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Plant Microbiomes and Its Beneficial Multifunctional Plant Growth Promoting Attributes

Ajar Nath Yadav[1*], Priyanka Verma[2], Divjot Kour[1], Kusam Lata Rana[1], Vinod Kumar[1], Bhanumati Singh[3], Vinay Singh Chauahan[3], TCK Sugitha[4], Anil Kumar Saxena[5] and Harcharan Singh Dhaliwal[1]

[1]*Department of Biotechnology, Akal College of Agriculture, Eternal University, India*

[2]*Department of Microbiology, Akal College of Basic Science, Eternal University, India*

[3]*Department of Biotechnology, Bundelkhand University, India*

[4]*Department of Agricultural Microbiology, Tamil Nadu Agricultural University, India*

[5]*ICAR-National Bureau of Agriculturally Important Microorganisms, India*

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***Corresponding author:** Ajar Nath Yadav, Department of Biotechnology, Akal College of Agriculture, Eternal University, Sirmour, India, Tel no: +91-9882545085; Email: ajarbiotech@gmail.com

Abstract

Plant microbiome (Epiphytic, endophytic and rhizospheric) plays important role in plant growth, development, and soil health. Plant and rhizospheric soil are valuable natural resource harbouring hotspots of microbes, and it plays critical roles in the maintenance of global nutrient balance and ecosystem function. The diverse group of microbes is key components of soil-plant systems, where they are engaged in an intense network of interactions in the rhizosphere/phyllospheric/endophytic. The microbes with plant growth promoting (PGP) attributes have emerged as an important and promising tool for sustainable agriculture. PGP microbes promote plant growth and development directly or indirectly, either by releasing plant growth regulators/phytohormones; solubilization of phosphorus, potassium and zinc; biological nitrogen fixation or by producing siderophore, ammonia, HCN and other secondary metabolites which are antagonistic against pathogenic microbes. The PGP microbes belonged to different phylum of archaea (Euryarchaeota); bacteria (Acidobacteria, Actinobacteria, Bacteroidetes, Deinococcus-Thermus, Firmicutes and Proteobacteria) and fungi (Ascomycota and Basidiomycota), which include different genera namely *Achromobacter*, *Acinetobacter*, *Agrobacterium*, *Alcaligenes*, *Arthrobacter*, *Aspergillus*, *Azoarcus*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Beijerinckia*, *Brevibacterium*, *Burkholderia*, *Collimonas*,*Curtobacterium*, *Diplococcus*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Flexibacterium*, *Gluconoacetobacter*, *Haloarcula*, *Halobacterium*, *Halococcus*, *Haloferax*, *Herbaspirillum*, *Klebsiella*, *Methylobacterium*, *Microbiospora*, *Micrococcus*, *Micromomospora*, *Nocardioides*, PaeniBacillus, *Pantoea*, *Penicillium*, *Piriformospora*, *Planomonospora*, *Pseudomonas*, *Rhizobium*, *Serratia*, *Streptomyces*, *Thermomonospora* and *Xanthomonas*. These PGP microbes could be used as biofertilizers/bioinoculants at place of chemical fertilizers for sustainable agriculture.

Keywords: Biodiversity; Endophytic; Epiphytic; Microbiome; Plant Growth Promotion; Rhizospheric; Sustainable Agriculture

Introduction

Plant-microbes interaction is a key for plant growth, development and soil health. An understanding of plant microbiome and their beneficial attributes could have multiple benefits towards sustainable agriculture. Recently, a great emphasis is given on decoding of microbial diversity associated with plants from diverse habitats. Microbial diversity is considered important for maintaining for the sustainability of agriculture production systems. In the 90s, the interaction of microbes with plants was simply thought of as being an effect, but today it is recognized as a process with a high level of complexity in which at least different type of microbes share information without sharing the same spaces from a cellular perspective. In general, there are three kinds of plant-microbes interactions are considered i.e. epiphytic, endophytic and rhizospheric.

