Chapter 12
Role of PGPR in Soil Fertility and Plant Health

Ram Prasad, Manoj Kumar, and Ajit Varma

12.1 Introduction

Plant growth-promoting rhizobacteria (PGPR) are naturally occurring soil bacteria that aggressively colonize plant roots and benefit plants health. Their use in crop production can reduce the agro-chemical use and support eco-friendly sustainable food production. Plant growth promotion by PGPR is due to root hair proliferation, root hair deformation and branching, increases in seedling emergence, early nodulation and nodule functioning, enhanced leaf surface area, vigor, biomass, phytohormone, nutrient, water and air uptake, promoted accumulation of carbohydrates, and yield in various plant species (Podile and Kishore 2006). PGPR bring nutrient elements into the ecosystem from atmospheric or mineral reserves in soluble form; the roots take up the nutrients, break down the detritus, and also protect the roots from pathogens. Microorganisms are great potential goldmine for the biotechnology industry because it offers countless new genes and biochemical pathways to probe for enzymes, antibiotics, and other useful molecules.

Soil is the natural habitat for microorganisms beneficial as well as harmful to plant community. They play an important role in soil processes that determine plant productivity. For successful functioning of introduced microbial bioinoculants and their influence on soil health, exhaustive efforts have been made to explore soil microbial diversity of indigenous community, their distribution and behavior in soil habitats. PGPR involved in various beneficial activities within the soil like decomposition of crop residues, mineralization of soil organic matter, immobilization of mineral nutrients, phosphate solubilizers, synthesis of soil organic matter, nitrification, nitrogen fixation, and plant growth promoters including nutrient acquisition (biofertilizers), phytohormone production (biostimulants), and suppression of plant

---

R. Prasad (✉) • M. Kumar • A. Varma
Amity Institute of Microbial Technology, Amity University, Sector-125, Noida, Uttar Pradesh 201303, India
e-mail: rprasad@amity.edu; mkumar9@amity.edu; ajitvarma@amity.edu

D. Egamberdieva et al. (eds.), *Plant-Growth-Promoting Rhizobacteria (PGPR) and Medicinal Plants*, Soil Biology 42, DOI 10.1007/978-3-319-13401-7_12

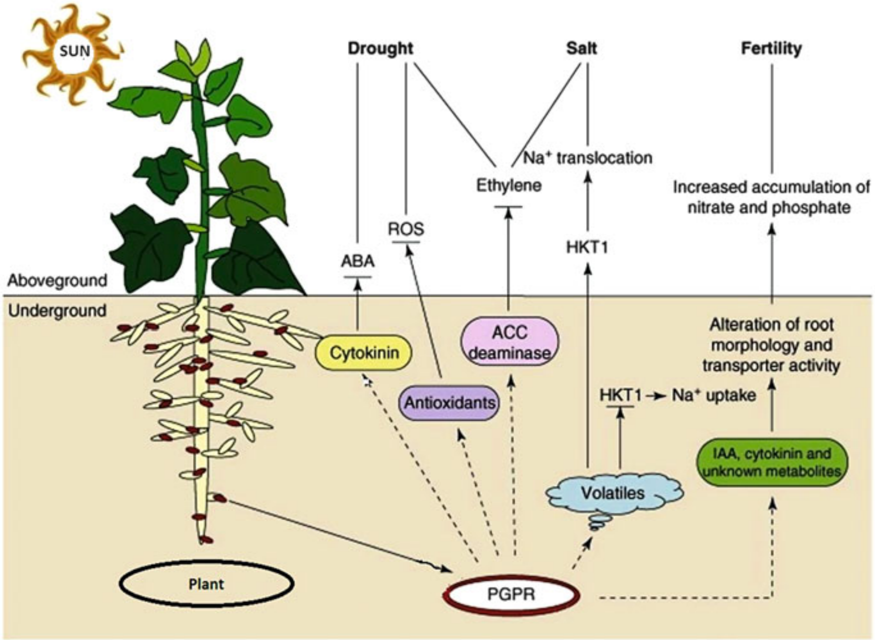


Fig. 12.1 Plant growth-promoting rhizobacteria has potential role in developing sustainable systems in crop production (Courtesy by: PakAgri farming)

disease (termed bioprotectants), which help in crop production and protection. Soil moisture content affects the colonization of the plant rhizosphere by the PGPR after inoculation (Shrivastava et al. 2014). In the recent era of sustainable crop production, the plant–microbe interactions in the rhizosphere play a pivotal role in transformation, mobilization, solubilization, etc. of nutrients from a limited nutrient pool and subsequently uptake of essential nutrients by plants to realize their full genetic potential (Fig. 12.1).

