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REVIEW ARTICLE

Root system architecture in rice: impacts of genes, phytohormones and root microbiota

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Abstract
To feed the continuously expanding world's population, new crop varieties have been generated, which significantly contribute to the world's food security. However, the growth of these improved plant varieties relies primarily on synthetic fertilizers, which negatively affect the environment and human health; therefore, continuous improvement is needed for sustainable agriculture. Several plants, including cereal crops, have the adaptive capability to combat adverse environmental changes by altering physiological and molecular mechanisms and modifying their root system to improve nutrient uptake efficiency. These plants operate distinct pathways at various developmental stages to optimally establish their root system. These processes include changes in the expression profile of genes, changes in phytohormone level, and microbiome-induced root system architecture (RSA) modification. Several studies have been performed to understand microbial colonization and their involvement in RSA improvement through changes in phytohormone and transcriptomic levels. This review highlights the impact of genes, phytohormones, and particularly root microbiota in influencing RSA and provides new insights resulting from recent studies on rice root as a model system and summarizes the current knowledge about biochemical and central molecular mechanisms.

Keywords Rice · Root system architecture · Root growth · Genetic regulation · Phytohormone · Microbiota

Introduction

Continuously increasing adverse climatic pressure and anthropogenic activities pose a serious threat to crop productivity and sustainable agriculture. Therefore, it is essential to improve plant tolerance to produce crops in increasingly hostile conditions and existing agricultural resources to feed the ever-increasing world population. Plants require water, specific micronutrients, and macronutrients to maintain their normal growth and development. They acquire these essential nutrients mainly through the root system, from the soil surrounded by active roots, i.e., the rhizosphere (Zhang et al. 2020a). As a result, the low surface area of active roots accounts for insufficient uptake of nutrients. This condition is more detrimental under low nutrient availability and negatively affects the overall crop development and yield. Therefore, increasing the active root surface area may improve resource exploration and uptake. The increased active root surface area can be attained by enhancing the three-dimensional root configuration or root system architecture (RSA). Thus, RSA modification plays a significant role in improving plant growth by enhancing soil resource utilization and is considered to be more productive under adverse conditions such as low nutrient availability (Paez-Garcia et al. 2015). The RSA primarily improves soil exploration and facilitates enhanced nutrient and water uptake that affects overall plant productivity and stress tolerance. Rice is one of the most widely cultivated and consumed staple crops that feed nearly half of the world's population. Improving rice productivity may contribute to global food security at a greater extent. Therefore, understanding the mechanistic details of RSA modification in rice would play an essential role in enhancing rice productivity.

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As a model plant, rice offers a functional experimental system to explore underlying molecular mechanisms of the fibrous root system of monocot plants (Coudert et al. 2010). Moreover, studying the adventitious roots system of *Arabidopsis* is insufficient to comprehend the genetic regulatory network for root development in monocot crops like rice, maize, and wheat. Consequently, understanding the hormonal and genetic regulation of rice root development will benefit in deciphering the regulatory network of root development in monocots. In addition, a detailed understanding of the critical genes/loci involved in RSA modification in rice would allow breeders and researchers to use genetic modification or marker-assisted selection to produce high-yield cultivars.

Several anatomical and developmental differences exist in dicots, and monocot roots. Embryonically derived primary or 'taproot' system is a typical feature of dicots, such as *Arabidopsis* root system (Bellini et al. 2014). In contrast, overall root architecture is more complex in the 'fibrous' root system of monocots. The monocot root system mostly constitutes seminal roots and shoot-borne crown and brace roots. These crown roots (CRs) in monocots also referred as adventitious roots emerged from root primordia during the developmental program (Hochholdinger et al. 2004). The CRs emerge 5–10 days post-germination from below-ground stem nodes, while brace roots emerge around 6 weeks after germination from above-ground stem nodes. For example, in maize, primary roots (PRs) were visible after 2–3 days of germination and seminal roots approximately 7 days after germination. Seminal roots are formed embryonically and emerge from the scutellar node in a similar manner as emergence of PRs (Singh et al. 2010). In cereals, lateral root (LR) initiation is also different as endodermal cells and pericycle both proceed to LR cells and create at the phloem poles than the xylem poles. *Arabidopsis* roots possess two xylem poles only, and LRs are initiated in an alternating left–right pattern at each pole. On the other hand, in cereal roots, there are ten or more phloem poles, resulting in a radial branching pattern around the parent root compared to that in *Arabidopsis* roots (Smith and De Smet 2012). Thus, in contrast to *Arabidopsis*, rice has a relatively complex root system, consisting of the embryonic PRs, seminal roots and post-embryonic adventitious roots. Primary and seminal roots have vital functions throughout the seedling stage, while adventitious roots form the functional root system (Steffens and Rasmussen 2016). Different rice cultivars have evolved adaptive root systems that adapt to various environmental stresses, including water and nutrient stress (Pedersen et al. 2021; Verma et al. 2021). For example, plants develop a deeper root system during water deficit conditions to obtain water from the subsoil portion to combat drought stress conditions (Lynch and Wojciechowski 2015). In addition to water uptake, a deeper root system would also be favorable for the rapid acquisition of nitrogen from the subsoil (Plett et al. 2020). In general, a thicker, branched, and deeper root system with a high root-to-shoot relationship can increase plant resistance to drought and nutrient stress (Klein et al. 2020). Therefore, studying the adaptive genetic variation (variation resulting from natural selection) in root system development and RSA modification would be more informative and beneficial for developing stress tolerance cultivars. Earlier research has shown that numerous factors can affect the root system development and alter the RSA through a complex regulatory network, as well as genetic, phytohormone and environmental stress factors. Genetic and phytohormones are two most prevalent factors affecting root development as well as shaping the RSA. Auxin and cytokinin (CK) are the most essential phytohormones required for the de novo genesis of root primordia. Other phytohormones such as abscisic acid (ABA) ethylene, gibberellic acid (GA) and salicylic acid (SA) are also involved in root formation, growth and modification of RSA (Qin et al. 2022). The crosstalk between these phytohormones and genetic factors affects a specific set of downstream regulators that lead to changes in gene expression, signal transduction, and metabolic conversions. For instance, CK induces the expression of auxin transporter, PIN1 and PIN7 via CYTOKININ RESPONSE FACTOR 2 (CRF2) and CRF6 which leads to modification of RSA (Šimášková et al. 2015). However, these interactions have been mainly characterized in dicot plants such as *Arabidopsis*, and translating this information into economically important monocot crop plants will open new research possibilities for increasing stress resilience and crop productivity by RSA modification.

