Review

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Communication between Plants and Rhizosphere Microbiome: Exploring the Root Microbiome for Sustainable Agriculture

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Abstract: Plant roots host various microorganisms around and inside their roots, known as the root microbiome. To become healthy and productive, plants should keep under surveillance niches around the roots to recognize disease-causing microbes and similarly exploit the services of beneficial microorganisms in nutrient acquisition, stress mitigation and growth promotion. Here we presented the communication strategies between plant roots and root-associated microbes in improving plant growth and yield. Understanding how plant root and root-associated microbes communicate is vital in designing ecofriendly strategies for targeted disease suppression and improved plant growth that will help in sustainable agriculture.

Keywords: plant-microbe interactions; signaling molecule; root exudate; disease suppression; crop production

1. Introduction

In time past microbial ecologists used to face high challenges in investigating multifaceted microbial societies. However, today the tide has changed thanks to the methodological advances like the high throughput deoxyribonucleic acid sequencing machinery that provides comprehensive information on the composition and structure of microbial groups [1–3]. Though, the bulk of the investigative practice emphasis a single property of the communities being examined. For instance, studies unfolding and relating the structure of microbial societies often concentrate on distinct lineages present or the total numbers of taxa in a given sample (alpha diversity) or between samples (beta diversity) [4,5]. The same attention has not been given when using sequence data to decipher indirect or direct collaboration among microbial taxa and plants [6–8]. With the availability of many sequence datasets from environmental samples, the focus now is to go beyond alpha and beta diversity and look more at the interactions between microbial taxa and their host [9,10]. Studying interactions between taxa across intricate and different inhabitants like plant microbiomes will aid in establishing useful roles or ecological niches engaged by beneficial microorganisms in promoting plant health [11–13]. Plants harbor diverse groups of microorganisms that live inside and outside their roots. The root microbiome is the active community of microbes connected with plant roots, be it inside or around the root, which is extensively involved in plant wellbeing and serves as a receptacle of extra genes that plants can acquire when required [14].

The concept and relevance of the root microbiome to plant health will improve our insight into the colossal power of these tiny giants in ecosystem function. The microbial communities and interaction networks inside the root, root surface and bulk soil are distinct, although the similarity in species structure can be seen [15,16]. With the use of bar-coded pyrosequencing of rRNA genes, NR Gottel, HF Castro, M Kerley, Z Yang, DA Pelletier, M Podar, T Karpinets, E Uberbacher, GA Tuskan, R Vilgalys, et al. [17] revealed that *Populus deltoides* root endophytic bacterial and fungal communities are discrete groups rather than opportunistic subgroups of the rhizosphere. Significant differences

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between the bacterial interaction networks and diversity of *Agave lechuguilla* rhizosphere and bulk soil were also reported by NE López-Lozano, A Echeverría Molinar, EA Ortiz Durán, M Hernández Rosales and V Souza [18] when they used the 16S rRNA gene sequence from *Agave lechuguilla* rhizospheric and bulk soil samples. Root microbiome is a significant driver for plant yield, health, and ecosystem functioning because it is the intersection point between a plant and the ecosphere. Furthermore, it is accountable for key functions such as nutrient acquisition and signals vital to plant development. Nevertheless, how plant roots and their associated microbes communicate to enhance plant development is incipient. Understanding the communication of plant roots with microbial communities will provide sustainable solutions in raising agronomic crop production. Thus, this review presented communications between root microbiome and plant root, the mechanism employed by root-associated microbes in promoting plant growth and applications of plant root collaborations and root microbiome in improving plant growth and yield through stress mitigation, disease suppression and nutrient acquisition.

2. Communication between root microbiome and plant root

The rhizosphere of plants has evolved into diverse and complex microbial groups with different information-processing systems involved in plant enlargement and growth, and plant defense response [19]. These information-processing systems and signals that are involved in the recognition of beneficial organisms in the rhizosphere and counteracting immune detection are still poorly understood [20]. As a result, recent research on immune signaling mediated by plant growth-promoting rhizobacteria is gaining considerable interest.