The rhizosphere is the zone of soil influenced by roots through the release of substrates that affect microbial activity. It is characterized by greater microbiological activity depending on the distance away from plant roots and constitutes a system especially suitable for obtaining culturable beneficial microbes. The rhizospheric microbes have the ability to attach to the root surfaces allowing these to derive maximum benefit from root exudates. Several factors such as soil type, its moisture, pH and temperature and, age and conditions of plants are known to influence the types of rhizospheric microbes. A number of microbial species belonging to different genera *Acinetobacter*, *Alcaligenes*, *Arthrobacter*, *Aspergillus*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Haloarcula*, *Halobacterium*, *Halococcus*, *Haloferax*, *Methylobacterium*, PaeniBacillus, *Penicillium*, *Piriformospora*, *Pseudomonas*, *Rhizobium* and *Serratia* were revealed from rhizosphere of different crop plants [1-8].

The phyllosphere is a common niche for synergism between microbes and plant. The leaf surface has been termed as Phyllosphere and zone of leaves inhabited by microorganisms as phyllo sphere. The plant part, especially leaves are exposed to dust and air currents resulting in the establishments of typical flora on their surface aided by the cuticles, waxes and appendages, which help in the anchorage of microorganisms. The phyllospheric microbes may survive or proliferates on leaves depending on extent of influences of material in leaf diffuseness or exudates. The leaf diffuseness contains the principal nutrients factors (amino acids, glucose, fructose and sucrose), and such specialized habitats may provide niche for nitrogen fixation and secretions of substances capable of promoting the growth of plants. The phyllospheric microbes may performs an effective function in controlling the air borne pathogens inciting plant disease. Microbes on leaf surface are said to be extremophiles as they can tolerate low/high temperature (5-55°C) and UV radiation. Many microbes such as *Achromobacter*, *Agrobacterium*, *Azotobacter*, *Bacillus*, *Beijerinckia*, *Brevibacterium*, *Burkholderia*, *Diplococcus*, *Flexibacterium*, *Methylobacterium*, *Microbiospora*, *Micrococcus*, *Micromomospora*, *Nocardioides*, *Pantoea*, *Penicillium*, *Planomonospora*, *Pseudomonas*, *Rhizobium*, *Streptomyces*, *Thermomonospora* and *Xanthomonas* have been reported in the phyllosphere of different crop plants [9-15].

The endophytic microbes are referred to those microorganisms, which colonizes in the interior of the plant parts, *viz*: root, stem or seeds without causing any harmful effect on host plant. The word endophyte means 'in the plant' and is derived of the Greek words end on (within) and python (plant). Endophytic microbes enter in host plants mainly through wounds, naturally occurring as a result of plant growth or through root hairs and at epidermal conjunctions. Endophytes may be transmitted either vertically (directly from parent to offspring) or horizontally (among individuals). A given endophytic microbiome can be modified by factors such as the physicochemical structure of the soil, plant growth phase and plant physiological state, as well as by diverse environmental factors [16,17].

The main colonization route used by endophytes seems to be the rhizosphere. Microbes reach the rhizosphere by chemotaxis towards root exudates components followed by attachment. The lipopolysaccharide and exopolysaccharide are bacterial components shown to play roles in attachment of endophytes to plant tissue. The preferred site of attachment and subsequent entry is the apical root zone with a thin-walled surface root layer, such as the cell elongation zone and the root hair zone with small cracks caused by the emergence of lateral roots. Root regions such as the differentiation zone and intercellular spaces in the epidermis have been suggested to be preferential sites for microbial colonization as well. Root cracks, wounds caused, for instance, by arthropods or nematodes, and emergence sites of lateral roots are generally considered as the main 'doors' for microbial penetration. Bacterial traits putatively involved in endophytic colonization of plant roots. For penetration, the bacteria have to produce cellulolytic enzymes required to hydrolyse the exothermal walls, such as endoglucanases and endopolygalacturonidases [18]. These enzymes also seem to be important for spreading through the intercellular space of the root cortex and beyond. Endophytes usually do not enter plant cells. Only a few of them can penetrate the endow dermal barrier and invade the xylem vessels. Endophytic microbes live in plant tissues without causing substantive harm to the host. Endophytic microbes exist within the living tissues of most plant species in form of symbiotic to slightly pathogenic. A large number of endophytic microbial species *Achromobacter*, *Azoarcus*, *Burkholderia*, *Collimonas*, *Curtobacterium*, *Enterobacter*, *Flavobacterium*, *Gluconoacetobacter*, *Herbaspirillum*, *Klebsiella*, *Microbiospora*, *Micromomospora*, *Nocardioides*, *Pantoea*, *Planomonospora*, *Pseudomonas*, *Serratia*, *Streptomyces* and *Thermomonospora* have been identified from different host plants [6,8,10,15,18-21].