Several microbes can affect root system development and RSA modification by altering hormonal, genetic and regulatory mechanisms (Valette et al. 2020; Batista et al. 2021). Thus, it is crucial to discover hormonal and genetic determinants governing root system development and RSA modification to decode the underlying mechanisms. The current review presents an overview focused on the genetic, hormonal, and microbial effects on root system development and RSA modification in rice and its relationship to the sustainable improvement of agricultural productivity.

Rice root system development

Rice forms a thick fibrous root system consisting of seminal, nodal and lateral roots (LRs) and post-embryonic adventitious roots (nodal roots or CRs) emerge from the basal nodes of the stem (Wang et al. 2020a). As soon as germination starts, the radicle finds its way out through the coleorrhiza and enveloping glume which forms the seminal root. Lateral roots emerge from the seminal roots, while adventitious roots emerge from the basal nodes with the advent of seedling growth. When seedlings emerge, most of the roots snapped off, but fresh roots develop very soon. The consecutive post-embryonic nodal roots or CRs differentiated from the nodal regions of stems and tillers. The bifurcation of the radicle and CRs results in longer LRs and shorter LRs. Longer LRs show positive geotropism and indeterminate growth, while shorter LRs are short, ageotropic and show determinate growth. Moreover, longer LRs emerge intermittently and carry expandable long or short LRs until the fifth branching order. Simultaneously, shorter LRs are larger in number and never develop a higher branching order. However, CRs differentiate from the stem but have similar characteristic features like root tissue (Mai et al. 2014). The radial structure of these CRs encompasses the stele (phloem and xylem), pericycle, endoderm, cortex, aerenchyma, sclerenchyma, exodermis, and epidermis locating from the center to periphery (Fig. 1). This radial structure reflects the capacity of rice roots to grow in both aerobic and anaerobic (flooding) environments (Maurel and Nacry 2020). Notably, the aerenchyma helps gas exchange with the shoot in anaerobic conditions (Pedersen et al. 2021). Additionally, pericycle and endodermal root cells proliferate to differentiate LRs and help the plant's nutrients and water uptake (Jing and Strader 2019). Overall, the rice root system is highly diverse between the different varieties and is affected by several edaphic and environmental conditions such as nutrient availability, organic content, and soil type.

Root system architecture (RSA) and RSA modification

The RSA is a three-dimensional spatial configuration of the root system in the supporting medium. It determines the distribution of different root types across the soil profile (Ogura et al. 2019). The RSA refers to the root system surface topography described in the medium, particularly the root axis geometry precision. 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. In addition, these components may be evolutionarily governed by complex and interactive genetic pathways that regulate growth and development to address environmental challenges. Hence, modifying RSA is an important strategy to enhance nutrient acquisition, especially under nutrient-deficient and water-stress conditions (Li et al. 2016).

Rice domestication started about 10,000 years ago, several rice varieties have grown in different ecosystems, including upland, rainfed lowland, flood-prone, and under different growing regimes ranging from conventional low-input to intensive high-input systems. A Gene bank at The International Rice Research Institute (IRRI), Philippines, contains over 100,000 rice genotypes (Wing et al. 2018). Many genotypes with variability in RSA establish a significant connection for identifying new genes involved in modifying RSA and root development in rice.. Several studies on "intrinsic pathway" or extrinsic "environmental response pathways" are significantly linked to the relationship between genetic and environmental factors listed in Table 1.

Genetic regulation of RSA

To decode the mechanism for RSA regulation by genes, the direct genetic approach was traditionally used earlier before the advent of reverse genetic approaches. The quantitative trait locus (QTL) identification in mapping populations was the starting point for the direct genetic approach. In 1995, Champoux et al. (1995) published the first study on rice root system architecture modification. In 2008, Kamoshita et al. (2008) reviewed a QTL associated with primary or secondary or integrated traits of RSA parameters correlated with drought stress in 15 mapping rice populations, including CT9993/IR62266 for RSA modification. They suggested genotype responses for stress tolerance such as deep and

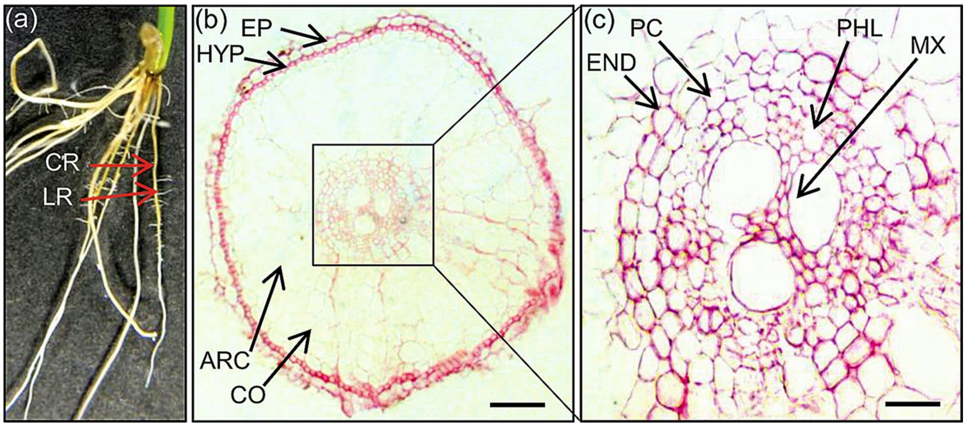

Fig. 1 Root architecture and the anatomy of rice. **a** Seedling root system (cultivar Nipponbare) after 15 days of germination, **b** transverse section of rice root stained with Safranin, **c** enlarge view of root stele. ARC, aerenchyma; CO, cortex; CR, crown root; END, endodermis; EP, epidermis; HYP, hypodermis; LR, lateral root; MX, metaxylem; PC, pericycle; PHL, phloem. Scale bars: **b** 50 µm, **c** 20 µm