Plants induce substantial selection pressure on the development of the rhizobiome are, achieved by the emission of exudates from plant roots. The secreted root exudates contain compounds of different kinds that attract the development of specific plant microbiota. The attracted organisms utilize these exudates as sources of energy and multiply in the vicinity [20]. Plant and microorganisms' ability to communicate before initiating somatic contact is crucial. It helps each partner to take full advantage of the association and alleviate the threat of damage. It also lets plants regulate the microbe they interact with throughout their development and growth process [21]. The formation of these relations entails synchronized crosstalk among the plant and a well-suited microbe that occurs in signals from the interacting organisms [21].

Plants have developed a myriad of communication systems to integrate information from the environment and to actively respond to abiotic and biotic factors [22]. They have equally developed a means of communication between plants and their associated microbes through transkingdom signaling [22]. Communication in the rhizosphere is highly sophisticated and controlled by a wide range of specialized exudates and metabolites. These exudates and metabolites end up in the altered gene expression in one or both of the interacting partners [20]. These exudates, mostly nutrients, are used by the rhizosphere organisms to colonize plant roots. This sophisticated form of communication results in plant growth promotion, control of soil-borne pathogens, availability of nutrients, biofilm formation and accumulation of soil microbes [20]. Nevertheless, numerous compounds in the rhizosphere, produced by plants or microbes, could likewise act as signals for communication [23].

Signals are low molecular-weight diffusible compounds produced by one organism and recognized by another organism that elicit, at low concentration, a specific response in the latter through a signal-transducing cascade [23]. Upon signal recognition, the molecules can be up or down-regulating gene expression and alter the physiology and activities of the receiving organism [24,25]. In the rhizosphere, there is a numerous number of these molecules whose concentration varies according to the distance from the point of emission. These deposits are collectively known as rhizodeposits that include sloughed-off tissue and cells, H^+ efflux, CO_2 from cell respiration, mucilage, intact root border cells and proteins [26]. The low molecular weight organic compounds, also known as root exudates, contain amides, sugars, phenolic, aromatic and amino acids. They facilitate communications and function as chemical attractants and repugnant that drive the root microbiome [27]. The recognition of these signals is important in driving the plant-microbe networking system. Plant-microbe communication through signal molecules can influence the stimulation and suppression of gene expression in both partners. This communication protects plants against abiotic and biotic stresses, enhanced nutrient acquisition and availability, and promotes plant growth and health [25]. With these root exudates, plants can interact with microbes to stimulate succor in environmental adjustment to relieve stresses such as drought-restrictive nutrient procurement, metal toxicity, and pathogen spell [28]. This synergy leads to more intricate collaborations, inducing plant growth and resource competition. Similarly, signal molecules are crucial for root colonization by rhizospheric microbes and for establishing plant-microbe interactions. *Pseudomonas fluorescens* establishes interaction and root colonization with tomato by the o-antigenic side chain of bacterial lipopolysaccharide [29], while the initial host recognition in cereals is achieved by the major outer membrane proteins (MOMP) in *Azospirillum brasilense* [30]. Plants also employ the rhizophagy cycle/process in recruiting beneficial microbes by producing the exudates they feed on. The root-associated microbes employ direct or indirect strategies to impact plant health status and growth [31]. Direct strategies include nutrient acquirement, phytohormones production, and phosphate solubilization. Indirect strategies occur by eliciting plant immune responses, preventing plant pathogens from proliferating and competing with their resources (Figure 1) [32]. For example, IA Stringlis, K Yu, K Feussner, R de Jonge, S Van Bentum, MC Van Verk, RL Berendsen, PA Bakker, I Feussner and CM Pieterse [33] showed that the probiotic-plant-rhizobacteria-collaboration elicited the root-specific transcription factor MYB72 and further led to the production and emission of MYB72-controlled β-glucosidase BGLU42-reliant scopolin and scopoletin, respectively, resulting in a well-established niche for microbial consortiums and resistance profits for the host plant against *Verticillium dahlia* and *Fusarium oxysporum* (soil-borne fungal pathogens). Bacterial assemblages connected with plant roots contribute a vital role in subduing soil-borne pathogens, and multispecies probiotic associations could boost disease suppression efficiency. For example, J Hu, Z Wei, V-P Friman, S-h Gu, X-f Wang, N Eisenhauer, T-j Yang, J Ma, Q-r Shen, Y-c Xu, et al. [34] reported that the addition of *Pseudomonas* consortia in *Solanum lycopersicum* rhizosphere microbiome reduced *Ralstonia solanacearum* concentration and lessened the disease incidence because of the meddling and increased resource competition with the pathogen. Similarly, an increase in the *Pseudomonas* consortia richness resulted in increased plant biomass and effective absorption of nutrients in *Solanum lycopersicum* plants.

