Plants require specific micro and macronutrients for their determinate developmental program. Plants acquire these essential nutrients from the soil surrounded by active roots, i.e., the rhizosphere (Zhang et al., 2020). Thus, the low surface area of active roots accounts for insufficient uptake of nutrients, which is more severe under low nutrient availability in the rhizosphere, negatively affecting overall plant development and crop yield. Thus, the root system modification plays a significant role in improving plant growth by enhanced soil resources utilisation and is considered more productive under adverse conditions, i.e. low nutrient availability in soil. The RSA primarily defines soil exploration by plant roots in order to facilitate enhanced nutrient uptake. Therefore, modifying RSA is an important strategy to enhance the acquisition of nutrients, especially under nutrient-deficient conditions (Li et al., 2016).

Since the domestication of rice (10,000 years ago), many rice varieties have grown in different ecosystems, including upland, rainfed lowland, flood-prone, and mangrove as different production systems ranging from conventional low-input to intensive high-input systems. The International Rice Research Institute (IRRI) Gene bank in the Philippines contains over 100,000 rice genotypes (Wing et al., 2018). The phenomics studies of root response suggested that some genotypes exhibited RSA variation, which gives a great idea and proof of concept for stress tolerance and root architecture modulation (Anupama et al., 2019). Many new genotypes with variability in RSA establish a significant connection for identifying new genes involved in modifying RSA and root development. The phenomic studies concentrate on some common genotypes that showed an extraordinary thought about RSA modification. The excess neglected broad changeability builds up a critical chance for the recognizable proof of new qualities associated with root improvement.

The RSA is a 3-dimensional spatial configuration of the root system in the supporting medium and decides the distribution of different root types in the root system across the soil profile (Ogura et al., 2019). The RSA referred to the root system's surface topography described in the medium, particularly the root axis's geometry precision. The RSA consists of a whole set of descriptors of the root systems, different from root anatomy, morphology, topology and redistribution of secondary roots. A primary RSA can be determined by numbers, patterns, lengths, orientation, angle and diameter of primary and secondary branches just like any other phenotypic signifier. These components may be evolutionally governed by complex and interactive genetic pathways that may also regulate growth and development to address environmental challenges. The "intrinsic pathway" or extrinsic "environmental response pathways" are significantly linked to the relationship between genetic and environmental factors (Malamy and Ryan, 2001) (Table 1).

Genetic regulation of RSA

Several studies have carried to date to understand the molecular mechanism behind root development and RSA modulation. A number of genes involved in manipulating plant root architecture to address nutrient and water imbalance have been reported. The root growth angle (RGA) is an essential component of RSA and used as a plant breeding parameter to determine variety. By influencing polar auxin transport

at root tip, *OSPIN2* plays a vital role in root gravitropic reactions and deciding RSA in rice (Wang et al., 2018). *OsARF12* is an auxin response factor regulating auxin synthesis and polar auxin transport through *OsYUCCAs*, *OsPINs*, and *OsPGPs*, resulting in shortened primary root length in rice plants (Qi et al., 2012). One more gene, *DEEPER ROOTING 1 (DRO1)*, an essential gene discovered by Uga and colleagues, changed RSA by controlling the RGA. *DRO1* triggers unidirectional root growth and lower root bending in response to gravity by causing cell elongation at root tip, and it is negatively regulated by auxin (Uga et al., 2013). Another significant gene *qSOR1* (quantitative trait locus for *SOIL SURFACE ROOTING 1*), a *DRO1* homolog showed shallower RGA, *qSOR1* is also negatively regulated by auxin, primarily expressed in root columella cells, and engaged in root gravitropic reactions (Singh et al., 2020). A root-specific α -expansin gene, *OsEXPA8*, improved RSA by lengthening primary roots, boosting lateral roots and root hair counts, and improving rice root development (Ma et al., 2013). Another expansin gene, *OsEXPB2*, can modify RSA and shoot length (Zou et al., 2015). A leucine-rich receptor-like kinase, *OsRPK1*, negatively controls rice roots development by controlling polar auxin transport (Zou et al., 2014). The *SOR1 (SOIL SURFACE ROOTING 1)* modified RSA by altering the gravitropic root response (Hanzawa et al., 2013). *OsARF16* also regulates RSA by regulating auxin transport and Fe homeostasis (Shen et al., 2015). *OsSIZ1* is concerned with RSA manipulation as mutant of *ossiz1* had short primary roots and adventitious roots than wild plants (Wang et al., 2015). A transcription factor *OsWOX4* played a pivotal role in primary root elongation by regulating auxin transport, indicating its importance in RSA modification of rice root system (Chen et al., 2020). The expression *OsMYB2P-1* also correlated with RSA regulation (Dai et al., 2012).