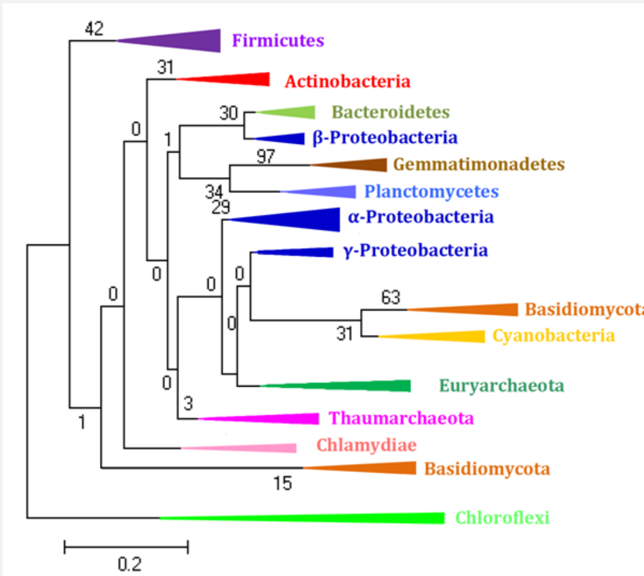

Figure 1: Phylogenetic tree showed the relationship among different groups of plant microbiome

The study on microbial biodiversity of plant associated microbes revealed representative microbes from archaea (Euryarchaeota); bacteria (Acidobacteria, Actinobacteria, Bacteroidetes, Deinococcus-Thermus, Firmicutes and Proteobacteria) and fungi (Ascomycota and Basidiomycota). Literature review suggested that the distribution of microbes although varied in all bacterial phyla, but Proteobacteria were most dominant and ubiquitous followed by Actinobacteria.

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Among different classes of Proteobacteria i.e. α, β, γ and δ-proteobacteria, the members of γ-proteobacteria were most dominant and have been reported from different crop plants. Least number of microbes was reported from phylum Deinococcus-Thermus and Acid bacteria followed by Bacteroidetes [18,22-26] (Figure 1). There are very few reports of archaea as PGP including rhizospheric as well as endophytic [27-29].

Actinobacteria is a phylum of gram-positive bacteria and divided into five classes' *viz*. Acidimicrobiia, Actinobacteria, Coriobacteriia, Nitriliruptoria, Rubrobacteria and Thermoleophilia. Members of class Actinobacteria are most dominant and found to associate with plants growing in different habitats as well as extreme environments. It also contains one of the largest of bacterial genera, *Streptomyces* [30-32]. The rhizospheric Actinobacteria are most dominant in nature and they are of great economic importance to humans because agriculture and forests depend on their contributions to soil systems. Among different groups of microbes, the member *Bacillus* and *Bacillus* derived genera are belonged to phylum Firmicutes, which most culturable and colonize with different plants such as wheat, rice, maize, soybean, and chickpea [33-37]. The phylum Firmicutes, have been further distributed into five families, *B*acillaceae, Bacillales Incertae Sedis, PaneniBacillaceae, *Planococcaceae* and *Staphylococcaceae* and reported from most of crop plants studies [6-8,10,12,15]. Among different phylum the Proteobacteria one of the predominant phylum including many dominant genera including *Brevundimonas terrae*, *Bosea* sp. and *Methylobacterium* sp. from α-proteobacteria; *Burkholderia* sp, *Burkholderia* cepacia, *Variovorax ginsengisoli*, *Janthinobacterium lividum* and *Janthinobacterium* sp. from β-proteobacteria and *Aeromonas*, *Pantoea*, *Providencia*, *Pseudomonas*, *Psychrobacter* and *Yersinia* from γ-proteobacteria class [6-8,18,38].

Table 1: Microbes with multifarious plant growth promoting attributes.