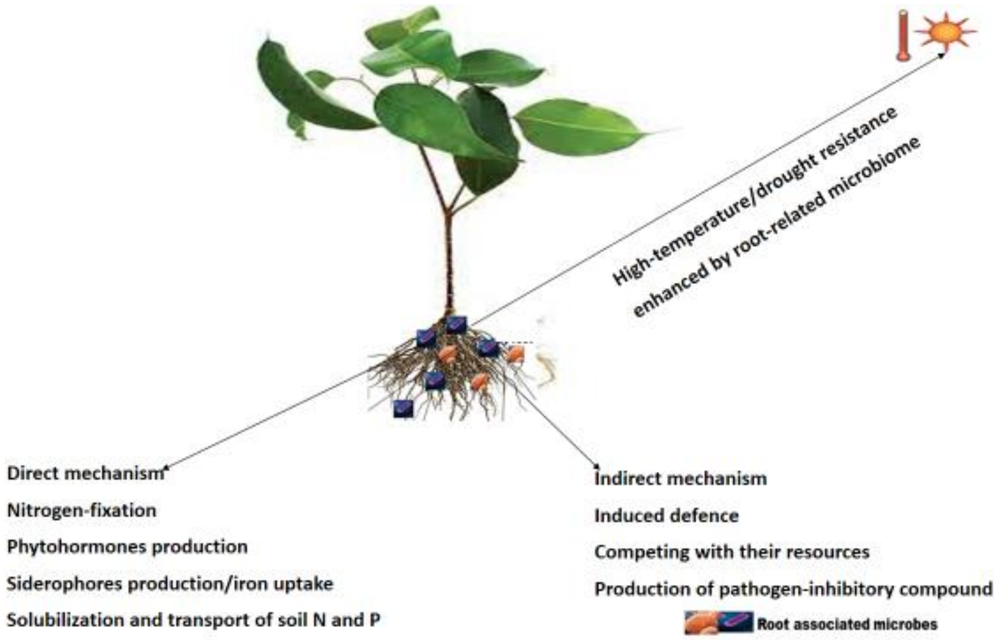

Figure 1. mechanisms employed by plant root-associated microbes in improving plant health.

Root-related microbes likewise produce communicating compounds ranging from antibiotics, organic acids, volatile signals, phytohormones, extracellular enzymes and quorum sensing molecules (QSM) [35]. These compounds aid plant roots associated microbe's relationship that facilitates plant growth. For instance, N-acyl-L-homoserine lactones (quorum-sensing molecules) were reported by R Ortiz-Castro [36] to influence the lateral root formation, root system architecture, primary root growth, and root hair development of *Arabidopsis thaliana* in their post-embryonic stage. Bacterial strains such as *Bacillus amyloliquefaciens* L3 use-communicating molecules like volatile organic compounds to stimulate reactions in fungi and plants and recruit induced systemic resistance (ISR) in plants, consequently eliciting expression of defense genes that mitigate the negative effect of viruses, oomycetes, bacteria, and fungi on plants [37–40]. Root-resultant exudates, apart from aiding plant fitness and longevity, also profit microorganisms that use them as a resource (carbon-rich products with other nutrients) that support microbial multiplication [41–43].

Alongside different rhizodeposits produced in the rhizosphere, different hormones are also produced that aid plant-microbe communication cascades [25]. These hormones include abscisic acid, auxin, cytokinins, gibberellin and peptide hormones that regulate plant growth and development. Several plant growth-promoting rhizobacteria have been reported to produce indole acetic acid in chemically defined medium with tryptophan precursor [44,45]. Auxin production enhances seed germination, nutrient uptake and root growth and development [25,46]. For instance, cytokinin was found to stimulate cell division, inhibit root elongation and affect root hair development [47], while gibberellin was reported to alter many physiological and developmental processes in plants by promoting seed germination, stem elongation, flowering and fruit setting in plants [48]. Gibberellin also facilitates cell-to-cell communication [25].