Further, RSA was substantially modified due to the overexpression of *OsMYB4P* gene in rice (Yang et al., 2014). *OsWRKYP74* conferred RSA modification as the transgenic plants provide better tolerance to low Pi stress through activating genes triggered by Pi starvation and modulating RSA (Dai et al., 2016). A small GTPase, *OsRab6a*, plays a critical role in manipulating Fe^{+2} absorption in rice plants by regulating physiological functions associated with the acquisition of Fe and RSA in response to Fe-deficiency (Yang and Zhang, 2016). Furthermore, in *RCc3* overexpression lines, local auxin biosynthesis and polar auxin transport increased auxin accumulation in root. *RCc3* generates pleiotropic phenotypes of reinforced RSA, such as expanded growth of primary roots, adventitious and lateral roots at the seedling stage (Wang et al., 2018). Another root growth controlling gene *OsWRKY28* influenced root growth at the seedling stage and fertility at the reproductive stage, likely by affecting jasmonic acid (JA) or other phytohormone homeostasis (Wang et al., 2018). The study showed that exogenous JA treatments mimicked *oswrky28* mutant phenotypes with inhibited root elongation. Further studies related to root growth suggested that *OsACS1* and *OsACS2* are concerned with regulating RSA modification, transcriptional regulation of genes induced by Pi starvation, and cellular phosphorus homeostasis. The study has shown that *OsACS* mutants, in particular, do not encourage lateral root growth in Pi-deficient condition, displaying the motivating involvement of ethylene in lateral root production under Pi-deficiency (Lee et al., 2019). An additional study by Singh et al., 2020 suggested that *OsJAZ9* modulates RSA in response to K deficiency, as *OsJAZ9* over expressed plants showed shorter seminal roots with longer lateral roots (Singh et al., 2020).

Lateral roots (LRs) play an essential role in RSA, allowing plants to search for water and nutrients from soil efficiently. However, in monocotyledonous plants, the mechanisms that regulate the evolution of LRs are poorly understood. According to Lee and colleagues, rice gene wavy root elongation growth 1 (*WEG1*) is involved in the formation of more extended and thick LRs (L-type LRs) via asymmetric cell growth in the elongation region (Lee et al., 2019). Apart from identifying and characterising RSA-related genes, several QTLs were also identified in diversified rice populations that affect the root system and grain yield. The complete knowledge may directly enhance rice irrigation and fertilizer efficiency in the molecular breeding of RSA (Zhou et al., 2016). Characterization of qRDWN6XB brings a different genetic resource for the breeding of rice cultivars and a reference point for strengthened grain yield and improved RSA under low nitrogen availability (Anis et al., 2019) (Table 2).

Hormonal regulation of root architecture

The key biochemical and molecular elements of the intrinsic pathways include hormones, their receptors, signalling components, and transcription factors (TFs). While related networks of environmental stimuli receptors, downstream signal transduction, and TFs are involved in extrinsic response pathways. Many environmental perception and response network components are inter-regulated by, or shared between, intrinsically and hormonally regulated to respond to external signals (Table 3).