	Microbes	P*	NF	IAA	Sidero	ACC	Referencs
1.	*Acinetobacter rhizosphaerae* BIHB 723	+	-	+	+	+	[66]
2.	*Aeromonas hydrophila* IARI-R-6	+	-	+	+	-	[49]
3.	*Arthrobacter methylotrophus* IARI-HHS1-25	+	+	+	+	+	[8]
4.	*Arthrobacter sulfonivorans* IARI-L-16	+	-	+	+	-	[45]
5.	*Bacillus altitudinis* IARI-HHS2-2	+	+	+	-	-	[8]
6.	*Bacillus amyloliquefaciens* IARI-HHS2-30	+	+	+	+	+	[15]
7.	*Bacillus amyloliquefaciens* IARI-R-25	+	-	+	+	-	[49]
8.	*Bacillus aryabhattai* IARI-HHS1-30	+	+	+	-	-	[8]
9.	*Bacillus firmus* IARI-L-21	+	-	+	+	+	[45]
10.	*Bacillus licheniformis* IARI-AL38	+	-	+	+		[43]
11.	*Bacillus muralis* IARI-AR28	-	-	+	+	-	[43]
12.	*Bacillus subtilis* IARI-L-69	+	-	+	+	+	[45]
13.	*Bordetella bronchiseptica* IARI-HHS2-29	+	+	+	+	-	[8]
14.	*Cellulosimicrobium cellulans* IARI-ABL-30	+	-	+	-	+	[45]
15.	*Desemzia incerta* IARI-L-46	+	-	+	+	-	[45]
16.	*Exiguobacterium antarcticum* IARI-HHS2-49	-	-	+	+	-	[8]
17.	*Flavobacterium psychrophilum* HHS2-37	+	-	+	+	+	[8]
18.	*Lysinibacillus sphaericus* IARI-AR11		-	+	-	+	[43]
19.	*Paenibacillus tylopili* IARI-AR36	+	-	+	+	-	[43]
20.	*Pantoea agglomerans* IARI-R-87	+	-	+	+	-	[49]
21.	*Pantoea dispersa* 1A	+	-	+	+	-	[67]
22.	*Providencia rustigianii* IARI-R-91	+	-	+	+	+	[49]
23.	*Pseudomonas cedrina* IARI-R-53	+	-	+	+	+	[49]
24.	*Pseudomonas fluorescens* PPRs4	+	-	+	+	-	[68]
25.	*Pseudomonas fragi* IARI-R-57	+		+	+	+	[49]
26.	*Pseudomonas geniculata* IARI-HHS1-19	+	+	+	+	-	[8]
27.	*Pseudomonas jessani* PGRs1	+	-	+	+	-	[68]
28.	*Pseudomonas koreensis* PBRs7	+	-	+	+	-	[68]
29.	*Pseudomonas lurida* M2RH3	+	-	+	+	-	[69]
30.	*Pseudomonas lurida* NPRs3	+	-	+	+	-	[68]

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31.	*Pseudomonas moraviensis* IARI-R-132	+		+	+	+	[49]
32.	*Pseudomonas putida* IARI-R-131	-		+	+	-	[49]
33.	*Pseudomonas* sp. NARs9	+	-	+	+	-	[70]
34.	*Pseudomonas* sp. PGERs17	+	-	+	+	-	[71]
35.	*Psychrobacter frigidicola* IARI-R-127	+		+	+	+	[49]
36.	*Rahnella* sp. BIHB 783	+	-	+	+	+	[72]
37.	*Sanguibacter suarezii* IARI-R-7	+	-	+	+	+	[49]
38.	*Stenotrophomonas maltophilia* IARI-HHS1-20	+	-	+	+	+	[8]

*P-Phosphorus; NF-Nitrogen fixation; IAA- Indole acetic acids; Sidero- Siderophores; ACC-1-aminocyclopropane-1-carboxylate (ACC) deaminase