Table 1 Effects of extrinsic factors in modulating root system architecture

Condition	Impact	Genes	Interactions	References
Root system submergence	CRP development	*SUB1*	GA, ethylene	Xu et al. (2006) and Fukao et al. (2011)
Drought	LR emergence	*OsABA8ox2*	ABA	Zhang et al. (2020b)
Low phosphate availability	Root foraging: increased LR initiation	*OsPTF1*, *Pho2*, *mir 399*	Auxin, CK, Ethylene, GA	Yi et al. (2005) and Bari et al. 2006
High Al^{3+}	Inhibition of LR initiation	*ART1*	Auxin, ethylene	Yamaji et al. (2009)

thick roots and maintaining water status were of immense importance for higher yield under stress. In advancement, Khowaja et al. (2009) identified the QTL by meta-QTL analysis in the Bala/Azucena population associated with drought stress. They evaluated RSA-related traits like root number, length, thickness, roots depths, and root-to-shoot ratio. The advancement of high-throughput root phenotyping and 3D imaging regain interest in QTL identification in mapping populations. However, the large population size of the confidence interval is the fundamental restriction of QTL detection in mapping populations. In comparison to mapping populations, genome-wide association studies (GWAS) in natural populations with quick linkage disequilibrium decay have recently emerged as powerful methods for improving the resolution in localizing QTLs. The first GWAS findings studying root characteristics in rice were released by Clark et al. 2013; Courtois et al. 2013. Even though the resolution of QTL location in GWAS is far better than in mapping populations, the number of potential candidate genes is still vast, necessitating further evidence to identify the functional genes. Several QTLs have been identified in diversified rice populations that affect the root system and grain yield. Comprehensive knowledge directly impacted rice irrigation and fertilizer efficiency in the molecular breeding of RSA (Zhou et al. 2016). For example, the characterization of qRDWN6XB resulted in a different genetic resource for breeding rice cultivars and a reference point for strengthened grain yields and improved RSA under low nitrogen availability (Anis et al. 2019). Apart from identifying and characterizing RSA-related QTLs, a number of genes involved in manipulating RSA to address nutrient and water imbalance were identified and characterized (Table 2).

Several studies were conducted to identify genetic regulators involved in modifying RSA. Auxin is the most important phytohormone involved in the regulation of RSA thus by modifying auxin transport it is possible to modify RSA. For instance, by influencing polar auxin transport at the root tip, *OSPIN2* plays a vital role in root gravitropic reactions and deciding RSA in rice (Wang et al. 2018a). Similarly, a leucine-rich receptor-like kinase *OsRPK1* negatively controls rice roots development by controlling polar auxin transport (Zou et al. 2014). *OsARF16* also regulates RSA by regulating auxin transport and Fe homeostasis (Shen et al. 2015). *OsARF12* is an auxin response factor that regulates auxin synthesis and polar auxin transport through *OsYUCCAs*, *OsPINs*, and *OsPGPs*, resulting in shortened length in rice plants (Qi et al. 2012). A transcription factor *OsWOX4* played a pivotal role in PR elongation by regulating auxin transport, indicating its importance in RSA modification of the rice root system (Chen et al. 2020). The root growth angle (RGA) is an essential component of RSA, and it is used as a plant breeding parameter to determine variety. RGA can be regulated by modifying the expression of genes such as, *DEEPER ROOTING 1* (*DRO1*), *qSOR1* (quantitative trait locus for *SOIL SURFACE ROOTING 1*), and *SOR1* (*SOIL SURFACE ROOTING 1*) involved in RSA modification by controlling root growth angle. *DRO1* triggers unidirectional root growth and lowers root bending in response to gravity by causing cell elongation at the root tip, and it is negatively regulated by auxin (Uga et al. 2013; Singh et al. 2021). Another gene, *qSOR1* (quantitative trait locus for *SOIL SURFACE ROOTING 1*), a DRO1 homolog, regulates the root growth angle. The *qSOR1* gene primarily expresses in root columella cells and engages in root gravitropic responses. Alternatively, *qSOR1* is negatively regulated by auxin (Kitomi et al. 2020). Another gene, *SOR1* (*SOIL SURFACE ROOTING 1*), modified RSA by altering the gravitropic root response (Hanzawa et al. 2013). *OsSIZ1* was concerned with RSA manipulation, as the *ossiz1* mutant had short PRs and adventitious roots compared to wild plants (Wang et al. 2015). The LR development and root hair emergence are of immense importance to increase active root surface area. For example, A root-specific α-expansin gene, *OsEXPA8*, improve RSA by elongating PRs, boosting LRs and root hair counts, and improving rice root development (Ma et al. 2013). Another expansin gene, *OsEXPB2*, also modifies RSA by LR elongation and shoot growth (Zou et al. 2015).

Transcription factors are master regulator involved in RSA modification by controlling the expression of RSA-related genes. Many transcription factors were identified and characterized to understand the molecular networking involved in RSA modification. For instance, RSA was substantially modified by the overexpression of

Table 2 Genes and their involvement in root growth and development

Gene	Function	References
DRO1	Regulating the root growth angle	Uga et al. (2013), Singh et al. (2021) and Kitomi et al. (2020)
OsARF12	Controlling PR length	Qi et al. (2012)
OsEXPA8	Lengthening PR, boosting LRs and root hair counts	Ma et al. (2013)
OsEXPB2	Modulating RSA and plant height by inhibiting cell growth	Zou et al. (2015)
OsWOX4	Primary root elongation by regulating auxin transport	Chen et al. (2020)
OsMYB2P-1	Regulation of root development under both phosphate sufficient and deficient conditions	Dai et al. (2012)
OsMYB4P	Regulation root development under phosphate deficient conditions	Yang et al. (2014)
OsRPK1	Negatively controls the development of rice roots	Zou et al. (2014)
SOR1	Modify RSA by altering gravitropic root response	Hanzawa et al. (2013)
OsARF16	RSA modification by regulating auxin transport	Shen et al. (2015)
OsSIZ1	RSA manipulation	Wang et al. (2015)
OsWRKYP74	RSA modification	Dai et al. (2016)
OsRab6a	The architecture of the root system in response to Fe-deficient medium	Yang and Zhang (2016)
OSPIN2	Root gravitropic response by affecting polar auxin transport at the root tip	Wang et al. (2018a)
RCc3	Expanded growth of PR, adventitious and LRs	Li et al. (2018a)
OsWRKY28	Influenced the root growth at the seedling stage	Wang et al. (2018b)
OsACS1 and OsACS2	Controlling the modification of RSA	Lee et al. (2019)
OsJAZ9	JA-mediated modulation of RSA	Singh et al. (2020)
OsGrx_C7	Improving root growth in response to arsenic	Verma et al. (2020)
WEG1	Increasing number, length and thickness of LRs	Lucob-Agustin et al. (2020)
qSOR1	Shallower root growth angle	Kitomi et al. (2020)
qRDWN6XB	Improving RSA under low nitrogen availability	Anis et al. (2019)
OsMED25	JA-mediated root development	Suzuki et al. (2021)
OsEIL1	Inhibition of primary root growth by activation of auxin, ABA biosynthesis and GA catabolism	Kin et al. (2022)
OsHDAC1	*OsHDAC1-GSK2/OsBZR1* module controls LR formation in rice	Hou et al. (2022)
OUR1/OsbZIP1	Promoting root development through repressing auxin signaling	Hasegawa et al. (2021)
OsMED25	JA-mediated root development	Suzuki et al. (2021)
OsFPFL4	Modulating the root by affecting auxin and ROS homeostasis	Guo et al. (2020)
MHZ1/OsHK1	Root growth regulation by inhibiting the ethylene receptors	Zhao et al. (2020)
OsZHD2	Promotes root meristem activity in rice by inducing ethylene biosynthesis	Yoon et al. (2020)
MAL	Maintaining cell viability in the meristem after the initiation of root primordial formation, mediated by cytokinin signaling and reactive oxygen species (ROS)	Jiang et al. (2020)
OsVST1	Influence meristem size through broad modulation of cell–cell communication or through specific signaling complexes	Shao et al. (2021)
CIPK9	$NH4^{+}$ dependent root growth	Xuan et al. (2019)
OsMADS57	Modulating root growth by regulating nitrate translocation from root to shoot	Huang et al. (2019)
LAZY1	Controlling shoot gravitropism and tiller angle by regulating the expression of auxin transporters	Zhu et al. (2020)
OsNAC2	Modulating rice root development by integrating auxin and cytokinin pathways	Chanjuan et al. (2020), Mao et al. (2020)
WOX11	*YUCCA*-Auxin-*WOX11* module controls CR development in rice	Zhang et al. (2018a, b)
OsMADS25	Regulating root system development via auxin signaling in rice	Zhang et al. (2018a, b)
OsAUX1	Auxin influx carriers involved in primary root and root hair elongation	Yu et al. (2015) and Wang et al. (2019)