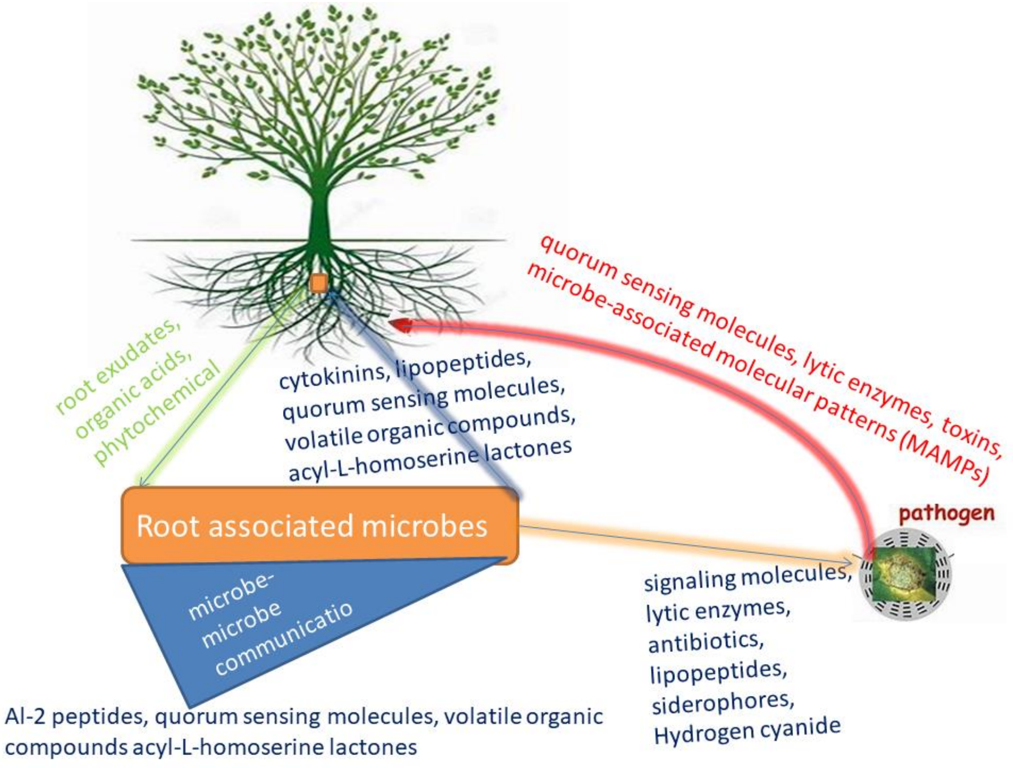

Figure 2. Plant root-root associated microbe communication.

3. Applications of plant root-associated microbes in improving plant growth and yield

The increase in farming productivity to meet the high food expectations of the human populace is a problem of great worry for all nations. Chemical fertilization to boost crop production has long alleviated these worries [49]. However, the prolonged misused of chemical fertilizers in farming has negatively imparted the ecosystem [50] and has led to the call for ecofriendly approach to boost crop production and to increase plant production is to make plant healthy [51,52]. To be healthy, plants must mitigate environmental disturbances. The plant root-associated microbes in mitigating abiotic and biotic stress, nutrient acquisition, and growth promotion need to be promoted to enhance sustainable agriculture [53,54].