Primary root initiation, elongation and development

In monocots, the primary root (PR) derived from the radical and established embryogenesis is the CRs-based fibrous root system's first root. The maintenance and development of quiescent centre (QC), stem cell population and cell identity differentiation create the PR's RAM. Auxin is one of the most critical phytohormones involved in regulating the root system. Changes in auxin levels able to transcriptionally regulate the different set of genes involved in root development and growth through the action of auxin/indole acetic acid (AUX/IAA) and Auxin Response Factor (ARF) modules (Guilfoyle and Hagen, 2007). The *ARFs* recognize and bind to auxin-responsive elements (AREs) in target gene promoters, thus activating or suppressing transcription. AUX/IAA proteins negatively regulate auxin response genes under no auxin or low auxin level by binding or inactivating ARFs activity (Abel et al., 1994). AUX/IAA proteins are intended for destruction by SCFTIR E3 ubiquitin ligase complex at higher auxin concentration (Gray et al., 2001). Another study suggested that *LATERAL ROOTLESS 2 (LRT2)*, a cyclophilin and is in control of cis/trans isomerisation of peptidylprolyl, acts on AUX/IAA proteins. *LRT2* catalyzes the isomerization of the tandem proline residues of the AUX/IAA necessary for recognition by *OsTIR1*. Also, the association of *LRT2* with *OsTIR1:OsIAA11* complex is increased by auxin and required for efficient degradation of AUX/IAAs (Jing et al., 2015). Perhaps other modules of the ARF regulation include miRNAs. For instance, the miR160 family assumes to take a considerable part in improving *Arabidopsis* PR and LR by tweaking ARF TFs, *ARF10*, and *ARF16*, which are functionally repetitive; however, both required for root cap cell foundation and upkeep. The overexpression of *miR160* in rice also led to serious root cap defects, implying equivalent regulatory pathways in monocots (Wang et al., 2005). Furthermore, rice gene *SLENDER RICE (SLR)* and homolog *SLENDER1 (SLN1)* in barley are negative GA-mediated root growth

regulators that tend to be influenced by auxin. When auxin is present, *DELLA* TFs are ubiquitinated and destroyed, allowing root cell division and elongation (Ikeda et al., 2001).

From initiation to elongation of CRs

Crown roots are adventitious roots specific to monocotyledons and called nodal root or roots that grow from shoots and account for the vast majority of its fibrous root system. CRs can be divided into two categories: the seminal roots of embryonic CRs that evolve during embryogenesis across the coleoptile node and the primary root (radicle), and the postembryonic CRs that occur during germination and plant life (Hochholdinger and Zimmermann, 2008). All CRs (embryonic and postembryonic), together with seminal PR, may be regarded as primary order roots because they emerge from the central plant stem and not from another root like LR.

Most of the studies regarding root development focused on PR and LR of dicots like *Arabidopsis*, primarily where existing understanding regarding genetic control of CRs is derived from research findings with mutants of rice and maize or based on *Arabidopsis* comparative studies of PR, LR, and adventitious root. The over-regulation of phytohormone, PR, LR, CR (monocots), and adventitious (dicots) gene families appear to have been predominantly conserved root growth (Coudert et al., 2010). Consequently, the roles of the specific genes in the developmental pathways can differ slightly. The initiation and progression of CRs are regulated by auxin-mediated signalling, equivalent to PR and LR development in *Arabidopsis* (Rebouillat et al., 2009).

Auxin signals are necessary for the correct division of parenchyma cells asymmetrically. Similar to LR production in *Arabidopsis*, cytokinins (CK) also played a secondary role in promoting CR formation by antagonising auxin-based signalling pathways. The *WUSCHEL RELATED HOMEODOMAIN11* (*WOX11*) is a rice gene that encodes auxin and CK-induced transcription factor, expressed in the early Crown Root Primordia (CRP) and actively divided areas of the apical meristem (Jain et al., 2006). CR growth was inhibited in *WOX11* knock out mutants, while its overexpression increased CR cell division rates, resulting in precocious CR growth. The transcription of CK and auxin-responsive genes has also been modified, indicating that *WOX11* could have a crucial role in incorporating auxin and CK signalling to regulate cell division rates in CRP. *RR2* can operate as a negative CK signalling regulator that represses the CR emergence by repressing the CR meristem's cellular proliferation (Zhao et al., 2009). The genetic and physiologic process also regulated CRP formation, and the productions of CRs in stem nodes have at least a part environmental impact (Mergemann and Sauter, 2000). Submergence induced ethylene accumulation kills epidermal cells above CRP in deepwater rice accessions, allowing CRs to emerge through the epidermis of submerged nodal branches. The development of CRP may also be regulated by auxin, as a study by Xu and co-worker suggested that *OsPIN1* gene RNAi-knockdown lines resulted in the discontinued development of CRP (Xu et al., 2005).

Recent studies have shown that gibberellic acid (GA) is also involved in CRP emergence and elongation with ethylene as a synergistic regulator. Furthermore, abscisic acid (ABA) also acts as an inhibitor of both GA and ethylene signalling pathways (Steffens and Sauter, 2005). Strigolactones can play a role in CR

elongation's positive regulation, potentially through modulation of auxin fluid, by promoting a meristematic cell root division (Arite et al., 2012). Rice dwarf mutants had a short CR phenotype due to an apparent decrease in cell division, resulting in a narrower meristematic region, for genes involved in SL biosynthesis (SL-deficient rice mutants max3/rms5/d17, max4/rms1/d10,d27) or SL (SL insensible rice mutants max2/rms4/d3 and d14) (Arite et al., 2012). This reduced cell distribution could be due to local auxin levels in SL modulation affecting the numbers of the meristem as seen in SL deficient and SL in PRs for homologous *Arabidopsis* genes.