OsMYB2P-1 (Dai et al. 2012) and *OsMYB4P* transcription factors in rice (Yang et al. 2014). *OsWRKYP74* conferred RSA modification as the transgenic plants better tolerate 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 the 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 the root. *RCC3* generates pleiotropic phenotypes of reinforced RSA, such as expanded growth of PRs adventitious and LRs at the seedling stage (Li et al. 2018a). Another root growth controlling transcription factor, *OsWRKY28,* influenced root growth at the seedling stage and fertility at the reproductive stage, which likely affects jasmonic acid (JA) homeostasis (Wang et al. 2018b). The study showed that exogenous JA treatments mimicked *oswrky28* mutant phenotypes with inhibited root elongation. Another study showed that *osmed25* mutants had longer PRs than WT and exhibited JA-insensitive phenotypes. Also, S-type LRs density was lower while L-type LRs density was higher in *osmed25* mutants than WT. This result suggested that *OsMED25* participates in JA-mediated root development in rice (Suzuki et al. 2021).

Further studies related to root growth suggested that *OsACS1* and *OsACS2* are concerned with regulating RSA modification, transcription regulation of genes induced by Pi starvation, and cellular phosphorus homeostasis. The study has shown that *OsACS* mutants do not encourage LR growth in Pi-deficient condition, displaying the role of ethylene in LR production under Pi-deficiency (Lee et al. 2019). An additional study by Singh et al. (2020) stated that *OsJAZ9* modulates RSA in response to potassium deficiency, as *OsJAZ9* overexpressed plants showed shorter seminal roots with longer LRs. Moreover, LRs play an essential role in RSA, allowing plants to efficiently search for water and nutrients from the soil. However, in monocotyledonous plants, the mechanisms that regulate the evolution of LRs are poorly understood. According to a recent study, rice gene wavy root elongation growth 1 (*WEG1*) is involved in the formation of more extended and thicker LRs (L-type LRs) via asymmetric cell growth in the elongation region (Lucob-Agustin et al. 2020). In this regard, further study is still needed to identify the major genetic determinants governing RSA modification to engineer more branched root systems. In the current scenario, adverse environmental as well as edaphic factors affect the plant health and productivity. Studies discussed here provide a base for future studies to generate a robust root system. The root system with improved RSA can be generated by overexpressing the above discussed genes in root by advanced molecular biology tools or by plant breeding. These improved roots can be used for grafting with elite cultivar without disrupting the crop quality.

Hormonal regulation of RSA

The key biochemical and molecular elements of the intrinsic pathways include hormones, receptors, signaling components, and transcription factors (TFs). Interconnected networks of environmental stimuli receptors, downstream signal transduction, and TFs are extrinsic response pathways. In addition, many ecological perception and response network components are inter-regulated or shared between, intrinsically and hormonally regulated to respond to external signals (Table 3).

Phytohormone regulation of primary root initiation, elongation, and development

In monocots, PR is derived from the radicle which established during embryogenetic development and forms the first CRs-based fibrous root system. Auxin is one of the critical phytohormones involved in regulating root system development and RSA modification. Changes in auxin levels can control the different sets 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). *ARF*s recognize and bind to auxin-responsive elements (AREs) in target gene promoters, activating or suppressing transcription. AUX/IAA proteins negatively regulate auxin response genes under no auxin or low auxin levels by binding or inactivating ARF 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). Jing and co-workers investigated a *LATERAL ROOTLESS 2* (*LRT2*), which acts on AUX/IAA proteins. *LRT2* is a cyclophilin that efficiently controls cis/trans isomerization of peptidylprolyl. *LRT2* catalyzes the isomerization of the tandem proline residues of AUX/IAA necessary for recognition by *OsTIR1*. Also, the association of *LRT2* with *OsTIR1:OsIAA11* complex is increased by auxin and required to efficiently degrade AUX/IAAs (Jing et al. 2015). Perhaps, other modules of ARF regulation include miRNAs. For instance, the miR160 family plays a considerable role in improving PR and LR growth by improving ARF TFs, *ARF10*, and *ARF16* functionally repetitive and required for root cap cell formation and maintenance. The overexpression of *miR160* in rice also led to severe root cap defects, implying equivalent regulatory pathways in monocots (Wang et al. 2005). Moreover, the 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). A recent study reported that the mutation of *OUR1*/*OsbZIP1*, a member of the leucine zipper TF family,

