Chapter 4
Ecology and Mechanisms of Plant Growth Promoting Rhizobacteria

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Abstract The rapid increase in population and climate change is calling for sustainable methods to improve food production such as soil microbial management. Here we review the ecology and mechanisms of action of plant growth-promoting rhizobacteria. Rhizosphere comprises both symbiotic and non-symbiotic microorganisms that influence plant growth positively by their effect on mineral nutrient uptake and bioavailability. Plant growth-promoting rhizobacteria facilitate resource acquisition and modulate phytohormone levels. Indirect mechanisms include production of antibiotics, lytic enzymes and siderophores, competition to harmful organisms, regulation of ethylene production, and induced systemic resistance. Plant growth-promoting substances suppress plant pathogens through competition for nutrients and space. Application of plant growth-promoting rhizobacterial increases crop yields. Numerous plant growth-promoting rhizobacteria are already marketed and are actually replacing mineral fertilizers and pesticides.

Keywords Siderophore · Induced systemic resistance · Phytohormones · Rhizosphere · Rhizobacteria · Plant growth · Crop yield · Soil microbiology

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Abbreviations

ACC	1-amino cyclopropane-1-carboxylic acid
DAPG	2,4 diacetyl phloroglucinol
IAA	Indole Acetic Acid
PGPR	Plant Growth-Promoting Rhizobacteria

4.1 Introduction

Free-living soil microorganism and rhizosphere bacteria that are beneficial to plants, are referred as plant growth-promoting rhizobacteria (PGPR). Plant inoculation with about 2–5% of rhizobacteria in a soil containing competitive microflora, is sufficient to sustain the plant growth and development to fulfil the requirement to some extent (Kusum et al. 2019; Dweipayan et al. 2016). PGPR terminology was first proposed by Kloepper in the 70s. According to the original definition, rhizobacteria include free-living bacteria, except nitrogen-fixing rhizobia and *Frankia*. Hence, growth stimulation which results from the biological nitrogen fixation by rhizobia or *Frankia* cannot be considered as a PGPR mechanism of action and are thus excluded from PGPRs. Plant growth-promoting rhizobacteria have the ability to colonize rhizosphere aggressively, that benefits plant and inhibit minor pathogens (Antoun and Prévost 2005). Plant growth-promoting rhizobacteria includes various types of bacterial groups including symbiotic ones viz., *Rhizobium, Bradyrhizobium, Actinomycetes* and free-living bacteria of genus *Acetobacter, Azotobacter, Azospirillum, Bacillus, Burkholderia, Enterobacter, Pseudomonas*. Many of the enlisted bacteria affect the plant metabolism either in the rhizospheric region or sometimes invade the plant tissue.

PGPRs have been classified based upon their activities as biofertilizers which increases the nutrient bioavailability to plant (Sushanto et al. 2017), phytostimulators which releases different phytohormone like chemicals resulting in plant growth promotion (Kloepper 2003), biocontrol agents which release a wide variety of antibiotics and antifungal compounds imparting plant resistance against biotic stress, sometimes also referred to as biocontrol plant growth-promoting bacteria (Bashan and Holguin 1997) and rhizo-remediators which promotes the plant growth by the removal of different organic pollutants present in the rhizosphere.

Plant growth-promoting rhizobacteria are sometimes classified into two groups, symbiotic and free-living based on their relationship with plants (Khan 2005), and they are studied as extracellular and intracellular PGPR (Gray and Smith 2005) based upon their occurrence in plant i.e., extracellular PGPR exist in the rhizosphere, on the rhizoplane, or in the spaces between cells of the root cortex, whereas intracellular PGPR exists inside the root cells. Due to their plant growth promotion effects, these beneficial microorganisms are termed as yield-increasing bacteria (Sayyed et al. 2010); plant health-promoting rhizobacteria, or nodule-promoting rhizobacteria as per their mechanism of action on the plant metabolism (Burr and Caesar 1984; Vessey 2003). Plant growth-promoting rhizobacteria can be present in proximity to the plant roots at different levels i.e., near roots of the plant, in the rhizoplane, within the root tissue, or in the case of symbionts as specialized structures known as nodules (Gray and Smith 2005). PGPR helps in water retention in the soil which can be combat drought to some extent (Wenjuan et al. 2018).

Apart from the issue of high cost, many of the agrochemicals used for fungal and bacterial disease control are hazardous to the living system along with humans and persist for a longer time resulting in bioaccumulation in natural ecosystems. Production of chemical fertilizers is also one of the major factors causing depletion of non-renewable resources. Fuels like petroleum oil and natural gas utilized in the production of fertilizers and other agrochemicals pose environmental hazards to human and other living community. Due to their biological nature, PGPR approach is environmentally safer and sustainable.

4.2 Applications and Mechanisms

Plant growth-promoting rhizobacterial action involves diverse mechanisms and generally, more than one mechanism is responsible for plant development. A summary of the effects of plant growth-promoting rhizobacteria on different crops under laboratory and field conditions are presented in Table 4.1.

4.2.1 Direct Mechanisms

4.2.1.1 Facilitating Resource Acquisition

Plant growth-promoting rhizobacteria may provide plants with lacking resources or nutrients like fixed nitrogen, iron, and phosphorus etc. (Munees and Mulugeta 2014). Nitrogen is the building block of the living cells and essential for growth, development and enhances productivity. Nitrogen facilitates from the atmosphere to the living system through microorganisms that resides in the soil. Nitrogen is fixed in the living system through symbiotic and non-symbiotic bacteria. A popular example of symbiotic nitrogen-fixing bacteria from family *Rhizobiaceae* that is associated with leguminous plants and *Frankia*, a soil actinomycete that do symbiosis in non-leguminous plants such as *Gymnostoma* (family Casuarinaceae), *Myrica* (family Myricaceae), *Comptonia* (family Myricaceae), *Casuarina cunninghamiana*, *Purshia tridentata*, *Allocasuarina decaisneana*, *Alnus*, *Hippophae*, *Coriaria*.