Root microbiota affects root development

The soil has an exceptionally diverse microbiome, susceptible to nutrient availability that influences the soil properties, including moisture, pH and nutrient content. According to a report that used deep sequencing techniques, soil type has a more significant impact on rhizosphere microbial communities than plant genotype (Xu et al., 2020). This finding suggested that soil properties are important in shaping the microbial communities of the soil and rhizosphere. Besides the land type, the nature and composition of root exudates secreted by plants in the rhizosphere are likely to influence microbial communities (Dennis et al., 2010). Root exudates comprise amino acids, carbohydrates, organic acids, phenolics, enzymes, fatty acids and flavonoids (Vives-Peris et al., 2019). Thus, the plant microbial interaction depends on soil and plant type (Ishaq, 2017). According to research, plants and rhizosphere inhabiting microbes have a rich chemical communication language, which alters the microbial community structure as well as plant growth and health (van Dam et al., 2016).

Rhizosphere microorganisms impact plant growth and agriculture by stimulating root development and increasing nutrient availability in the rhizosphere. Additionally, these microbes diversely improve plant growth and development by secreting specific chemicals that involve root growth and development. Plants exude a diverse range of photosynthate compounds in the rhizosphere through their roots. These compounds contain polysaccharides, sugars (glucose, galactose, mannose and glucuronic acid), aromatic acids, amino acids, fatty acids and aliphatic acids (Hu et al., 2018). These compounds help in plant-microbe interaction by attracting and sustaining microorganisms (Venturi and Keel, 2016). Rhizospheric microbes reinforce plants growth by nutrient solubilization, storage, and uptake; humification of recalcitrant organic matter (Tfaily et al., 2014); averting pathogens entry and from colonizing in plants roots (Enebe and Babalola, 2019); harmonizing host immunity via induced systemic resistance (ISR); (Bruno et al., 2020) and regulating signalling pathways (Van Wees et al., 2008). Several microbes produce extracellular enzymes like cellulases, proteases, chitinases, lipases and β -1-3 glucanases that hydrolyze a wide range of cell wall compounds, such as cellulose, chitin, hemicelluloses and protein (Lugtenberg et al., 2017). These enzymes help to improve soil fertility by releasing organics nutrients like N, P, and K into the plant rhizosphere (Doni et al., 2019).

Apart from this, several rhizospheric microorganisms can modify RSA to improve nutrient and water exploration (Vacheron et al., 2013) through distinct mechanisms. The central mechanism of microbial modulation of RSA encompasses the altering hormonal balance in plant roots either by secreting plant

hormone or producing secondary metabolites interfering with hormonal pathways concerned with root development such as CK, auxin, ethylene, GA, and ABA (Ghosh et al., 2019). Microbes have been shown to influence postembryonic root development by modifying cell division and differentiation inside the PR and root hair emergence and LR formation (Zhang et al., 2017). The most characteristic root phenotype of plant tolerance in nutrient stress is PR growth inhibition, along with the proliferation of LRs and root hairs result in increased nutrient assimilation and improved shoot biomass. A rise in shoot biomass accompanied by an increase in PR growth or deep root system is another phenotype. Both effects are dependent on nutrient type and availability. The plant root growth is also affected by both the microbial density as well as the distance between the bacteria and plant root (Ortíz-Castro et al., 2009). One of the critical mechanisms recently studied that several microbes affect root development by cell division and differentiation mainly at two sites, i.e., meristem zone and LR formation zone (Wu et al., 2018). These changes affect the plants' overall RSA, usually accompanied by changes in endogenous plant responses. Because several rhizospheric microbes have been identified as a producer of these hormones, it is tempting to speculate that microbial hormones may directly induce root system changes. The different studies summarize in Table 4 and impact of root microbiota on RSA in rice illustrated in Figure 2.

Plant growth promoter

Phytohormone production and secretion, such as indole-3-acetic acid (IAA) by rhizospheric microbes, may also be responsible for RSA reconfiguration. Microbes can also alter the signals that control for root morphogenesis in plants and modulate RSA (Ortíz-Castro et al., 2009). Thus, using rhizospheric microbes promises to be a novel and environmental friendly method of improving a crop's RSA and ultimately ensuring a long-term strategy for improving crop quality and yields.