Table 3 Hormones and their involvement in root growth and development

Phytohormone	Function	References
Auxin (IAA) NAA	Increases CRP initiation and outgrowth	Sreevidya et al. (2010)
2,4-D	Increases CRP initiation through cell division (but does not promote cell elongation and root outgrowth)	Sreevidya et al. (2010) and Debi et al. (2005)
Kinetin, trans-zeatin	Stimulates elongation of LRs	Sreevidya et al. (2010), Ashikari et al. (2005), Jain et al. (2006), Kurakawa et al. (2007) and Debi et al. (2005)
Kinetin, trans-zeatin	Stimulates CRP formation	Debi et al. (2005), Hirose et al. (2007) and Zhao et al. (2009)
Gibberellins (GA3)	Interacts with ethylene to promote CRP outgrowth and elongation	Steffens et al. (2006)
Gibberellins	Controlling root development by regulating local auxin biosynthesis and polar auxin transport by modulating the expression of OsYUCCA6 and PIN	Li et al. (2020a, b)
Ethylene	Promotes CR formation at submerged nodes–internodes	Lorbiecke and Sauter (1999)
Ethylene	Promotes CR emergence at submerged nodes through induction of epidermal cell death	Mergemann and Sauter (2000)
Strigolactones (SLs)	Promote CR elongation by inducing meristematic cell division	Arite et al. (2012)
Abscisic acid	Promotes root hair elongation by regulating auxin homeostasis in root tips	Wang et al. (2017)
Auxin and melatonin	Regulates root architecture by modulating auxin response in rice	Liang et al. (2017)

promotes root development by suppressing auxin signaling in rice (Hasegawa et al. 2021). As a result, rice is a suitable model for studying how the auxin-dependent gene regulatory network has developed to control post-embryonic root growth.

Phytohormone regulation of initiation and elongation of CRs

CRs are adventitious roots and specific to monocotyledons. CRs are also designated as nodal roots or roots that grow from shoots and account for most of its fibrous root system. CRs can be divided into adventitious roots and post-embryonic CRs. As soon as seedlings begin to grow, adventitious roots evolve from the coleoptile node of PR (radicle). When seedlings are pulled out, most of the roots get torn off, but very soon fresh post-embryonic CRs evolve and persist for whole plant life (Hochholdinger and Zimmermann 2008). All CRs (embryonic and post-embryonic) and seminal PR may be primary order roots because they emerge from the central plant stem and not from another root like LRs. However, most of the studies regarding root development focused on PR and LR in dicots like *Arabidopsis*. Until now most of the studies regarding genetic control of CRs development have been derived from research on *Arabidopsis* roots. Recent studies on rice and maize mutants suggest that the initiation and progression of CRs are regulated by auxin-mediated signaling, equivalent to PR and LR development in *Arabidopsis* (Rebouillat et al. 2009). However, the role of specific genes in developmental pathways can differ in the rice root system. Like *Arabidopsis* root development auxin signals are necessary for the equitable and asymmetric division of parenchyma cells which lead to formation of CRs. On the other hand, CK played a secondary role in promoting CR formation by antagonizing auxin-based signaling pathways. For example, *WUSCHEL-RELATED HOMEOBOX11* (*WOX11*), 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 CR development and 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 signaling to regulate cell division rates in CRP. Another gene *RR2* operate as a negative CK signaling regulator that represses CR emergence by repressing meristem cellular proliferation (Zhao et al. 2009).

Studies on genetic and physiological processes also suggest the regulation of CRP formation and the production of CRs in stem nodes in response to environmental impacts (Mergemann and Sauter 2000). For instance, submergence-induced ethylene accumulation kills epidermal cells above CRP in deepwater rice accessions, allowing CRs to emerge through the epidermis of submerged nodal branches. CRP development is regulated by auxin as a study suggested that *OsPIN1* RNAi-knockdown resulted in the discontinued development of CRP in rice (Xu et al. 2005). Recent studies suggest that GA is involved in CRP emergence and elongation with ethylene as a synergistic regulator. Furthermore, ABA acts as an inhibitor of GA and ethylene signaling pathways (Steffens and Sauter 2005). Similarly, strigolactones play a role in the positive regulation of CR elongation, potentially through modulation of auxin translocation and promoting meristematic cell division in the root (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*). This reduced cell distribution could be due to local auxin levels in SL-insensible rice mutants where SL modulation affects the numbers of the meristem as seen in PRs for homologous *Arabidopsis* genes (Arite et al. 2012). Even though numerous genes have been studied involving CR development in rice, our understanding of this process remains disorganized, and understanding its molecular mechanisms requires significant elucidation.

Role of jasmonic acid, salicylic acid, and brassinosteroids in RSA modification

Jasmonic acid and salicylic acid are also involved in regulation of root growth. JA increases auxin levels by inducing the expression of auxin biosynthetic gene *ASA1*, which leads to root growth inhibition (Sun et al. 2009). The potential interaction between JA and auxin signaling also occurs via *AUXIN RESISTANT 1* (*AXR1*). In addition to its role in auxin signaling, *AXR1* also shows JA-mediated root growth inhibition (Tiryaki and Staswick 2002). Taken together, the above reports suggest that JA signaling is linked to auxin homeostasis, leading to root growth inhibition. Similarly, SA can also modulate root growth by regulating root apical meristem (RAM) activity. As the 30 µM SA reduces the number of cells expressing cell division marker *CYCLIN B1;1* (*CYCB1;1*) in the proximal meristem which causes the decreased root length (Pasternak et al. 2019). A treatment with higher SA concentrations (150 µM) results in enlarged proximal meristem cells without any *CYCB1;1* signal in more than a half of treated roots (Pasternak et al. 2019). SA regulates root growth in interaction with plant hormones. Concentration-dependent effects on root growth were also shown for auxin (indole-3-acetic acid, IAA), ABA, and brassinosteroids (Bagautdinova et al. 2022). SA also cross-talks with CK for root growth regulation (Argueso et al. 2012). For instance, CK, benzyl adenine (BA), inhibits PR growth in the wild type *Arabidopsis* at 50 nM, whereas in SA biosynthesis mutant (eds16), this occurs at a lower (5 nM) concentration. In addition, endogenous auxin controls apoplast acidification and alkalization, which are required for the activation or repression of root cell elongation, respectively (Barbez et al. 2017). For ethylene, CK, and JA only inhibitory effects on root growth were demonstrated, while for gibberellins only stimulating effects on root growth were shown in various species (Kudo et al. 2012). Brassinosteroids (BRs) are steroidal hormones that play an essential role in many aspects of plant growth. BRs, in low concentrations, promote root growth through the control of root meristem size and cell elongation (Lv et al. 2018 and promote LR initiation (Bao et al. 2004). Moreover, treatments of rice seeds with BRs may also affect the root length as well as the LR density in rice (Vázquez-Glaría et al. 2021).