Rhizobia also establish symbiosis in relation with non-legume plant such as *Parasponia.* Their symbiosis results in the nodulation for bacteria and those bacteria assist in providing atmospheric nitrogen to plants (Raklami et al. 2019). In contrast, non-symbiotic microorganisms may be free-living, associative or endophytic in

Table 4.1 The effects of plant growth promoting rhizobacteria and their mechanisms of action

PGPR	Crop system	Trial setup	Soil modification	Effects on plant	Mechanism of action	References
Acinetobacter calcoaceticus SE370	*Cucumis sativus*	*Pot trial*	–	Increase in biomass and chlorophyll contents, water potential and decrease in electrolytic leakage	Stress adaptation imparted through: 1. Reduced antioxidant enzyme activity of catalase, peroxidase, polyphenol oxidase. 2. Decreased polyphenol content. 3. Decreased abscisic acid and increased salicylic acid and gibberellin levels.	Kang et al. (2014)
Acinetobacter sp.	Bean and wheat	*Field trial*	Improvement in the amount of soil organic matter	Increased plant growth, leaf production, shoots, and root system	PGPR influenced efficient colonization of bean and wheat plant roots by the mycorrhizal consortium	Raklami et al. (2019)
Bacillus amyloliquefaciens	Rice	*Pot trial*	–	Increased stress adaptation against various abiotic stresses	Elevated phytohormone induced stress tolerance	Tiwari et al. (2017)
Bacillus cereus	*Sunflower*	*Pot trial*	Enhancement in the accumulation of Cu, Co, Fe, and Zn	Increased tolerance towards drought and heavy metal stress	Increase in the translocation and accumulation of micronutrients	Khan et al. (2018)
Bacillus megaterium	*Phaseolus vulgaris*	*Pot trial*	Increased phosphorus availability	Increased nodulation, shoot weight and root weight	Increased N2 fixation by legume-*Rhizobium* symbiotic association	Korir et al. (2017)
Bacillus sp. B55	*Nicotiana attenuata*	*Petri dish*	–	Increased germination and seedling growth	Emission of volatile organic compounds	Meldau et al. (2013)
Bacillus sp.	Durum wheat	*Field trial*	Increased mycorrhizal colonization	Increased biomass, elevated N and P content	Increased phosphate transferase gene expression	Saia et al. (2015)
Bacillus sp.	*Spartina maritima*	*Pot trial*	–	Increased belowground biomass	Decreased antioxidant enzyme activity along with slower respiration rate	Mesa-Marín et al. (2018)

Burkholderia cepacia SE4	*Cucumis sativus*	*Pot trial*	–	Increase in biomass and chlorophyll contents, water potential and decrease in electrolytic leakage	Stress adaptation imparted through: 1. Reduced activity of catalase, peroxidase, polyphenol oxidase 2. Decreased total polyphenol 3. Decreased abscisic acid and increased salicylic acid and gibberellin levels	Kang et al. (2014)
Burkholderia phytofirmans	*Arabidopsis thaliana*	*Pot trial*	Increased root colonization	Improved plant tolerance towards lower temperature stress	Strengthening of the cell wall in mesophyll	Su et al. (2015)
Burkholderia sp.	*Schizolobium parahyba*	*Field trial*	Increased mycorrhizal association and increased nutrient supply	Increased biomass and wood yield	Improved nutrient acquisition	Cely et al. (2016)
Enterobacter cloacae and *Bacillus drentensis*	Mung bean	*Field trial*	–	Improvement in stomatal conductance, transpiration, relative water content, chlorophyll content, plant height, leaf area, dry biomass, seed yield, and salt tolerance	Mitigation of the adverse effects of salinity due to the additive effect of PGPR and Si foliar spray on various physiological factors	Mahmood et al. (2016)
Enterobacter hormaechei	Foxtail millet	*Pot trial*	–	Improved drought tolerance and increased seed germination and seedling growth	ACC deaminase activity and exopolysaccharides production which enhance drought tolerance	Niu et al. (2018)
Paenibacillus polymyxa	*Phaseolus vulgaris* L.	*Pot trial*	Increased phosphorus availability	Increased nodulation, shoot weight and root weight	Increased N2 fixation by legume-*Rhizobium* symbiotic association	Korir et al. (2017)
Paenibacillus polymyxa NSY50	Cucumber seedlings	*Pot trial*	–	Increased defence against pathogenic attack by *Fusarium*	Elevated defence related to protein metabolism	Du et al. (2016)

(continued)

Table 4.1 (continued)

PGPR	Crop system	Trial setup	Soil modification	Effects on plant	Mechanism of action	References
Planomicrobium chinense	Sunflower	*Pot trial*	Enhancement in the accumulation of Cu, Co, Fe, and Zn	Increased tolerance towards drought and heavy metal stress	Increase in the translocation and accumulation of micronutrients	Khan et al. (2018)
Promicromonospora sp. SE188	*Cucumis sativus*	*Pot trial*	–	Increase in biomass and chlorophyll contents, water potential and decrease in electrolytic leakage	Stress adaptation imparted through: Reduced catalase, peroxidase and polyphenol oxidase activity, decreased total polyphenol content. Decreased abscisic acid and increased salicylic acid and gibberellin levels	Kang et al. (2014)
Pseudomonas fluorescens, P. migulae	Foxtail millet	*Pot trial*	–	Improved drought tolerance; increase in seed germination and seedling growth	ACC deaminase activity and exopolysaccharide production enhance drought tolerance	Niu et al. (2018)
Pseudomonas sp.	Maize	*Pot trial*	Increase in Pseudomonas population	Better plant growth and development.	Increased root colonization by Pseudomonads	Vacheron et al. (2016)
Rahnella aquatilis	Bean and wheat	*Field trial*	Improved amount of total organic matter and carbon content	Increased plant growth, leaf production, shoots, and root system	PGPR influenced efficient colonization of bean and wheat plant roots by the mycorrhizal consortium	Raklami et al. (2019)
Rhizobium sp.	*Schizolobium parahyba*	*Field trial*	Increased mycorrhizal association resulting in increased nutrient supply	Increased biomass and wood yield.	Improved nutrient acquisition	Cely et al. (2016)