Auxin and Cytokinin

The potent regulator of plant organogenesis is the balance of auxin and CK, which regulate the root development and shapes RSA (Jing and Strader, 2019). The endogenous ratio of auxin to CK in plants may be influenced by auxin and CK secretion by rhizospheric microbes and microbial metabolites that may interact with these hormonal pathways. To date, IAA is the most well-studied auxin produced by large number of rhizospheric microbes (Mohite, 2013). Exogenous IAA regulates a broad range of plant development and root growth; for example, low IAA levels can promote the elongation of the PR, while higher IAA levels encourage LR formation, enhances root hair formation while reduces PR growth (Zhang et al., 2018). Microbial metabolites like 2,4-diacetyl phloroglucinol (DAPG) and nitric oxide (NO) can also stimulate RSA changes in plants by interfering with auxin synthesis pathway. DAPG is a well known natural phenolic compound found in some specific strains of gram-negative bacteria and responsible for antimicrobial properties of *Pseudomonas fluorescens* (Weller et al., 2007). DAPG serve as a signal molecule for plants at low concentrations, stimulates root exudation (Phillips et al., 2004) and improves root branching (Brazelton et al., 2008). An auxin-dependent signalling pathway can be interfered by DAPG, consequently modify RSA (Brazelton et al., 2008). Similarly, inoculation of rice endophyte

Phomopsisliquidambari B3 significantly enhanced auxin, CK, and ethylene level in rice under varying N levels (Li et al., 2018). Additionally, *Azospirillum brasilense* has nitrite reductase activity and produces NO during root colonization which is involved in auxin signalling pathway to regulate the development of LR (Rondina et al., 2020).

Cytokinin regulates RSA in rice by CK-signalling and its interaction with auxin signalling (Neogy et al., 2020). Plant growth has been stimulated by inoculating plants with rhizospheric microbes that produce CK (Li et al., 2020) (Kieber and Schaller, 2018). Cytokinin production has been reported in various microbes like *Arthrobactergia comelloi*, *Azospirillum brasilense*, *Paenibacillus polymyxa*, *Bradyrhizobium japonicum*, *Pseudomonas fluorescens* and *Bacillus licheniformis* (Cacciari et al., 1989; Perrig et al., 2007; García de Salamone et al., 2001; Timmusk et al., 1999).

Ethylene

Another important phytohormone that inhibits root elongation is ethylene. It also inhibits auxin transport, induces senescence, and abscission of different organs, all of which contribute to fruit ripening (Iqbal et al., 2017). Apart from senescence, abscission and fruit ripening, ethylene also modulates plant defence pathways (Yang et al., 2017). Rhizospheric microbes affect ethylene level in plants by degrading precursors of ethylene. Rhizospheric microbes secrete 1-aminocyclopropane-1-carboxylic acid deaminase (ACCd), which degrades ACC (immediate precursor of ethylene) into α -ketobutyrate and ammonium. Microbes used the produced ammonium as carbon and nitrogen source (Kim et al., 2020). Thus, microbial ACCd activity is thought to reduce root ethylene production by reducing the abundance of the ethylene precursor ACC (Gamalero and Glick, 2015), thereby reducing the repressive effect of ethylene on root growth.

Abscisic acid (ABA) and gibberellic acid (GA)

Several reports have revealed that rhizospheric microbes produce ABA and GA, or compounds that control the concentration of these phytohormones in plants (Wang et al., 2020). These phytohormones, however, play distinct roles during LR development (Chen et al., 2018). An endophytic bacterium, *Bacillus amyloliquefaciens* RWL-1, produces ABA under saline conditions, and thus inoculation with this microbe improves salinity stress tolerance in rice (Shahzad et al., 2017).

GAs, particularly GA₃, influence rice root elongation and modulate local auxin production and polar auxin transport (Li et al., 2020). Gibberellins are produced by a number of microbes, including *Achromobacter xylosoxidans*, *Acinetobacter* spp., *Azospirillum* spp., *Bacillus* spp., *Herbaspirillum seropedicae*, *Gluconobacter diazotrophicus*, and *Gelvizobia* (Dodd et al., 2010). The application of GA in rice at amount comparable to that produced by *Azospirillum* endorses root growth (Bottini et al., 2004).