At present, the use of biological approaches is becoming more popular as an additive to chemical fertilizers for improving crop yield in an integrated plant nutrient management system. In this regard, the use of PGPR has found a potential role in developing sustainable systems in crop production. A variety of symbiotic (*Rhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Allorhizobium*, *Sinorhizobium*, *Mesorhizobium*) and free-living nitrogen-fixing bacteria or associative nitrogen fixers, viz. *Azospirillum*, *Azotobacter*, *Enterobacter*, *Klebsiella*, and *Pseudomonas*, are now being used in enhancing plant productivity (Cocking 2003). In the rhizosphere, rhizobacteria not only benefit from the nutrients secreted by the plant root but also beneficially influence the plant in a direct or indirect way, resulting in a stimulation of its growth. These PGPR can be classified according to their beneficial effects. For instance, biofertilizers can fix nitrogen, which can subsequently be used by the plant, thereby improving plant growth when the amount of nitrogen in the soil is limiting. Phytostimulators can directly promote the growth of plants, usually by the production of hormones. Biocontrol agents are able to protect plants from infection by phyto-pathogenic organisms. However, this may be a function of the type of bacterium utilized since high moisture content may decrease the oxygen content of the soil.

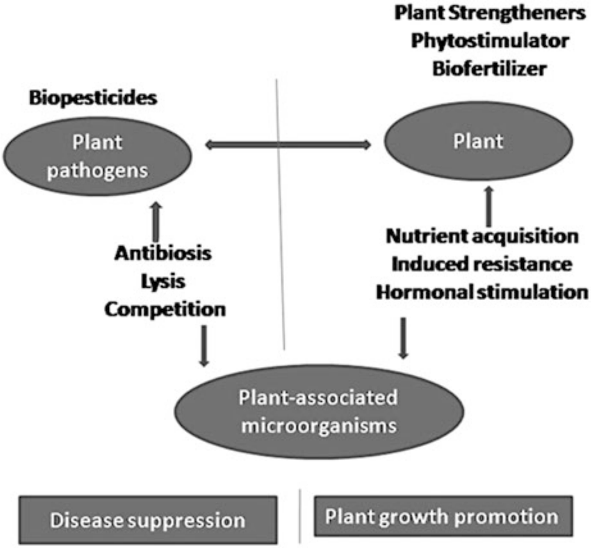
12.2 The Rhizosphere

Hiltner (1904) discovered that the rhizosphere, i.e., the layer of soil influenced by the root, is much richer in bacteria than the surrounding bulk soil. These rhizosphere microbes benefit because plant roots secrete metabolites that can be utilized as nutrients. This rhizosphere effect is caused by the fact that a substantial amount of the carbon fixed by the plant, 5–21 %, is secreted mainly as root exudates (Marschner 1995). The rhizosphere is the zone of soil surrounding a plant root where the biology and chemistry of the soil are influenced by the root. As roots grow through soil, they release water-soluble compounds such as amino acids, sugars, and organic acids that supply food for the microorganisms. The food supply means microbiological activity in the rhizosphere is much greater than in soil away from plant roots. In return, the microorganisms provide nutrients for the plants. Some microorganisms, including bacteria and mycorrhizal fungi, form associations with roots that are mutually beneficial to both the plant and the microorganism. The rhizosphere is a center of intense biological activity due to the food supply provided by the root exudates. Most soil microorganisms do not interact with plant roots, possibly due to the constant and diverse secretion of antimicrobial root exudates. However, there are some microorganisms that do interact with specific plants. These interactions can be pathogenic (invade and kill roots and plants), symbiotic (benefit plant growth), harmful (reduce plant growth), saprophytic (live on plant debris), or neutral (no effect on plants). Interactions that are beneficial to agriculture include mycorrhizae, legume nodulation, and production of antimicrobial compounds that inhibit the growth of pathogens (Fig. 12.2). Rhizosphere microorganisms produce vitamins, antibiotics, plant hormones, and communication molecules that all encourage plant growth (Shrivastava et al. 2014).