terms of nitrogen fixation; cyanobacteria (*Anabaena, Nostoc*, *Azospirillum, Azotobacter, Azoarcus*) are the prevalent example of non-symbiotic microorganisms. They provide lesser nitrogen to plants in contrast to symbiotic microorganism all nitrogen fixation capacity depends on the requirement of the plant. Nitrogenase enzyme plays important role in nitrogen fixation based on metal cofactor. This enzyme is classified into three categories; (i) Mo- nitrogenase (ii) V- nitrogenase (iii) Fe- nitrogenase and *nif* gene responsible for nitrogen fixation (Raklami et al. 2019).

Most of the soil phosphorus is insoluble (inorganic apatite or as organic inositol phosphate (soil phytate, phosphomonoesters, or phosphodiester) and therefore unavailable for plant growth. Phosphorous fertilizer is also immobilized immediately after application and becomes unavailable to plants. An important trait of plant growth-promoting rhizobacterial action is to convert the phosphorus into available form for the plant by phosphate-solubilizing bacteria, which is carried out by a variety of different phosphatase enzyme synthesis (Sivasakthi et al. 2015). Bacteria such as *Azotobacter, Bacillus, Enterobacter, Flavobacterium, Rhizobium* are categorized under phosphate solubilizing bacteria. Plants always need phosphorus for nutrition. Now-a-days biotechnology approaches are used for efficient use of P from soil to plants involving PGPR bacterial inoculation (Elizabeth et al. 2017). Due to providing nutrition to plants, phosphate solubilizing rhizobacteria are used as an alternative to chemical fertilizers for development and production in *Triticum aestivum* var. Galaxy 2013 (Batool and Iqbal 2019).

Aerobic soils contain iron in the ferric form which is not readily accessible by plants. Bacteria considered under plant growth-promoting rhizobacteria secrete siderophores which are soluble in water, produce iron chelators that assist the soil ferric ions to get accessible by plants. Therefore, PGPR-mediated iron sequestration is one of the important to survive with such a limited supply of iron. It is mediated through low-molecular-mass siderophores (~400–1500 Da) that bind with Fe^{+3} and attach to bacterial membrane receptors to form Fe-siderophore complex, thereby microorganisms facilitate the reduction of iron and compensate the iron nutrition in the plants.

In some non-Gramineae plants rhizosphere needs acidification for efficient utilization of iron. Generally, iron in soil is present in ferric form. Siderophores increases the solubility of iron through proton extrusion; because it lowers the soil pH and this process enhances the trans-plasma membrane redox activity for ferric to ferrous reduction via ferric chelate reductase transport ferrous form into root cell via iron regulator transporter1 (IRT1) and in some plant such as Gramineae they secrete mugineic phytosiderophore via efflux transporter of mugineic acid (TOM1) present in the plant for solubilizing ferric ion in the rhizosphere and transport into the plant via yellow stripe 1 transporter with the help of Fe(III) phytosiderophore complex (Cely et al. 2016). In this way, iron availability to plants is in under circumference of redox potential and pH of the soil and siderophores secreting microbes are quite helpful in the absorption of iron; apart from the uptake of iron they also assist in tackling and controlling the stress conditions imposed on plants by high heavy metal content present in soil (Saif and Khan 2018). Generally, bacteria produce few kinds of siderophore such as hydroxamate, catecholate, salicylate, carboxylate; and their amount gets changed according to the PGPR bacteria.

The leguminous plants need more iron-containing protein for nodulation in comparison to non-nodulating plants. It has been observed that Fe deficiency in soil can induce signals for phenolic exudation which alters the rhizosphere microbial environment (Jin et al. 2014). Under the PGPR section, *Escherichia coli, Salmonella, Klebsiella pneumoniae, Vibrio cholerae, Vibrio anguillarum, Aeromonas, Aerobacter aerogenes, Enterobacter, Yersinia and Mycobacterium* species, *Geobacter sulfurreducens,* are very popular. The ferrous amount converted from Ferric present in soil can be measured from Ferrozine assay and determine its concentration from UV spectrophotometer. Further, scanning electron microscopy, energy disperse spectroscopy, Fourier transformed infrared spectroscopy, and X-ray diffraction are used for analysis. Malachite green is used for the cross-check of iron content and quantification (Polgari et al. 2019; Kooli et al. 2018; Kannahi and Senbagam 2014).

4.2.1.2 Modulating Phytohormone Levels

Phytohormones play significant roles in plants related to cell division, cell growth, cell development, vascular bundle development, and are ultimately involved in plant growth. Apart from these attributes, they have the ability to cope in adaption in the changing environmental conditions including reduction of stress conditions (Dilfuza et al. 2017). Endogenous phytohormones of the plant are variable in relation to the environmental conditions and are adjusted accordingly in order to tackle the negative effects of environmental stress. Soil bacteria are reported for phytohormone production in several reports especially Plant growth Promoting bacteria and can produce either cytokinins or gibberellins or both or auxins, such as indole acetic acid viz. within the acellular strains of *Acinetobacter* sp., *Rhizobium* sp., *Mycobacterium, Pseudomonas sp., Bacillus sp., Rahnella, Arthrobacter, Klebsiella,* and *Paenibacillus polymyxa* (Verma et al. 2016). Moreover, plant growth promotion by auxin, cytokinin, gibberellins, and other phytohormones is involved in different activity related to plants growth and development.