Modification of root tissue structural properties

Changes in plant gene expression caused by microbes involved in cell wall expansion or loosening will mainly cause changes in the root cell wall's ultrastructure. The endophytic microbe *Azospirillum irakense*

induces polygalacturonase expression in roots of inoculated rice (Sekar et al., 2000). Furthermore, another study found that exogenous application of auxin improves the role of the induced polygalacturonase found in rice roots inoculated with *Azospirillum irakense* (Dobbelaere et al., 2002).

Impact on plant transcriptome

The rice root architecture could be improved by changing the hormonal level or gene expression of the root architecture. For instance, the up-regulation of *DRO1* in a shallow-rooted rice cultivar relates to root enhancement due to improved root growth angle, with even more downward root growth and high yield under drought condition (Uga et al., 2013). Furthermore, inoculation with *Rhizophagus irregularis* and *Acanthamoeba castellanii* increased the number of lateral roots (Kreuzer et al., 2006). In comparison to the findings of Kreuzer et al., *Azospirillum lipoferum* inoculation increased the root numbers, root surface area and total root length (Chamam et al., 2013). Low level of IAA induces PR elongation, whereas high concentration promoted LR development, increased root hair formation, and decreased PR length, according to previous studies (Perrig et al., 2007; Remans et al., 2008).

Microbial strains may either directly supply IAA to the host plant or modify auxin pathways in the plant by controlling auxin-responsive genes expression. For example, *Klebsiella* and *Azospirillum* transformed tryptophan into IAA, which accounted for altering rice root growth (El-Khawas and Adachi, 1999). Similarly, a study reported that isolates from rice rhizospheric able to produce IAA and influenced rice seedlings root length (Ashrafuzzaman et al., 2009). A recent study showed that the inoculation of *Bacillus altitudinis* strain FD48 could modify root architecture by increasing root thickness and the number of rising LR while reduce the root length. The IAA modulation in rice root caused by *Bacillus altitudinis* strain FD48 is due to variation in the expression level of the AUX/IAA gene family. An early study suggested the association of *Azospirillum* with the expression of plant genes, as the inoculation of *Azospirillum brasilense* Sp245, enhances the expression of ethylene receptors in two rice cultivars with contrasting nitrogen acquisition capacities (Vargas et al., 2012). To create a positive relationship between the plant and bacteria, all ethylene receptors can need to be accumulated. In term of endophytes, *Azoarcus* was found to have differential rice root colonisation (Miché et al., 2006). A mild defensive response occurred in a less compatible interaction and followed by the stimulation of proteins linked to pathogenesis and proteins sharing domains with receptors such as pathogens induced kinases, which were also stimulated by jasmonate (Miché et al., 2006). Rice roots inoculation with endophytic microbes *Herbaspirillum seropedicae* caused the expression of auxin and ethylene responsive genes and the repression of PBZ1 proteins and thionins associated with defence (Brusamarello-Santos et al., 2012; Shidore et al., 2012). These findings suggested that plant defence responses can be modulated during colonization of endophytes.

Plant-associated *Bacillus* can change the expression level of auxin-responsive genes, modulating auxin concentration in the root and thus changing the early stages of root architecture in rice seedlings (Ambreetha et al., 2018). Further studies suggested that AM fungi, *Rhizophagus irregularis* causes host to develop more LR (Chen et al., 2018; Paszkowski and Gutjahr, 2013), which is dependent on receptor-like

kinase *OsCERK1*, implying that the recognition of chitin oligomers is critical in AM fungal-mediated induction of LR growth in rice. Another study reported that *R. Irregularis* triggers plant signalling responsible for induction of LR production, involving a receptor kinase CHITIN ELICITOR RECEPTOR KINASE 1 (CERK1) in rice (Chiu and Paszkowski, 2020; Chiu et al., 2018).

Impact on plant metabolome

Microbes are capable of altering the composition and volume of metabolites in addition to influencing root exudation. For example, when inoculated with *Herbaspirillum seropedicae*, rice plants showed higher amount of malate content in shoot tissues (Curzi et al., 2008). The early effect of numerous *Azospirillum* strains on rice root and shoot secondary metabolite profiles has been investigated in recent studies. Secondary metabolite profiling of two rice cultivars inoculated with two different strains of *Azospirillum* has shown that secondary metabolite profiles have been modified with phenolic compounds like flavonoids hydroxyl cinnamic derivatives (Chamam et al., 2013). The relatively high concentration of quaternary compounds, glycine betaine was observed in rice infected with *Pseudomonas pseudoalcali* (Jha et al., 2011).