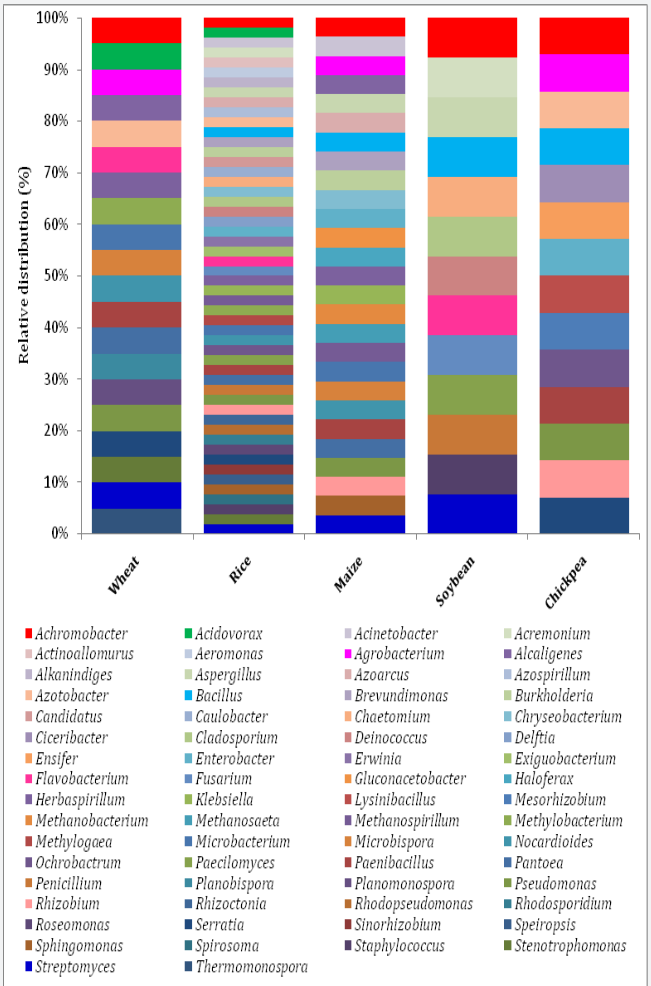

Figure 2: Diversity and relative distribution of microbes isolated from different crops.

Plant associated microbes have been shown be beneficial by promoting plant growth either directly, e.g. by fixation of atmospheric nitrogen, solubilization of minerals such as phosphorus, potassium and zinc; production of Sidero pores and plant growth hormones such cytokinins, auxins and gibberellins or indirectly, via production of antagonistic substances by inducing resistance against plant pathogens [3,38-41]. Biological nitrogen fixation (BNF) is one of the possible biological alternatives to N-fertilizers and could lead to more productive and sustainable agriculture without harming the environment. Many associative microbes are now known to fix atmospheric nitrogen and supply it to the associated host plants. A variety of nitrogen fixing microbes like *Arthrobacter*, *Azoarcus*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Enterobacter*, *Gluconoacetobacter*, *Herbaspirillum*, *Klebsiella*, *Pseudomonas*, and *Serratia* have been isolated from the rhizosphere of various crops, which contribute fixed nitrogen to the associated plants [18,42-44] (Figure 2) (Table 1).

Plant-associated microbes typically produce plant growth hormones such as auxins and gibberellins. The gibberellins production is most typical for the root-associated microbes and auxins production is common to all plant-associated microbes. Auxins can promote the growth of roots and stems quickly (by increasing cell elongation) or slowly (through cell division and differentiation). The production of such growth regulators by microbes provides numerous benefits to the host plant including the facilitation of root system expansion, which enhances the absorption of water and nutrients and improves plant survival. The ability to synthesize these phytohormones is widely distributed among plant-associated microbes [45-47]. Diverse microbial species possess the ability to produce the auxins phytohormone indole acetic acid (IAA). Reviewing the role of bacterial IAA in different microorganism–plant interactions highlights the fact that microbes use this phytohormone to interact with plants as part of their colonization strategy, including phyto-stimulation and circumvention of basal plant defense mechanisms. The IAA application has also been suggested to promote plant growth or suppress weed growth.

Phosphorus (P) is major essential macronutrient for biological growth and development. Microbes offer a biological rescue system capable of solubilizing the insoluble inorganic P of soil and make it available to the plants. The ability of some microbes to convert insoluble P to an accessible form, like orthophosphate, is an important trait in PGP microbes for increasing plant yields. The rhizospheric P-utilizing microbes could be a promising source for plant growth promoting agent in

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agriculture. P-solubilization is a common trait among microbes associated with different crops. For instance, the majority of microbial populations from wheat, rice, maize, and legumes were able to solubilise mineral phosphates, and a vast number of PGP microbes with P solubilizing property have been reported which include members belonging to *Burkholderia*, *Enterobacter*, *Halolamina, Pantoea*, *Pseudomonas*, *Citrobacter* and *Azotobacter* [48-54] (Table 1). Possible mechanisms for solubilization from organic bound P involve either enzymes namely C-P lyase, non-specific phosphatases and phytases [55,56]. However, most of the bacterial genera solubilize P through the production of organic acids such as gluconate, ketogluconate, acetate, lactate, oxalate, tartarate, succinate, citrate and glycolate. Type of organic acid produced for P solubilization may depend upon the carbon source utilized as substrate. Highest P solubilization has been observed when glucose, sucrose or galactose has been used as sole carbon source in the medium [27,57].