Phytohormone affects differently in different parts of plants such as auxin is involved in the plant cell division, cell development, cell elongation, tissue differentiation, apical dominance, root growth formation and assist in the germination. Indole 3 acetic acid (IAA) is well-known auxins produced by many PGPRs. IAA effects on branching number, weight, size, enhance the surface area in the soil which increase the nutrition exchange, re-differentiate root tissue from stem tissue, and overall IAA support plant growth (Gouda et al. 2018). Different PGPRs have different pathways for the synthesis of IAA such as *Rhizobium, Bradyrhizobium, Azospirillum* synthesize via indole 3 pyruvic acid pathways; some pathogenic bacteria *Agrobacterium tumefaciens, Pseudomonas syringe, Pantoea agglomerans, Rhizobium, Bradyrhizobium* and *Erwinia herbicola* synthesize IAA via Indole 3 acetamide pathways; and *Bacillus subtilis*, *B. licheniformis*, *B. megaterium*, etc. produce IAA via. tryptamine pathway.

Indole acetic acid is produced in *Azospirillum brasilense* by the independent pathway of L-tryptophan. Cytokinins involved in the shoot development, cellular proliferation, differentiation activity, influence physiological processes, involved in chlorophyll production, enhanced root hair production, promotion of seed germination and assist in grain filling stage. Plant growth-promoting strains of bacteria isolated from barley, canola, bean, and Arabidopsis plants produce cytokinins. The bacteria belong to the genera, *Pseudomonas Azospirillum*, *Bacillus, Proteus*, *Klebsiella, Escherichia*, *Xanthomonas*, *Rhizobium, Bradyrhizobium* etc. Zeatin and Kinetin are abundant cytokinins widely produced by plant growth-promoting rhizobacteria.

Abscisic acid plays important role in adaption and growth regulation. Gibberellic acid shows the importance in their shoot growth, seed germination, stem elongation, flowering, and fruit setting and assist in maintaining the metabolism of plants. Among *Bacillus* sp., two strains show prominent production of gibberellic acid; *B. pumilus* and *B. licheniformis*. Besides, *Azospirillum* sp. and *Rhizobium meliloti*, *Acetobacter diazotrophicus*, *Herbaspirillum seropedicae* are also popular PGPRs (Gouda et al. 2018). Ethylene hormone is also quite essential for growth and development. PGPRs microbes involved in ethylene regulation possess the enzyme 1-aminocyclopropane 1-carboxylate deaminase enzyme which protects plants from adverse environmental situations, and also reduces senescence and facilitates nodulation (Muhammad et al. 2007). *Pseudomonas putida* UW4, *Azospirillum lipoferum* 4B, *Rhizobium leguminosarum* bv *viciae* 128C53K, *Agrobacterium* spp., *Achromobacter* spp., *Burkholderia* spp., *Ralstonia* spp., *Enterobacter* spp. *Mesorhizobium*, *Phyllobacterium brassicacearum* STM196 isolated from *Arabidopsis thaliana* seedlings are responsible for regulation of ethylene production.

Several microbes produce groups of phytohormone that aid plant growth and development such as *Pseudomonas putida, Enterobacter asburiae, Pantoea agglomerans, Rhodospirillum rubrum, Pseudomonas fluorescens, P. aeruginosa, Paenibacillus polymyxa, Stenotrophomonas maltophilia, Mesorhizobium ciceri, Klebsiella oxytoca, Bacillus subtilis, Azotobacter chroococcum and Rhizobium leguminosarum* stimulate the auxins, gibberellins, kinetin and ethylene production (Dilfuza et al. 2017).

4.2.2 Indirect Mechanisms

Indirect action of plant growth-promoting rhizobacteria is related to its ability to act against phytopathogenic species and thus promote the plant growth and development by providing safe uncompetitive surrounding to the plants. Understanding the indirect mechanism of plant growth-promoting rhizobacterial action may add to the exploration of the best biocontrol agents replacing the commercial chemical pesticides and other agro-additives used presently for the control of plant diseases.

4.2.2.1 Antibiotics and Lytic Enzymes

Antibiotic synthesis by plant growth promoting bacteria is an important trait that prevents the proliferation of plant pathogens (Beneduzi et al. 2012). Some of these biocontrol PGPR strains have been commercialized. To prevent antibiotic resistance development, some biocontrol strains synthesizing hydrogen cyanide as well as one or more antibiotics have been utilized. Some biocontrol bacteria produce lytic enzymes that can lyse portion of the cell wall of many pathogenic microorganisms. Plant growth promoting bacteria which are able to synthesize one or more of these antibiotic is found to have biocontrol activity against a range of pathogenic microorganism including pyrrolnitrin and 2,4 DAPG antibiotics from *P. fluorescens* BL915 for *Pythium*; Phenazine antibiotic from *Pseudomonas* for *Fusarium oxysporum;* Circulin, polymyxin and colistin antibiotics from *Bacillus* sp. for gram-negative, gram-positive bacteria and pathogenic fungi; and Fngycin and iturin antibiotics from *Bacillus subtilis*. Apart from these other well-known antibiotics are Oomycin A, Viscosinamide, Butyrolactones, Kanosamine, Pseudomonic acid, Azomycin produced by PGPRs (Tariq et al. 2017).

4.2.2.2 Siderophores

Siderophores are low molecular weight organic compounds consisting of hydroxamates (composed of a hydroxyl group closely associated with a nitrogenous portion of the molecules) which have a high affinity for multivalent iron chelators that transport iron into bacterial cells. Siderophores produced by Plant growth promoting bacteria acquire iron in sufficient quantity, and thus, can prevent some phytopathogens growth and thereby limiting their ability to proliferate (Beneduzi et al. 2013). It is one of the effective mechanisms of biological control by plant growth promoting bacteria which are able to produce siderophores that forms a complex with iron and deprive pathogenic microorganism and lead them for starvation by causing non-availability of iron. The concentration of siderophore in the soil is approximately 10^{-30} M. Siderophore-producing bacteria usually encountered are *Pseudomonas fluorescens* and *Pseudomonas aeruginosa* which release pyochelin and pyoverdine type of siderophores like, Fe–ferrioxamine for oat, Fe–pyoverdine for Arabidopsis, Fe–erobactin for soybean and oat, Fe–rhizoferrin for tomato, barley, and corn and *Bacillus subtilis* GB03 form *Arabidopsis* (Nadeem et al. 2015; Chaparro et al. 2012; Sayyed et al. 2013; Jin et al. 2014).