Concluding remarks and future perspectives

It is not surprising, then, that rhizospheric microbes influence rice root development. The latest evidence on the impacts of rhizospheric microbes on root development is summarised in this review. It will encourage the use of naturally growing soil microbes in order to facilitate plant growth and health while minimising herbicides and synthetic fertilisers in the field. Future research combining the study of plant developmental biology and plant-microbe interactions will shed light on how soil microbes influence root development. This research will assist us in better understanding these complex cross-kingdom interactions, root developmental biology, and microbial signalling. Finally, this knowledge will aid in developing sustainable plant growth-promoting technologies, which can significantly improve crop yield and food security.

Declarations

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Declaration of Interest

All the authors declare no conflict of interest.

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Tables

Table 1. Effects of extrinsic factors in modulating root system architecture.

Condition	Impact	Genes	Interactions	References
Root system submergence	Crown root primordia development	SUB1	GA, ethylene	(Xu et al., 2006; Fukao et al., 2011)
Drought	LR emergence	SUB1	ABA	(Zhang et al., 2020)
Low phosphate availability	Root foraging: increased LR initiation	OsPTF1, Pho2, mir 399	Auxin, CK, Ethylene, GA	(Yi et al., 2005; Bari et al., 2006)
High Al ³⁺	Inhibition of LR initiation	ART1	Auxin, ethylene	(Yamaji et al., 2009)

Table 2. Genes and their involvement in root growth and development

Gene	Function	Reference
<i>DRO1</i>	regulating the root growth angle	(Uga et al., 2013)
<i>OsARF12</i> ,	controlling primary root length, shortened primary root	(Qi et al., 2012)
<i>OsEXPA8</i>	lengthening primary root, boosting lateral roots and root hair counts	(Ma et al., 2013)
<i>OsEXPB2</i>	modify RSA	(Zou et al., 2015)
<i>OsWOX4</i>	primary root elongation by regulating auxin transport	(Chen et al., 2020)
<i>OsMYB2P-1</i>	RSA regulation	(Dai et al., 2012)
<i>OsMYB4P</i>	RSA	(Yang et al., 2014)
<i>OsRPK1</i>	negatively controls the development of rice roots	(Zou et al., 2014)
<i>SOR1</i>	modify RSA by altering root gravitropic response	(Hanzawa et al., 2013)
<i>OsARF16</i>	RSA modification by regulating auxin transport	(Shen et al., 2015)
<i>OsSIZ1</i>	RSA manipulation	(Wang et al., 2015)
<i>OsWRKYP74</i>	RSA modification	(Dai et al., 2016)
<i>OsRab6a</i>	architecture of the root system in response to Fe-deficient medium	(Yang and Zhang, 2016)
<i>OSPIN2</i>	plays an important role in root gravitropic reactions and in determining RSA in rice by affecting polar auxin transport at the root tip	(Wang et al., 2018)
<i>RCc3</i>	expanded growth of primary roots, adventitious roots and lateral roots	(Wang et al., 2018)
<i>OsWRKY28</i>	influenced the root growth at the seedling stage	(Wang et al., 2018)
<i>OsACS1</i> and <i>OsACS2</i>	controlling the modification of RSA	(Lee et al., 2019)
<i>OsJAZ9</i>	modulating RSA	(Singh et al., 2020)

<i>OsGrx_C7</i>	Improve root growth in response to arsenic	(Verma et al. 2020)
<i>WEG1</i>	formation of higher number of long and thick lateral roots	(Lee et al., 2019)
<i>qSOR1</i>	shallower root growth angle	(Singh et al., 2020)
<i>qRDWN6XB</i>	improved RSA under low nitrogen availability	(Anis et al., 2019)