Root microbiota affect root system development and RSA modification

The soil contains an exceptionally diverse microbiome, susceptible to nutrient availability that is influenced by soil properties, including moisture, pH and nutrient content. Recent deep sequencing techniques suggest soil type significantly impacts rhizosphere microbial communities compared to plant genotype (Xu et al. 2020). These findings suggested that soil properties are essential in shaping the microbial communities. In addition to the soil type, the nature and composition of root exudate by plants roots are also likely to influence microbial communities (Dennis et al. 2010). Plants exudate contain polysaccharides, sugars, aromatic acids, amino acids, fatty acids and aliphatic acids and help in plant–microbe interaction by attracting and sustaining microorganisms (Hu et al. 2018; Venturi and Keel 2016; Vives-Peris et al. 2019). These microbes reinforce plant growth by nutrient solubilization, humification of recalcitrant organic matter and improving nutrient uptake and distribution; (Tfaily et al. 2014); averting pathogens' entry and colonizing in plants' roots (Enebe and Babalola 2019); harmonizing host immunity via induced systemic resistance (ISR); (Bruno et al. 2020) and regulating signaling 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 and chitin hemicelluloses and proteins (Lugtenberg et al. 2017). These enzymes improve soil fertility by releasing organic nutrients like N, P, and K into the plant rhizosphere (Doni et al. 2019).

Apart from this, several rhizospheric microorganisms are able to modify RSA to improve nutrient and water exploration through distinct mechanisms (Vacheron et al. 2013). The central mechanism of microbial modulation of RSA encompasses the altering hormonal balance in plant roots either by secreting plant hormones or producing secondary metabolites interfering with hormonal pathways concerned with root development such as CK, auxin, ethylene, GA, and ABA (Ghosh et al. 2019). For instance, *Azospirillum brasilense*, *Klebsiella pneumoniae* and *Bacillus altitudinis* induces IAA production which resulted in increased root length. Microbes such as *Phomopsis liquidambari* B3 (Zhu et al. 2021), *Azospirillum brasilense* (Zaheer et al. 2022) and *Rhizophagus irregularis* (previously known as *Glomus intraradices*) (Mitra et al. 2021) affect the CK level which resulted in more LRs. As discussed above, these chemical signals alternatively affect the expression of root-related genes in plants. In addition, microbes have been shown to influence post-embryonic root development by modifying cell division and differentiation in 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. The proliferation of LRs and root hairs results in increased nutrient assimilation and improve shoot biomass. Another phenotype is an increase in shoot biomass accompanied by an increase in PR growth or deep root system. Both effects are dependent on nutrient type and availability. Plant root growth is also affected by microbial density and the distance between the bacteria and plant roots (Ortíz-Castro et al. 2009). One of the critical mechanisms reported by a study is 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 overall RSA of plants, usually accompanied by differences in endogenous plant responses. Because several rhizospheric microbes have been identified as producers of these hormones, it is tempting to speculate that microbial hormones may directly induce root system changes. The different studies are summarized in Table 4, and the impact of root microbiota on RSA in rice is illustrated in Fig. 2.

Impact of microbial phytohormone on RSA improvement

Rhizospheric microbes can modify RSA and the structure of root tissues mainly through their ability to interfere with plant hormonal balance. Changes in RSA may result from interference of microbes with the main hormonal pathways involved in regulating plant root development: auxin, CK, ethylene, gibberellins, and ABA. In addition, phytohormone production and secretion, such as indole-3-acetic acid (IAA) by rhizospheric microbes, becomes a significant player in RSA reconfiguration. Finally, microbes can also alter the signals that control plant root morphogenesis and modulate RSA (Ortíz-Castro et al. 2009). Thus, using rhizospheric microbes promises to be a novel and environmentally friendly method of improving RSA and ultimately ensuring a long-term strategy for improving crop quality and yields.

Impact of microbial 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 well-studied auxin produced by a 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 PR, while higher IAA levels encourage LR formation, enhance root hair formation, and reduce PR growth (Zhang et al. 2018a, b). Microbial metabolites like 2,4-diacetyl phloroglucinol (DAPG) and nitric oxide can also stimulate RSA modification in plants by interfering with the auxin synthesis pathway. DAPG is a well-known natural phenolic compound found in some specific strains of gram-negative bacteria and is responsible for the antimicrobial properties of *Pseudomonas fluorescens* (Weller et al. 2007). DAPG serves 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 signaling pathway can be interfered with by DAPG, consequently modifying RSA (Brazelton et al. 2008).

The rice endophyte *Phomopsis liquidambari* B3 induces auxin and CK production as the endophyte's inoculation in rice root significantly enhanced auxin, CK, and ethylene levels in plant under varying nitrogen levels (Li et al. 2018b). Additionally, *Azospirillum brasilense* has nitrite reductase activity and produces nitric oxide during root colonization involved in regulating LR development by modulating the auxin signaling pathway (Rondina et al. 2020).

CK is the next most crucial phytohormone that regulates RSA in rice by CK signaling and CK interaction with auxin signaling (Neogy et al. 2020). Plant growth has been stimulated by inoculating plants with rhizospheric microbes that produce CK (Li et al. 2020a; Kieber and Schaller 2018). CK 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). However, the role of CK synthesis by PGPR in RSA alterations is yet to be speculative.

Ethylene

Another important phytohormone that inhibits root elongation is ethylene, which induces senescence, abscission of different organs, and contributes to fruit ripening (Iqbal et al.