4.2.2.3 Competition

Disease incidence and severity depends upon the competition between pathogens and nonpathogenic plant growth promoting bacterial species. PGPR microorganism assists in controlling pathogen growth by producing a limiting factor for the pathogenic microorganism in the nutrition and their fundamental niche. Similarly, it is observed that the leaf bacterium *Sphingomonas* sp. produces a shield to plants from the bacterial pathogen *Pseudomonas syringae* and *Bacillus* sp. shows the competition for nutrition to *Botrytis cinerea* (Innerebner et al. 2011; Kundan et al. 2015).

4.2.2.4 Ethylene

The presence of phytopathogens forms a typical stress response resulting in ethylene production in plants which exacerbates the effects of the stress on the plant (Muhammad et al. 2007). Thus, regulation of plant's ethylene is quite responsive to cope up the plants from biotic and abiotic stresses. It assists the plants in PGPR colonization and elimination of phytopathogen and root formation by regulating auxin transport within root tip zone of the root. Gene coding ethylene synthesis enzymes such as ACC synthase, ACC oxidase, ACC deaminase containing plant growth-promoting rhizobacteria can easily mediate this effect and maintain the homeostasis of the hormone.

4.2.2.5 Induced Systemic Resistance

Plant growth-promoting rhizobacteria and pathogenic microorganism induce the phenomenon of induced systemic resistance and systemic acquired resistance, respectively, in the plants; which trigger against a broad spectrum of a plant pathogen. There is a slight difference in the induction of the plant immune system through PGPR microorganisms and pathogenic microorganisms. PGPR-related induced systemic resistance involves primarily jasmonic acid and ethylene phytohormone in the defense process while systemic acquired resistance related to plant-pathogen involves salicylic acid which induced the pathogenesis-related proteins. Therefore, induced systemic resistance and systemic acquired resistance regulate different signaling pathways for defense in plants. These phytohormones are involved in the host plant's defense stimulation which results in tackling responses against a range of pathogens.

However, both induced systemic resistance and systemic acquired resistance are related to defense activity but induced systemic resistance defense is faster, higher, and more effective than systemic acquired resistance defense. Several enzymes activated for defense in induced systemic resistance is chitinase, β-1, 3-glucanase, phenylalanine ammonia lyase, polyphenol oxidase, peroxidase, lipoxygenase, Superoxide Dismutase, Catalase, and Ascorbate peroxidase along with some proteinase inhibitors (Annapurna et al. 2013; Romera et al. 2019).

4.3 Ecology of Interactions of Plant Growth-Promoting Rhizobacteria

Understanding ecological aspects of plant growth-promoting rhizobacterial interactions are of prime importance to achieve sustainable agriculture in the present climatic scenario. Rhizosphere ecology is very complex involving physical and chemical interactions of different PGPRs, plants, and other organisms which overall affects the soil fertility and crop yield which is of main interest to humankind for understanding the plant growth-promoting rhizobacterial ecology. Thus, there is a need to understand such synergistic PGPR interactions under phyto-microbiome through holistic studies which include PGPR symbionts, soil microbiota, and other components constituting this ecosystem (Hol et al. 2013).

4.3.1 Symbiotic Organisms

Rhizobium and Leguminosae symbiotic association are one of the crucial sources of nitrogen supplementation in the soil. However, this association is influenced by various abiotic and biotic factors in the rhizosphere. It has been observed through various studies that several mutualistic species benefit the plants much in comparison to a single mutualistic relationship (Hol et al. 2013). Such observations are also seen in the case of successful nodulation in leguminous plants by different *Rhizobium* sp. Several plant growth-promoting rhizobacteria are observed to increase the nodulation efficiency of *Rhizobium* strains, and thus, nitrogen fixation (Subramaniam et al. 2015). Apart from the nodulation, at biochemical levels, plant growth-promoting rhizobacteria had been observed to increase the nitrogenase activity which in turn increases crop yield.

The nodulation incrementation, however, varies on the *Rhizobium* and plant growth-promoting rhizobacterial strains used for the study. In addition to PGPR effect on nodulation, it was observed that such a system also helps in tackling abiotic and biotic stresses. In a report, plant growth-promoting rhizobacterial inoculation helped in escaping low-temperature stress in Chickpea (Nascimento et al. 2016). Similarly, the synergistic relationship of rhizobium, PGPR, and phosphate solubilizing bacteria helps in better development of legume crops increasing production, nitrogenase activity, mineral uptake, shoot and root development, chlorophyll content and fresh and dry weight. However, effect of PGPR varies according to inoculation modes of PGPR and rhizobia controlling infection, nodulation and nitrogen fixation (Tajini et al. 2012).

Similar to the rhizobial symbiotic associations, mycorrhizal symbiotic associations influence the water and nutrient absorption in plant roots and thus help in plant growth and development along with protection against many plant diseases. Arbuscular Mycorrhiza fungi are seen to be associated with 80% of plant species where they act as the inter-connections between soil and root in the form of spores, hyphae, propagules, or extraradical hyphae (Carolina et al. 2000). Mycorrhizal association starts with intraradical hyphae growing along with the cortical cells and arbuscules formation establishing root colonization and this process is influenced by rhizosphere microbiota.

It is well established that both endo as well as ectomycorrhizal associations are influenced by the microbial population of the rhizosphere and such interactions are of prime interest. However, the complexity of such interactions hinders the better utilization of these symbiotic associations for crop sustainability (Pravin et al. 2016). Beneficial effects of the PGPR on mycorrhizae had been reflected in many studies which include enhancements in root colonization, soil improvement in terms of nitrogen content and organic matter, potential incrementation of plant resistance against pathogen attack, stress adaptation, etc. These all parameters are influenced by extracellular factors from rhizobacteria as well as the plant which influences the mycorrhizal association and thus there is a need of elucidation of the physical and chemical factors (Beneduzi et al. 2012; Sood 2003).