Table 3. Hormones and their involvement in root growth and development

Phytohormone	Function	References
Auxin (IAA) NAA	Increases lateral root primordia initiation and outgrowth	(Sreevidya et al., 2010)
2,4-D	Increases lateral root primordia initiation through cell division (but does not promote cell elongation and root outgrowth)	(Sreevidya et al., 2010) (Debi et al., 2005)
Kinetin, trans-zeatin	Stimulates lateral root elongation	(Sreevidya et al., 2010) (Ashikari et al., 2005) (Jain et al., 2006) (Kurakawa et al., 2007) (Debi et al., 2005)
Kinetin, trans-zeatin	Stimulates crown root primordia formation	(Debi et al., 2005), (Hirose et al., 2007; Zhao et al., 2009)
Gibberellins GA3	Interacts with ethylene to promote crown root primordia outgrowth and elongation	(Steffens et al., 2006)
Ethylene	Promotes crown root formation at submerged nodes-internodes	(Lorbiecke and Sauter, 1999)
Ethylene	Promotes crown root emergence at submerged nodes through induction of epidermal cell death	(Mergemann and Sauter, 2000)
Strigolactone SLs	Promote crown root elongation by inducing meristematic cell division	(Arite et al., 2012)

Table 4. Effects of microbes in modulating root system architecture

Microbes	Function	Effects	References
<i>Azospirillum brasilense</i>	IAA production	Increase in root elongation, root surface area, root dry matter and development of lateral roots	(El-Khawas and Adachi, 1999)
<i>Klebsiella pneumoniae</i>	IAA production	Increase in root elongation, root surface area, root dry matter and development of lateral roots	(El-Khawas and Adachi, 1999)
Rhizosphere isolates PGG2 and PGB4	IAA Production	Increases root length	(Ashrafuzzaman et al., 2009)
<i>Bacillus altitudinis</i> strain FD48	Induced IAA modulation in rice root is due to a change in the expression level of the <i>OsIAA</i> gene family	modifies the early events of root architecture	(Ambreetha et al., 2018)
<i>Acanthamoeba castellanii</i> (Protozoa) and <i>Betaproteobacteria</i>	Nutrient solubilization	Elongated (L-type) laterals, branched root systems	(Kreuzer et al., 2006)
<i>Phomopsis liquidambari</i> B3	Enhanced auxin, cytokinin, and ethylene level	Nitrogen mediated lateral root growth	(Li et al., 2018)
<i>Pseudomonas fluorescens</i>	Stress related induction	Increases root length	(Kandasamy et al., 2009)
<i>Azospirillum brasilense</i> Sp245	Enhances the expression of ethylene receptors	increase in lateral root numbers	(Vargas et al., 2012)
<i>Herbaspirillum seropedicae</i>	Improve the expression of auxin and ethylene-responsive genes	lateral root initiation	(Brusamarello-Santos et al., 2012) (Shidore et al., 2012)
<i>Bacillus amyloliquefaciens</i>	ABA	lateral root development	(Shahzad et al., 2017).
<i>Azospirillum lipoferum</i> 4B <i>Azospirillum</i> B510	Alters rice secondary metabolite profiles	increased the number of roots, total root length and root surface	(Chamam et al., 2013)
<i>Azospirillum irakense</i>	Induce polygalacturonase expression	Modification of root tissue structural properties	(Sekar et al., 2000) (Dobbelaere et al., 2002)
<i>Glomus intraradices</i>	Affect the expression of <i>OsCYCLOPS1</i>	Increases in root mass, thickness, length, and LR number, induces the formation of long LRs	(Yano et al., 2008; Gutjahr et al., 2009)

	<i>OsLRT1</i> and also alters Auxin, ABA, CK, Ethylene concentration		
<i>Rhizophagus irregularis</i>	Perception of chitin oligomers	increased growth of LRs	(Chiu et al., 2018) (Paszkowski and Gutjahr, 2013)

Figures

Figure 1

Root architecture and anatomy of rice. (a) Seedling root system (cultivar Nipponbare) after 15 days of germination, (b) transverse section of rice root stained with Safranin, (c) enlarge view of root stele. Abbreviations: ARC, aerenchyma; CO, cortex; CR, crown root; END, endodermis; EP, epidermis; HYP, hypodermis; LR, lateral root; MX, metaxylem; PC, pericycle; PHL, phloem. Scale bars: (b) 50 μm, (c) 20 μm.

Figure 2

Impact of root microbiota on RSA in rice. Rhizospheric microbes can modulate root growth and development via the production of secondary metabolites and phytohormones. Microbes can influence plant nutrition by phosphorus solubilization, nitrogen fixation and siderophore production, and also alter gene transcription and metabolite biosynthesis in plant cells which effect root physiology. Abbreviations: CK, cytokinin; ET, ethylene; GA, gibberellic acid; IAA, indole acetic acid; NF, nitrogen fixation; PS, phosphate solubilization; SP, siderophore production.