3.1. *Root microbiome role in abiotic stress tolerance*

Crops are often exposed to physical stresses such as soil salinization, submergence, extreme temperatures, nutrient imbalances, drought, to mention but a few [55]. The fact that these stresses will rise in nearby days makes it a big concern as plant growth, yield, and productivity will be hindered. To overcome these abiotic stresses, plants must undergo adaptive modifications or solicit the help of beneficial microbes to live and will promote plant function [2,56]. Root-associated microbes can stimulate the growth and defend the host via many molecular pieces of machinery in abiotic stress circumstances (Table 1). CM Ribeiro and EJBN Cardoso [57] revealed that strains of *Bacillaceae, Enterobacteriaceae,* and *Pseudomonadaceae* isolated from the *Araucaria angustifolia* root were tremendous plant growth-promoting bacteria. Some of these bacterial strains are P-solubilizing microbes that help the crops tolerate drought, salt, and extreme temperature conditions through the production of numerous phytohormones, antioxidants, exopolysaccharide, 1-aminocyclopropane-1-carboxylate deaminase, enrichment of nutrient uptake, many volatile compounds, and initiation of the buildup of osmolytes. They also help in the regulation of stress-responsive genes [58,59]. Under drought settings, T Yuwono, D Handayani and J Soedarsono [60] found that osmotolerant rhizobacterial inoculated with rice increased root and shoot dry weight. It was also proven that under stress conditions, these isolates had what it took to produce betaine, signifying that the drought tolerance was because of the increase in osmolyte. They also revealed that the rhizobacteria-plant interaction led to indole acetic acid production. Under drought experiment conducted by JM Ruiz-Lozano, C Collados, JM Barea and R Azcón [61] showed that co-inoculation of *Glomus mosseae* and *Bradyrhizobium japonicum* in drought-stressed soybean plants resulted in increased leghemoglobin content, acetylene reductase activity and protein content by 25%, 112% and 15% respectively compared with well watered soybean plants and plants colonized by *Bradyrhizobium* alone.

Root associated microbes also use other strategies to retain ion homeostasis in plants facing salt stress. For instance, bacterial exopolysaccharides fix to Na^+, and confine Na^+ inflow into roots. They produced volatile organic compounds (VOCs) during stress conditions so that VOCs can activate high-affinity K^+ transporter (HKT1) reduction in root and stimulate HKT1 in shoots, thereby restraining Na^+ entrance into roots and easing shoot-to-root Na^+ retransmission. The K^+/Na^+ ratio is increased by arbuscular mycorrhizal fungi by immensely improving Ca^{2+} and K^+ absorption and eluding the movement of toxic Na^+ under salty circumstances. Furthermore, for effective water assimilation in saline-strained plants, root closely associated microbes control the processes of genes encrypting the plasma membrane integral proteins to aquaporin activity [62–64]. Boosting the antioxidative systems in plants for ROS (reactive oxygen species), scavenging, and production of polyamines and proline are also part of mechanisms employed by root-associated microbes for mitigating salt stress in plants. A Bano and M Fatima [65] induced salt stress conditions and co-applied *Pseudomonas* and *Rhizobium* at the seedling stage of maize. Their findings showed that under sodium chloride conditions alone, a harmful effect on maize growth and development was seen. Furthermore, improved sodium chloride tolerance of maize upon co-inoculation with *Pseudomonas* and *Rhizobium* is linked with reduced electrolyte leakage, increased proline production and conservation of leaf water contents. The improvement of nutrient uptake to boost plant survival under salt conditions is another mechanism employed by root-associated microbes. For instance, the introduction of *Bacillus aquimaris* to wheat plants resulted in a substantial rise in phosphorus, nitrogen and potassium in wheat leaves (Upadhyay and Singh 2015). The root-associated microbe can also aid plants to withstand high or low-temperature conditions, either by increasing or decreasing anthocyanin, proline and sugar contents. [66] reported that under low temperatures, *Burkholderia phytofirmans* strain PsJN bacterized with grapevine plant, increased physiological activity and grapevine growth through a substantial increase in proline, starch deposition, carbohydrates and phenol contents compared with the control.

Table 1. Root microbiome and their mitigation on abiotic stress confronting plant.