Table 4 Effects of microbes in modulating root system architecture

Microbes	Function	Effects	References
Azospirillum brasilense	IAA production	Increased in root elongation, root surface area, root dry matter and development of LRs	El-Khawas and Adachi (1999)
Azospirillum brasilense Sp245	Enhances the expression of ethylene receptors	Increasing numbers of LRs	Vargas et al. (2012)
Azospirillum brasilense CA-10	IAA production	Enhanced PG (polygalacturonase) activity in roots, better root morphogenesis	Sekar et al. (2000)
Azospirillum lipoferum 4B	Alters rice secondary metabolite profiles	Increased the number of roots, total root length and root surface	Chamam et al. (2013)
Azospirillum B510			
Azospirillum irakense	Induces polygalacturonase expression	Modification of root tissue structural properties	Sekar et al. (2000) and Dobbelaere et al. (2002)
Acanthamoeba castellanii (Protozoa) and *Betaproteobacteria*	Nutrient solubilization	Elongated (L-type) laterals, branched root systems	Kreuzer et al. (2006)
Bacillus altitudinis strain FD48	IAA production	Modifies the early events of root architecture	Ambreetha et al. (2018)
Bacillus altitudinis (strain FD48)	Modulates the expression of AUX/IAA family genes	Modifies the root architecture	Ambreetha et al. (2018)
Bacillus amyloliquefaciens RWL-1	ABA	LR development	Shahzad et al. (2017)
Bacillus amyloliquefaciens	Induces the expression of auxin-responsive *OsASR6*	Root improvement	Agarwal et al. (2019)
Burkholderia pyrrocinia (R-46)	Auxins, siderophore production	Improves root length and diameter	Ferreira Rêgo et al. (2014)
Herbaspirillum seropedicae	Improves the expression of auxin and ethylene-responsive genes	LR initiation	Brusamarello-Santos et al. (2012)
Klebsiella pneumoniae	IAA production	Increased in root elongation, root surface area, root dry matter and development of LRs	El-Khawas and Adachi (1999)
Phomopsis liquidambari B3	Enhanced auxin, cytokinin, and ethylene level	Nitrogen-mediated growth of LRs	Li et al. (2018b)
Pseudomonas fluorescens	Stress-related induction	Increased root length	Kandasamy et al. (2009)
Pseudomonas putida REN5, *Pseudomonas fluorescens* REN1	IAA, ACC deaminase, siderophore production	Increase length, fresh weight and dry weight, branching	Etesami and Alikhani (2016)
Pseudomonas fluorescens (R-55)	Auxins, siderophore production	Improves root length and diameter	Ferreira Rêgo et al. (2014)
Glomus intraradices (Rhizophagus irregularis)	Affects the expression of *OsCYCLOPS1* *OsLRT1* and also alters auxin, ABA, CK, ethylene concentration	Increases in root mass, thickness, length, and LR number, induces the formation of long LRs	Yano et al. (2008) and Gutjahr et al. (2009)
Rhizophagus irregularis	Perception of chitin oligomers	Increases growth of LRs	Chiu et al. (2018)
Rhizosphere isolates PGG2 and PGB4	IAA Production	Increases root length	Ashrafuzzaman et al. (2009)
Trichoderma koningiopsis NBRI-PR5 and T. asperellum NBRI-K14	Altered lignification patterns and packing of the sclerenchyma and exodermis cells	Stimulated the root growth	Anshu et al. (2022)

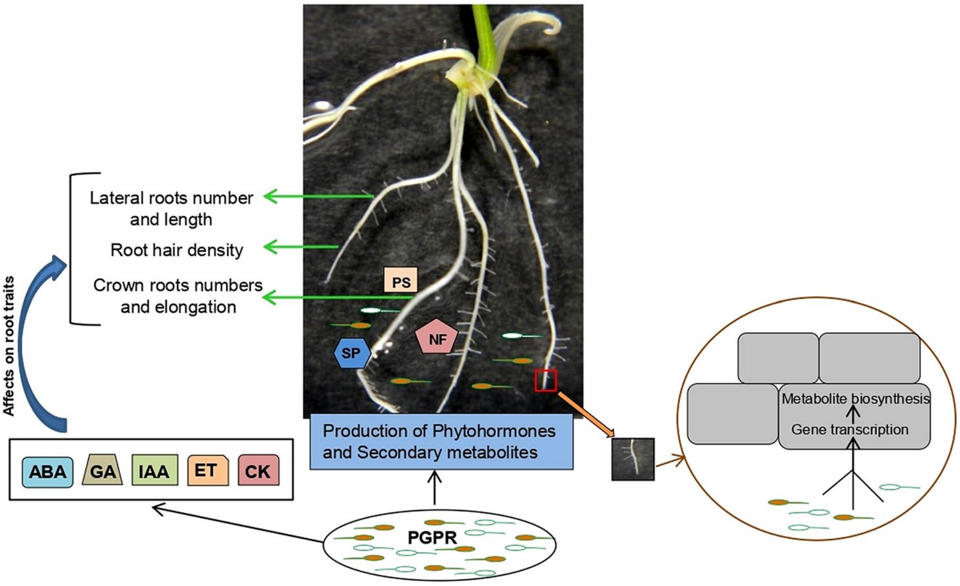

Fig. 2 Impact of root microbiota on RSA in rice. Rhizospheric microbes can modulate root growth and development via the production of secondary metabolites and phytohormones. Microbes can influence plant nutrition by phosphorus solubilization, nitrogen fixation and siderophore production, and alter gene transcription and metabolite biosynthesis in plant cells that affect root physiology. CK, cytokinin; ET, ethylene; GA, gibberellic acid; IAA, indole acetic acid; NF, nitrogen fixation; PS, phosphate solubilization; SP, siderophore production

2017). Apart from senescence, abscission and fruit ripening, ethylene also modulates plant defence pathways (Yang et al. 2017). Rhizospheric microbes affect ethylene levels in plants by degrading ethylene precursors. These microbes secrete 1-aminocyclopropane-1-carboxylic acid deaminase (ACCd) coded by a gene *acdS*, which degrades ACC (immediate precursor of ethylene) into α-ketobutyrate and ammonium. Microbes use ammonium as a carbon and nitrogen source (Kim et al. 2020). Thus, microbial ACCd activity is thought to reduce root ethylene production by reducing the abundance of ethylene precursor ACC (Gamalero and Glick 2015), thereby decreasing the repressive effect of ethylene on root growth. Meanwhile, minimal impacts on RSA were seen when plants were infected with an acdS bacterial mutant or when plants impaired their ethylene signaling pathway (Contesto et al. 2008; Galland et al. 2012). Thus, it implies that ethylene is involved in RSA modification but not as a significant participant. Overall, the physiological significance of bacterial ACCd function requires further investigation.

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. 2020b). It is well-studied that ABA plays a significant role in drought tolerance; however, it also plays a distinct role during LR development. 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). Gibberellins, particularly GA3, influence rice root elongation and modulate local auxin production and polar auxin transport (Li et al. 2020b). Gibberellins are produced by many microbes, including *Achromobacter xylosoxidans*, *Acinetobacter* spp., *Azospirillum* spp., *Bacillus* spp., *Herbaspirillum seropedicae*, *Gluconobacter diazotrophicus*, and *Gelhizobia* (Dodd et al. 2010). The application of GA in rice at an amount comparable to that produced by *Azospirillum* endorses root growth (Bottini et al. 2004). In addition to their involvement in RSA modification in plants, these hormones have also shown engagement in plant defensive systems. However, even though PGPR-mediated hormone production has been well studied, the genetic variables involved in their biosynthesis are mostly unknown. As a result, bacterial origin hormones in RSA modulation by interaction or hormonal balance in plants have not been fully understood.