4.3.2 Other Microorganisms

The effect of plant growth-promoting rhizobacteria on the rhizosphere microbiota has been extensively worked out under different conditions including gnotobiotic, greenhouse, and native natural conditions. Studies related to the microbiota of rhizosphere reflected that it is very variable and changes from crop to crop, soil to the soil as well as during different stages of the plant (Shahbaz et al. 2017). plant growth-promoting rhizobacteria are also seen to be the modifier of rhizosphere microbiota due to their influence on different ecological interactions (Probanza et al. 1996). Zhang et al. 2019 worked on the sweet pepper system and reported the effect of plant growth-promoting rhizobacterial consortium on rhizosphere biota which results in disease suppression and protection against stress conditions. It has been observed that plant growth-promoting rhizobacteria acts on soil health improvement in terms of total nitrogen, organic carbon, ammonium nitrogen form, potassium and phosphorus availability, thus transforming rhizosphere ecology which favours the plant growth and development escaping adverse effects of the abiotic and biotic stress conditions (Cummings 2009). Plant growth-promoting rhizobacteria-mediated induced systemic resistance is determined by the presence of lipopolysaccharides, siderophores, and salicylic acid which are its major determinants.

4.3.3 Soil Fauna

Rhizosphere ecology accompanies efficient nutrient cycling which is controlled by the interrelationship of plant roots, microorganisms, and animals and it acts as a determinant of mineral nutrient availability from soil to plant root system (Mohamed et al. 2019). The release of root exudates initiates the process of the microbial loop in the soil which is responsible for the increase in microbial biomass. Microbial growth results in the sequestration of nutrients which are re-mobilized for plant uptake due to the microbial consumption by soil fauna. Protozoa and nematodes constitute an important population in this process which is responsible for 70% and 15% respectively of total respiration of soil animals. Protozoa and saprozoic nematodes show plant growth-promoting activity indirectly, mainly due to their key role in N-mineralization.

Interactions between protozoa and rhizobacteria in the rhizosphere which acts through the mechanism which is identified as "the microbial loop in soil" are well-known to have positive effects on plant growth. Protozoa-mediated plant growth promotion occurs due to their effect on the plant root system, rhizosphere microbiota composition, and nutrient cycling which also includes the addition of nutrients from the digestion of bacterial biomass consumed by them for their development and growth. This effect is very similar to what we termed as the "plant-growth-promoting" or "hormonal" effect. Nematodes usually inhibit plant growth and development, and thus, plant growth-promoting rhizobacteria-nematodes interactions have mainly been studied from the biocontrol point of view. Several genera are reported to have biocontrol activity against nematodes due to the production of extracellular hydrolytic enzymes, cyanide and oxidizing agents. Nematicidal activities has been reported from the following genera *Agrobacterium*, *Alcaligenes*, *Bacillus*, *Clostridium*, *Desulfovibrio*, *Pseudomonas*, *Serratia,* and *Streptomyces* (Cetintas et al. 2018).

4.3.4 Host Rhizospheric and Endophytic Relationships

Plant-rhizobacteria relationship enhances the nutrient availability to the root system and this involves intricate physical as well as chemical interactions to modify the rhizosphere ecology which favours plant growth and development. Similarly, endophytes are the beneficial microorganisms residing in the apo-plastic space and favours the plant growth and developments due to their traits like siderophore production, 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activity, and inorganic phosphate solubilization (Lally et al. 2017). Therefore, plant growth-promoting rhizobacteria and host relationships are mainly categorized into two levels of complexity i.e., rhizospheric and endophytic (Vinayarani and Prakash 2018). Recently, Cheng et al. (2019) worked on the rhizospheric and endophytic PGPR communities of an invasive plant *Sinecio vulgaris,* and reported different types of PGPR imparting plants to develop efficiently due to phosphate solubilization and nitrogen fixation. In the same study, some of these PGPRs also improve plant capacity to potentially fight against different biotic as well as abiotic stresses. Recently, endophytic and rhizospheric culturable bacterial communities were characterized from Maize roots which were irrigated with municipal and industrial wastewater and their findings are interesting to notice that most of the PGPR isolated are salinity and heavy metal resistant. Plant growth-promoting rhizobacteria have more potential of heavy metal tolerance than the endophytic ones along with their increased root colonization under wastewater irrigation in comparison to control (Abedinzadeh et al. 2019).

4.4 Improving Rhizobacterial Potential by Genetic Modification

The identification of genes related to the ability of rhizobacterial strains to plant growth promotion creates the potential to improve the capability of biocontrol strains or to construct novel biocontrol strains by genetic modification tools. With the advancements in molecular biology techniques, the genetically-modified rhizobacteria have been developed with additional features such as contaminant-degrading genes that have been transferred to conduct the bioremediation in the rhizosphere. However, many technologies have been developed including high throughput sequencing of bacterial genomes and genome editing techniques which facilitate the genome modification apart from improvements in the visualization and imaging techniques for more close observation in biocontrol behaviour (Glandorf 2019). Table 4.2 enlists few genetically modified plant growth-promoting rhizobacteria.

Important issues related to the selection of compatible strain for gene modification and incorporation into the rhizosphere includes: (1) Stability of the strain after cloning and the high expression of the target gene in the host strain; (2) Tolerance of the strain towards contaminants or insensitiveness to the contaminants; and (3) Survival of the strains as some strains can survive only in specific plant rhizosphere even after genetic modification. Before marketing genetically modified biocontrol agents registered as a plant protection product, the effect of genetically modified plants on humans and the environment must be ascertained.