Ethylene is a stress-induced plant hormone that can inhibit plant growth. Some microbes can lower the level of ethylene in the plant by cleaving the plant-produced ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC). Inoculation of such microbes can mitigate the effect of various stressors by sustaining plant growth in the face of ethylene. ACC-deaminase producing microbes may play a role in regulating ethylene levels after such bursts, ensuring that ethylene levels stay below the point where growth is impaired. Ethylene is a key regulator of the colonization of plant tissue by bacteria which in turn suggests that the ethylene inhibiting effects of ACC-deaminase may be a microbial colonization strategy. Generally, ethylene is an essential metabolite for the normal growth and development of plants [58-61]. This plant growth hormone is produced endogenously by approximately all plants and is also produced by different biotic and abiotic processes in soils and is important in inducing multifarious physiological changes in plants. Apart from being a plant growth regulator, ethylene has also been established as a stress hormone. Under stress conditions like those generated by salinity, drought, water logging, heavy metals and pathogenicity, the endogenous level of ethylene is significantly increased which negatively affects the overall plant growth. PGP microbes which possess the enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, facilitate plant growth and development by decreasing ethylene levels, inducing salt tolerance and reducing drought stress in plants. Microbial strains exhibiting ACC deaminase activity have been identified in a wide range of genera such as *Acinetobacter*, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia* and *Rhizobium* [6,8,61-65] (Figure 2)(Table 1).

The indirect mechanism of plant growth occurs when microbes lessen or prevent the detrimental effects of pathogens on plants by production of inhibitory substances or by increasing the natural resistance of the host [66-72]. Phytopathogenic microbes can control by releasing siderophore, chitinases, antibiotics, fluorescent pigment or by cyanide production [73,74]. Biocontrol systems are eco-friendly, cost-efficient and involved in improving the soil consistency and maintenance of natural soil flora [75-77]. To act efficiently, the Biocontrol agent should remain active under large range of conditions *viz*., varying pH, temperature and concentrations of different ions. Biocontrol agents limit growth of pathogen as well as few nematodes and insects. Biocontrol microbes can limit pathogens directly by producing antagonistic substances, competition for iron, detoxification or degradation of virulence factors; or indirectly by Inducing Systemic Resistance (ISR) in plants against certain diseases, signal interference, competition for nutrients and niches and interference with activity, survival, germination and speculation of the pathogen. Iron is a necessary cofactor for many enzymatic reactions and is an essential nutrient for virtually all organisms. In aerobic conditions, iron exists predominantly in its ferric state (Fe^{3+}) and reacts to form highly insoluble hydroxides and ox hydroxides that are largely unavailable to plants and microorganisms. To acquire sufficient iron, siderophore produced by bacteria can bind Fe^{3+} with a high affinity to solubilizing this metal for its efficient uptake.

Bacterial siderophores are low-molecular-weight compounds with high Fe^{3+} chelating affinities responsible for the solubilization and transport of this element into bacterial cells. Some bacteria produce hydroxamate-type siderophores, and others produce catecholate-types [78,79]. In a state of iron limitation, the siderophore-producing microorganisms are also able to bind and transport the iron-siderophore complex by the expression of specific proteins. The production of siderophores by microorganisms is beneficial to plants because it can inhibit the growth of plant pathogens. siderophores have been implicated for both direct and indirect enhancement of plant growth by plant growth promoting microbes.

Conclusion and Future Prospect

The microbes are capable of colonizing the rhizosphere, phyllosphere as well as living inside the plant tissues as endophytes. Biotechnology has opened up new possibilities concerning the application of these microbes for the beneficial applications in soil for the promotion of plant growth and the biological control of soil-borne pathogens. The nutritional and environmental requirements of these microbes are very diverse. Due to the diverse range of activities as well as the number of microbes in varying habitats around the world, these are important bioresources towards rationalized use of chemicals fertilizers in agriculture. An understanding of plant microbiome for major crops will be of significant importance for exploring efficient use of these microbes.

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Competing Interests

The authors declare no conflict of interest.

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