Role of polyamine and GABA in plant–microbe interaction and RSA modification

Plant growth substance like GABA, and polyamines (PAs) also affect the plant–microbe association which in turns leads to the RSA modification. Studies suggest that PAs enhance nodule tolerance to the oxidative stress caused by the establishment of the symbiotic interaction. Research on *Lotus japonicus* showed that the expression of PA biosynthesis genes *LjSPDS* and *LjSPMS* were higher in early stage of nodulation (Efrose et al. 2008). In addition, metabolites derived from PAs catabolism also have important role in nodulation. For instance, GABA (γ-Aminobutyric acid) produced from 4-amino butanal has a dual role, acting as signaling molecule during plant-bacteria communication and functioning as an amino acid precursor in bacterial metabolism (Sulieman and Schulze 2010). In this trend, feeding with

GABA into the phloem sap of *Medicago truncatula* plants causes a short-term increase in nodule activity and a remarkably increment in the amino acid and organic acid content in nodules (Sulieman and Schulze 2010). The mycorrhizal-plant root symbiosis is also affected by PAs and GABA in the same manner. For example, PAs increases the mycorrhizal symbiosis by increasing total free PA pools in *Lotus glaber* following colonization by *Rhizophagus irregularis* (Sannazzaro et al. 2007). In turn *Rhizophagus irregularis* modulate the expression of *OsCYCLOPS1, OsLRT1* and alter the phytohormone such as auxin, CK, ABA and ethylene concentration. This altered phytohormone concentration increases root mass, thickness, length, and LR number. Thus, PAs and GABA increase the microbial colonization which leads to the modification of RSA.

Root microbiota impact on modification of root tissue structural properties in rice

Changes in plant gene expression by microbes occur via cell wall expansion or loosening of cell wall which is caused by changes in the ultrastructure of the root cell wall. For example, *Bacillus subtilis* GB03 enhances *Arabidopsis* development by generating volatile organic compounds found to influence the expression of 38 genes linked with the cell wall structure, in which 30 genes were responsible for expanding or loosening cell walls (Zhang et al. 2007). The endophytic microbe *Azospirillum irakense* induces polygalacturonase expression in inoculated rice roots (Sekar et al. 2000). Another study found that exogenous auxin application improves the role of induced polygalacturonase found in rice roots inoculated with *Azospirillum irakense* (Dobbelaere et al. 2002). PGPRs also play a significant role in changes in the chemical composition of the root cell wall. El Zemrany et al. (2007) conducted a study and observed that maize root cell walls had lower lignin content when inoculated with *Azospirillum lipoferum* CRT1 than uninoculated ones. Consequently, lower lignin content may promote cell elongation, which leads to root elongation. However, the impact of microbes on gene expression involving cell wall expansion and lignin deposition in rice root has not been well studied and needs further clarification.

Root microbiota impact on plant transcriptome in rice

The rice RSA could be improved by changing the hormonal level or expression of the root architecture-related genes discussed above. For instance, the up-regulation of *DRO1* in shallow-rooted rice cultivars correlates to root enhancement due to improved root growth angle, with even more downward root growth and high yield under drought conditions (Singh et al. 2021; Uga et al. 2013). Furthermore, inoculation with *Rhizophagus irregularis* and *Acanthamoeba castellanii* increased the number of LRs (Kreuzer et al. 2006). *Azospirillum lipoferum* inoculation increased the root numbers, root surface area, and total root length by altering the expression of root-related genes (Chamam et al. 2013). Moreover, a low level of IAA induces PR elongation, whereas high concentration promotes LR development, increases root hair formation, and decreases PR length (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 the expression of auxin-responsive genes. For example, *Klebsiella* and *Azospirillum* transformed tryptophan into IAA, which accounted for altering rice root growth (El-Khawas and Adachi 1999). Similarly, microbial isolates from rice rhizospheric soil produce IAA and influence rice seedling's 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, raising LRs while reducing 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). All ethylene receptors need to be accumulated to create a positive relationship between the plant and bacteria. In terms of endophytes, *Azoarcus* was found to have differential rice root colonization (Miché et al. 2006). A mild defensive response occurred in a less compatible interaction followed by the stimulation of proteins linked to pathogenesis and proteins sharing domains with receptors such as pathogen-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 thionin associated with defence (Brusamarello-Santos et al. 2012). These findings suggest that plant defence responses can be modulated during the colonization of endophytes and rhizospheric microbes. Furthermore, Plant-associated *Bacillus* spp. able to regulate auxin-responsive genes' expression level, modulating auxin concentration in the root and thus changing the early stages of root system architecture in rice seedlings. In addition to bacterial species, an AM fungus, *Rhizophagus irregularis*, causes the host to develop more LRs (Chen et al. 2018), 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. Furthermore, another study reported that *R. irregularis* triggers plant signaling responsible for the induction of LR formation, involving a receptor kinase *CHITIN ELICITOR RECEPTOR KINASE 1* (*CERK1*) in rice (Chiu and Paszkowski 2020; Chiu et al. 2018).

Furthermore, microbes can alter the composition and volume of metabolites and influence root exudation. For example, when inoculated with *Herbaspirillum seropedicae*, rice plants showed a higher 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). In addition, a relatively high concentration of quaternary compounds, glycine betaine, was observed in rice infected with *Pseudomonas pseudoalcali* (Jha et al. 2011). Thus, establishing beneficial associations requires mutual recognition and substantial coordination of plant and microbial responses in controlling RSA and improving crop production and quality.

Concluding remarks and future perspectives

Significant progress has been made to improve understanding of the genetic, hormonal and microbial regulation of root development and RSA modification in rice. Detailed research on genes controlling root traits will open the door for additional in-depth molecular and genetic studies of rice and other cereal root system development. Despite the identification of numerous genes involved in root growth, our understanding of molecular mechanisms behind CR growth, root elongation, LR development and root hair formation is still unsatisfactory. Most investigations focus on identifying through mutants or QTL analyses of particular genes that restrict our overall understanding of root growth development mechanisms. Integrating functional genomics, proteomics, transcriptomics, and phenomics will significantly expand our knowledge of the molecular mechanisms underlying RSA modification. However, several genes involved in RSA have been identified, still a limited data is available about how these genes could be utilized to strengthen the root system through breeding or genetic engineering techniques. Cloning genes from QTL analysis is a viable method for identifying potential candidates for molecular breeding; nevertheless, identifying QTLs with minor effects. Another primary strategy for improving crops is genetic manipulation. It offers the chance to modify specific genes for particular requirements. The CRISPR/Cas9 method allows for more focused genome editing of RSA-related alleles to improve locus performance. Additionally, using novel technologies to examine RSA in natural soils and complex environments, such as magnetic resonance imaging and X-ray micro-computed tomography, will allow for a more accurate assessment of root traits and identification of associated genes.

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

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Declarations

Conflict of interest All authors declare that they have no conflict of interest.

Ethical approval The manuscript does not involve any animal study.

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