Some studies have shown that gene introduction into plant growth-promoting rhizobacteria enhanced the capability of rhizobacteria (Maxime et al. 2014). Several genes are identified through whole-genome sequencing includes, *pqq* gene for Phosphate solubilization, *acdS* gene for ACC deaminase activity, *phzF* gene for phenazine production, *pvd* gene for siderophore production, *chiA* gene for chitinase production, *cry* gene for insecticidal activity, *nif* gene of *Rhizobium* for nitrogen fixation and *phl* gene for phloroglucinol synthesis. Few genes are transferred into PGPR strain such as *nif* gene in *Paenibacillus* strains via horizontal gene transfer from Frankia.

Phosphate solubilizing *Pseudomonas* sp. strain P34 enhanced the growth of wheat and can be utilized as biofertilizer (Liu et al. 2019). The genes transferred from *P. fluorescens* WCS365 have also been shown to improve the competitive colonization capability of other *Pseudomonas* isolates. *Pseudomonas capeferrum* (WCS$_{35}$8r) has been modified to produce naturally occurring secondary metabolites like, phenazine carboxylic acid or 2,4 diacetyl phloroglucinol (DAPG); these secondary metabolites help plants in defence and are indirectly involved in enhancing

Table 4.2 Genetic Engineering of plant growth-promoting rhizobacteria. Various plant growth-promoting rhizobacteria are modified through genetic modification for desired traits for better utilization

S. no.	Plant growth-promoting rhizobacteria	Plants	Genetic modifications	Traits	References
1	*Pseudomonas fluorescens*	*Oryza sativa L.*	EMS mutation; UV mutation	Improved production of plant growth-promoting substances and phosphate solubilization	Sivasakthi et al. (2015)
2	*Bacillus subtilis*	*Oryza sativa L.*	EMS mutation UV mutation	Improved production of plant growth-promoting substances & phosphate solubilization	Sivasakthi et al. (2015)
3	*Pseudomonas aeruginosa*	Tobacco	Expression of salicylic acid biosynthesis genes	Improvement of salicylic acid production	Maurhofer et al. (1998)
4	*Pseudomonas*, *Bacillus*, *E. coli*, *Proteus*, *Shigella*	Fenugreek	Physical agents (UV) and chemical agent (EMS)	Seed germination promotion	Queen et al. (2016)
5	Bacterial isolates	*Withania somnifera*	Physical agent (UV B exposure)	Seed germination promotion	Rathaur et al. (2012)
6	*Bacillus amyloliquefaciens* subsp. plantarum SA5	–	Protoplast fusion technique	Improving the nematicidal potential	Abdel-Salam et al. (2018)
7	*Lysinibacillussphaericus* Amira strain	–	Protoplast fusion technique	Improving the nematicidal potential	Abdel-Salam et al. (2018)
8	*Sinorhizobium* strains	Lettuce (*L. sativa*)	–	High growth-promoting effect	Galleguillos et al. (2000)
9	*Azospirillum brasilense* Sp245	Wheat	ipdC gene expression which codes for IAA production	Better phyto-stimulatory properties	Baudoin et al. (2010)
10	*Azospirillum brasilense* Sp6	*Sorghum bicolor* L.	Gene mutation and tagging	Overproduction of indole-3-acetic acid	Basaglia et al. (2003)

EMS ethyl methane sulfonate, *UV* ultraviolet

productivity (Glandorf 2019). Genetic modified *Azospirillum* strains known for higher production of IAA, promote the growth and nitrogen uptake. Several studies are already done on genetically modified PGPR strains expressing 1-amino cyclopropane-1-carboxylic acid (ACC) deaminase activity gene for plant growth and protection plant from diseases (Gupta and Pandey 2019).

Advancement in technology includes next-generation sequencing, Transcriptome engineering, genetic editing, microarray-based gene expression analysis, gene expression profiling, qRT-PCR, metabolomics, proteomics, and other omics technologies that provides a new direction in understanding rhizospheric microbes ecology, biology, and chemistry. The present need for agriculture is to enhance soil fertility and plant growth for better yield without chemical additives. These technologies provide convenient insight into microbial ecology to fulfil the requirement of present agriculture.

Rhizosphere engineering related to plant growth-promoting rhizobacteria may also contribute to plant development and growth for more production. Microbial exudates such as metabolites, small peptides, lipids, proteins stimulate the growth of plants by different interactions (Canarini et al. 2019). In rhizosphere engineering, synthetic biology techniques are used to incorporate the beneficial PGPR microbial strains in the rhizosphere to harvest maximum benefits of microbes. Besides introducing plant growth-promoting rhizobacterial strains, genetically engineered plants are also exploited to alter the rhizosphere (Rondon et al. 1999). Genetically modified plants change their root exudate profile and manipulate gene expression levels which facilitates interaction with plant growth-promoting microorganisms around the root zone of plants.

The Root exudates serve as communicating molecules for biological and physiological interactions in the rhizospheric zone. Even simple inoculation of plant growth-promoting rhizobacterial strains in plants may alter expression of some of the genes. In spite of specific, these changes are random and it require lots of exercises in order to reduce time for engineering. In context to plants several transporters such as UMAMIT transporter, CAT transporter, GDU transporter for amino acid, SWEET transporter for sugar, ALMT/Malate, MATE/citrate transporter for organic acid has been modified to enhance the root exudates. Under control of constitutive promoter *GOS2* and root-specific promoter *RCc3,* overexpression of *OsNAC10* gene in rice increases plant tolerance to drought, high salinity, and low temperature at the vegetative stage (Jeong et al. 2010).

Gene transition in transgenic plants has been constructed for higher efficiency of remediation in compare to bacterial transgenic. A popular example is a transgenic plant of ACC deaminase gene expression exhibits much more advantages over its expression in the bacterial system: (1) the ACC deaminase activity in bacteria is much lower than in the -in transgenic plants during initial stages; (2) it leads to a higher metal accumulation due to constant stimulation of the plant growth; (3) increase in the shoot/root ratio in some cases. However, sometimes constitutive expression of some genes may lead to such modified plants which may perform worse than the original plant because of the fact that transfer of even single trait can have profound effect on plant-rhizosphere interaction which may have adverse effect on plant performance.