Stress type	Root associated microbes	Plant host	Inoculated with	Activities	The effect on plant	Reference
Drought	*Enterobacter, Bacillus, Moraxella* and *Pseudomonas*	*Acacia arabica*	*Triticum aestivum* L	indole-3-carboxylic acid, Indole-3-lactic acid and indole-3-acetic acid production	Improvement in shoot length, tillers and number of spikelets and increases in spike length and seed weight of *Triticum aestivum* L .	[67]
Salt	*Halomonas* and one *Bacillus*	*Salicornia rubra, Sarcocornia utahensis,* and *Allenrolfea occidentalis*	Alfalfa	-	The total biomass of alfalfa increased, and root length were improved by 2.6 and 1.5 fold in *Halomonas* and *Bacillus* inoculated plants, respectively, compared with the uninoculated alfalfa	[68]
salt or drought	*Bacillus amyloliquefaciens* SB-9	grapevine	Grapevine plantlet	melatonin secretion, 5-hydroxytryptophan, serotonin, and *N*-acetylserotonin	Lessen the antagonistic effects of salt- and drought-induced stress by decreasing the secretion of malondialdehyde, O_2^- and H_2O_2 (reactive oxygen species) in roots.	[69]
Heavy metal stress	*Phialocephala fortinii, Rhizodermea veluwensis*, and *Rhizoscyphus* sp	*Clethra barbinervis*	*Clethra barbinervis* seedling	Siderophores	Improved K absorption in shoots and decreased the concentrations of Cd, Zn, Pb, Cu, and Ni in roots.	[70]
Heavy metal	*Penicillium ruqueforti* Thom	Solanum *surattense* Burm	Wheat seedling	indole-3-acetic acid	It led to low concentrations of heavy metals in the root and shoot. In increase nutrient uptake and higher plant growth,	[71]
Heat	*Thermomyces* sp	*Cullen plicata*	cucumber	Increase in antioxidant enzyme activities, soluble proteins, flavonoids, saponins, and total sugars.	It maintains the optimal quantum efficiency of photosystem II, water use efficiency, and photosynthesis rate and increases the root length, induced accumulation of saponins, total sugars, soluble proteins, flavonoids, and antioxidant enzyme activities	[72]
High temperature, salinity, and	Ochrobactrum cytisi strain IPA7.2	*Solanum tuberosum* L.	*Solanum tuberosum* L	.indole-3-acetic acid and type II 5-enolpyruvylshikimate-3-phosphate synthase	Improved the mitotic index of root meristem cells, the number of roots, the number of	[73]

glyphosate pollution					leaves and the length of shoots	
Flood	*Klebsiella variicola* AY13	soybean	soybean	Indole acetic acid production	Plants' growth improved with enriched chlorophyll content and quantum efficiency of chlorophyll fluorescence	[74]

3.2. Root microbiome role in nutrient acquisition

Most micronutrients and macronutrients important for plant growth are available in the soil in insoluble forms. Plants devise several mechanisms for the acquisition of these nutrients in the soil. The plant root microbiome enhances the uptake of major micronutrients by mineralizing or solubilizing them and ensuring their bioavailability through acidification [75,76], secretion of hydrolytic enzymes such as phytase or phosphatase, excretion of proton and production of siderophore [77]. Endophytes, rhizospheric microbiomes and Arbuscular mycorrhizal fungi (AMF) help the plant in the acquisition of nutrients from the soil through the solubilization of nutrients such as sulphur (S), potassium (K), calcium (Ca), iron (Fe), zinc (Zn) and phosphorus (P) [78–80]. Some notable root microbiome genera associated with maize, wheat rice and legumes such as *Streptomyces, Pantoea, Citrobacter, Azospirillum, Bacillus, Herbaspirillum, Achromobacter, Gluconacetobacter, Burkholderia, Chryseobacterium, Bacillus, Klebsiella, Azotobacter* and *Pantoea* have been reported to enhance plant development and growth via the uptake of micronutrients and stimulate the development of plant roots [81–84]. Siderophores secreted by endophytes aid plant's iron uptake from the soil; this is because iron cannot directly penetrate the plant cell even through transporters [85]. Root endophytes, such as *Azoarcus, Herbaspirillum, Acetobacter* and diazotrophicus, have been reported to be active in nitrogen fixation. Some diazotrophic endophytic microbial communities, such as *Bacillus, Gammaproteobacteria*, and *Actinobacteria* have been largely reported as an atmospheric nitrogen fixer in rice [85–87]. Rhizobia, most importantly, *Burkholderiales* form root nodules with legumes, which convert atmospheric nitrogen into ammonia, which is readily available to the plant, while the plant, in return, produces carbon compounds [88,89]. Some root microbiomes such as *Brevibacillus, Kineococcus, Microbacterium, Rhizobium, Burkholderia, Nocardia, Bacillus, Rhodococcus, Methylobacterium, Mesorhizobium,* and *Paenibacillus*, associated with Eucalyptus plant have been reported to be involved in the fixing of nitrogen [85,90]. A summary of other studies on nutrient acquisition attributes of some plant root microbiomes is presented in Table 2.