4.5 Commercialization of Plant Growth Promoting Rhizobacteria

Plant Stress management in agriculture needs different strategies for sustainable agricultural productivity. Plant growth-promoting rhizobacterial inoculation is one of the crucial strategies employed for an increase in crop yield. However, the results are not satisfactory in many cases due to the limitation in the accurate knowledge about the plant-PGPR system and its mechanism of action. Commercial use of plant growth-promoting rhizobacteria belonging to the microbial genera like, *Agrobacterium, Azospirillum, Azotobacter, Bacillus, Burkholderia, Paenibacillus, Pantoea, Pseudomonas, Serratia, Streptomyces, Rhizobium* are used commercially for the efficient crop cultivation (Backer et al. 2018). Bacterial bio-inoculants as biocontrol agents are also recently available in the markets which belong mostly to the genera *Azospirillum, Bacillus, Pseudomonas, Serratia, Streptomyces, etc.* for improving the disease-fighting potential of plants (Bushra et al. 2017).

Although commercial use of plant growth-promoting rhizobacteria as biofertilizers, biocontrol agents is very lucrative and presents an eco-friendly solution to the recalcitrant chemical pesticides, fertilizers, their application is limited by the knowledge gap related to the following parameters viz. mechanism of action involved, growth parameters, large-scale production, cost-effective formulation, marketing, ease of use, and farmer awareness (Rachel et al. 2018). These constraints can be tackled by the multidisciplinary study of plant-PGPR-surrounding interactions and identifying the different physical and chemical principles involved in the establishment of conditions favouring the efficient growth and development of plants.

This requires extensive studies of direct as well as indirect mechanisms utilized by PGPR which include growth regulator production, nitrogen fixation, siderophore production, phosphate solubilisation, antibiotics production, extracellular secretion of different hydrolases, and competitive inhibition of pathogens (Bushra et al. 2017). The need for sustainable substitutes to the chemical agro-additives is necessary for the enhancement of crop yield under the changing climatic conditions but it should be carried out keeping the fact that PGPR can also pave potential eco-hazards due to microbial nature (Carlos et al. 2019). This, therefore, necessitates the evaluation of biosafety aspects of different PGPR released for commercialization and used for agricultural production.

4.6 Perspective

Plant growth-promoting rhizobacteria are emerging as an efficient alternative to chemical agro-additives, which are being used under formulated regulations and sometimes forbidden completely (Anwar et al. 2017; Mohd et al. 2019). Agricultural applications depend upon the better elucidation of PGPR properties and mechanisms underlying at both molecular as well as the genetic levels which strongly promotes the performance of PGPR as agro-additive. Such understanding also narrows the gap occurring in beneficial effects under gnotobiotic conditions and at the field applications (Nailwal et al. 2014; Rocheli et al. 2015). This will also impart the potential to enhance the plant growth promotion activity of plant growth-promoting rhizobacteria utilizing the advanced genetic modification methods.

Plant growth promoting activity can also be supplemented using consortium strategies i.e., combination of different plant growth-promoting rhizobacteria in place of using a single strain and in most of the cases this helps in increasing the crop productivity (Carlos et al. 2019). The beneficial effects are also achieved if we include the soil studies and inoculation of plant growth-promoting rhizobacteria as per the native nature of the soil. The success of plant growth-promoting rhizobacterial inoculation depends upon the soil factors including both the abiotic as well as biotic. We know that plant and beneficial microbes form a holobiont system in which plant provides the microbes with reduced carbon and other important metabolites and in return, microbes provide better nutrient bioavailability, assimilation, soil texture modification, root colonization, pathogen control, etc. This takes place by a large array of chemical secretion from the plant as well as microbes (Lally et al. 2017). Thus, presently researches are carried to study plant root exudate which comprises various chemical compounds which act as root colonization signals for the beneficial microorganisms.

Similarly, analysing the microbial signalling in the rhizosphere helps in developing a better agro-inoculant and alleviates problems associated with the failure of most of plant growth-promoting rhizobacteria under the field study. The genetic-engineering technologies and their advanced variations greatly expand the extension and degree of bioremediation (Patel et al. 2016). However, applications are constrained due to a lack of understanding of genetic mechanisms underlying the plant growth-promoting rhizobacterial action especially the establishment of the plant growth-promoting rhizobacteria in its host plant rhizosphere which is affected by various contaminants including high concentrations of heavy metals (Ojuederie and Babalola 2017; Saima and Mohammad 2017; Shukla et al. 2011). Thus, this requires a holistic study of the biochemical nature of the signalling compounds which helps in the establishment of plant-PGPR holobiont system along with the elucidation of genetic changes that control such signalling. Therefore, it is the utmost requirement to decipher the interrelations of this system by genomics, metabolomics, and proteomics high throughput tools.

4.7 Conclusion

The plant-microbe interrelationships as understood by various research works represents the necessity of analysing in detail what we term as “Phytomicrobiome”. Studies related to the composition of Phytomicrobiome, signalling and variations at different stages of the plant as well as in different plants revealed many interesting factors which influence plant growth and development. It is now well established that the success of plant growth-promoting rhizobacteria-based agro-additives doesn't only requires isolation and study of a plant growth-promoting rhizobacterial strain but needs also to carry out the detailed study of compatibility between the plant growth-promoting rhizobacteria, plant, and phytomicrobiome. This will result in the potential application of plant growth-promoting rhizobacteria for sustainable crop management. Presently, we are at infancy in understanding such interrelationships and require studying the phyto-PGPR system by applying advanced methods of analysis. Thus, presently plant growth-promoting rhizobacterial research has a similar impetus as in previous decades, and it's revealing the many intricate plant-microbe relationships in soil with the help of advanced life science technologies.

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