Table 2. Nutrient acquisition attributes of notable plant root microbiomes.

Root Microbiomes	**Host plant**	**Phosphorus (P)**	**Potassium (K)**	**Nitrogen fixers (N_2F)**	**Siderophore (Sid)**	**Zinc (Zn)**	**References**
B. amyloliquefacien	Rice	+	+	+	+	+	[91]
A. sulfonivorans	Wheat	-	-	-	+	+	[92]
A. amazonense	Sugarcane	-	-	+	-	-	[93]
B. megaterium	Soybean	+	-	+	+	-	[94]
P. agglomerans	Rice	+	-	+	-	-	[91]
P. putida	Soybean	-	-	+	+	-	[95]
B. silvatlantica	Sugarcane	-	-	+	-	-	[96]
B. aryabhattai	Soybean	-	-	-	-	+	[97]
K. pneumoniae	Rice	-	-	-	+	-	[98]
B. tropica	Sugarcane	-	-	+	-	-	[99]
P. putida	Rice	+	-	-	-	-	[100]
P. dispersa	Wheat	-	-	-	+	+	[91]
B. vietnamiensis	Rice	-	-	+	-	-	[101]
R. leguminosarum	Beans	+	-	-	+	+	[102]
B. licheniformis	Chickpea	+	-	-	-	-	[103]
B. subtilis	Soybean	-	-	+	+	-	[104]

P. polymyxa	Maize	-	-	+	-	-	[105]
P. thivervalensis	Maize	-	-	-	+	-	[106]
E. asburiae	Maize	-	-	-	+	-	[106]
R. endophyticum	Beans	+	-	-	-	-	[107]
R. irregularis	Tomato	+	-	-	-	-	[108]

+ =Active, - = Inactive

3.3. *Root microbiome role in disease suppression/biocontrol*

Insect and pathogens attack plants and retard their yield, growth and health. However, plant root microbiomes have been reported to be a reservoir of many bioactive metabolites that can protect and enhance plant resistance against attacks from pathogens and pests [85]. Phyllospheric microorganisms isolated from different crop plants showed the abundance of *Firmicutes* that is capable of secreting volatile organic compounds active in the protection of crops from several fungal and bacterial pathogens/diseases [109]. Plant root microbiome protects the plant through induced systemic resistance (ISR) or antibiosis from insects, pathogens and herbivores. Siderophores, antibiotics, salicylic acid, N-acyl homoserine lactones, lipopolysaccharide, jasmonic acid and flagella secreted by endophytic bacteria have been reported to be capable of inducing systemic resistance in plants [110]. Also, endophytic fungi, majorly of the phyla *Glomeromycota, Basidiomycota, Ascomycota*, and *Zygomycota* are capable of secreting inhibitory compounds, some of which are terpenoids, polyketones, phenols, chlorinated compound, alkaloids, peptides, steroids and flavonoids, which aid the protection of plants from insects, pathogens and herbivores [111]. Actinomycetes have also been widely studied due to its ability to secrete notable antimicrobial compounds active against plant pathogens. *Streptomyces* spp. secretes many antimicrobial compounds such as indolo-sesquiterpene antimicrobial compounds, munumbicins, coronamycin and kakadumycins [85,112,113]. Studies have also revealed that siderophore can induce ISR in plants and enhance biocontrol activities. For example, strains of endophytic methylobacterium successfully suppressed *Xylella fastidiosa* (a pathogen responsible for chlorosis in citrus trees) via siderophore production [53]. Rhizobiomes such as Actinobacteria, Proteobacteria and Firmicutes have been linked with the inhibition of *Rhizoctonia solani* commonly attacking sugar beet [85], while the *Gammaproteobacteria* also successfully inhibit the disease via non-ribosomal peptide synthesis (NRPS) [114]. A high abundance of bacteria such as *Streptomyces*, *Bacillus*, *Paenibacillus*, and *Rhizobium* in the root microbial community of cucumber cultivated and monitored in suppressive soil [115]. A summary of similar studies on the biocontrol attributes of some plant root microbiomes is presented in Table 3.

Table 3. Biocontrol activities of some plant root microbiomes.

Root Microbiomes	**Host plant**	**Pathogens active against**	**Activities and metabolites secreted/Induced**	**References**
Pseudomonas sp., *Pantoea* sp.	Grapevine	*A. tumefaciens, A. vitis*	-	[116]
A. calcoaceticus	Soybean	*P. sojae* 01	Siderophore and indole acetic acid	[95]
Bacillus sp.	Soybean	*C. truncatum, R. solani, F oxysporum, S. rolfsii, A. alternata*, and *M. phaseolina*	Siderophore and Hydrogen cyanide.	[117]
B. subtilis	Rice	*R. solani, F. verticelloides*, and *S. rolfsii*	Lipopeptides	[118]
B. gladioli 3A12	Maize	*S. homoeocarpa*	-	[119]
P. fluorescens 63-28	Pea	*P. ultimum* and *F. oxysporum* f. sp. pisi	Induced peroxidase, polyphenoloxisae, Superoxide dismutase and phenylalanine amonialyase.	[120]
P. aeruginosa FTR	Maize	*F. oxysporium, P. aphanidermatum, Alternaria* sp., *R solani*, *M. phaseolina, Alternaria* sp. and	-	[106]

Glomus etunicatum	Wheat	*S. rolfii*, *G. graminis*	Isozyme	[121]
B. velezensis CB3	Citrus	*P. digitatum*	-	[122]
G. versiforme and *T harzianum*	Cowpea	*E. flexuosa*	-	[123]
B. velezensis	Maize	*T. funiculosus*, *P. oxalicum*, and *F. verticillioides*	Lipopeptide	[124]
R. leguminosarum RPN5	Beans	*M. phaseolina*, *F. oxysporum*, *S. sclerotiorum* and *F. solani*.	-	[102]
Serratia (B17B), *Enterobacter* (E), and *Bacillus* (IMC8, Y, Ps, Psl, and Prt)	Papaya and Bean	*P. capsici*	-	[125]
Acremonium sp., *Leptosphaeria* sp., *T. flavus*, and *P. simplicissimum.*	Cotton	*V. dahliae* strain Vd080	-	[107]
Bacillus sp.	Millet	*R. solani*, *S. rolfsii*, and *F. solani*	Antimicrobial peptides	[126]
B. subtilis	Rice	*M. oryzae*	Enhanced activity of peroxidase, polyphenol oxidase and superoxide dismutase	[127]
Pseudomonas sp.	Wheat	*F. graminearum*	-	[128]
B. subtilis EB-28	Tomato	*B. cinerea*	-	[129]
F. mosseae	Wheat	*X. translucens*	-	[130]
R. irregularis	Tomato	*A. solani*	-	[108]
F. mosseae	Wheat	*B. graminis*	-	[131]
F. mosseae and *P. fluorescens*	Wheat	*G. graminis*	-	[132]

4. Conclusion and future prospects

It is evident that plant-microbe signaling cascades are essential regulators of plant development and growth, and these signal molecules can alter the morphology and physiology of the host plant. Plants develop complex interactions and communicate with various microbes in their rhizosphere through different signals that affect plant growth and modulate plant-specific core root microbiome. These signals, secreted by micro- and macro-symbionts, can enhance root development, increase nutrient and water uptake, and promote tolerance to biotic and abiotic stresses. As a result of the roles plant growth-promoting organisms played in improving plant growth and yield, the role of plant-microbe signals in sustainable agriculture and the recovery of marginal lands cannot be overemphasized. It is, therefore, important to focus future research on the understanding of intra- and inter-communication that can lead to the identification of more signal molecules and similarly improve plant growth and development. Thus, the need to develop efficient technologies for isolating and identifying signal compounds useful for sustainable development.

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