12.3 Plant Growth-Promoting Rhizobacteria

Rhizosphere represents a nutrient-rich habitat for microorganisms; on the other hand, the microbial colonization of the rhizosphere also affects the whole plant (Hartmann et al. 2008). Kloepper and Schroth (1978) suggest the term "PGPR" for an important group of rhizosphere bacteria that have beneficial effects on plant growth when colonizing roots. Such effects are earlier seedling emergence, and increased vigor, biomass, yield, as well as proliferation of the root system in various plants (Kloepper 1993). PGPR as biological control agents and the ineffectiveness

Fig. 12.2 PGPR promoting plant growth and health: mode of action and potential use in biotechnological applications



of PGPR in the field have often been attributed to their inability to colonize plant roots (Bloemberg and Lugtenberg 2001). A variety of bacterial traits and specific genes contribute to this process, but only a few have been identified (Benizri et al. 2001). These include motility, chemotaxis to seed and root exudates, production of pili or fimbriae, production of specific cell surface components, ability to use specific components of root exudates, protein secretion, and quorum sensing (Lugtenberg et al. 2001). Several rhizospheric bacteria are plant growth promoters stimulating seedling growth and development; while mycorrhizal fungi provide vegetation with increased efficiency of nutrient uptake, increased productivity and abiotic stress may contribute to plant diversity. These facts, among others, are leading to a possible paradigm shift to a more microbial dominated or at least highly reciprocal view of the relationship between plant and associated microbiota. PGPR enhance plant growth either by producing plant hormones or by enhancing nutrient uptake or absence of pathogens (Van Loon 2007).

12.4 Applications of PGPR

PGPR enhance plant growth due to various factors, among which the release of phytohormones, nitrogen fixation, and regulation of ethylene production in roots, solubilizing nutrients such as phosphate, siderophore production, promoting mycorrhizal function, and decreasing heavy metal toxicity are the most important (Whipps 2001). The plant properties that are improved by PGPR during phytoremediation include biomass, contaminant uptake, and plant nutrition and health. Grain yields also an indication of plant health and growth. Plant growth benefits due to the addition of PGPR include increases in germination rates, root growth, yield including grain, leaf area, chlorophyll content, magnesium content, nitrogen content, protein content, hydraulic activity, tolerance to drought, shoot and root weights, and delayed leaf senescence. Another major benefit of PGPR use is disease resistance conferred to the plant, sometimes known as "biocontrol" (Lucy et al. 2004).

The following genera of endophytes isolated from agricultural crops harbor PGPR-active strains: *Pseudomonas*, *Bacillus*, *Enterobacter*, and *Agrobacterium. Pseudomonas* spp. are typical PGPR and their reaction with arbuscular mycorrhizal fungi has been studied by Barea et al. (1998). *Pseudomonas* spp. had a positive effect on the spore germination and mycelial development of AMF in the soil as well as in root colonization. These bacteria (*Pseudomonas* spp.) have been called mycorrhization helper bacteria (Garbaye 1994). PGPR have stimulatory effect on the arbuscular mycorrhizae formation and plant nutrition (Barea et al. 2004). The ability to enter the root interior might help these microorganisms to evade the highly competitive rhizosphere habitat (Whipps 2001).

Siderophores, including salicylic acid, pyochelin, and pyoverdin, which chelate iron and other metals, also contribute to disease suppression by conferring a competitive advantage to biocontrol agents for the limited supply of essential trace minerals in natural habitat (Loper and Hankels 1997). Siderophores produced by PGPR inhibit the root pathogens by creating iron-limiting conditions in the rhizosphere and reduce probability of plant disease (Podile and Kishore 2006). Some siderophores such as pseudobacin and pyoverdin (yellow green fluorescent pigment of *Pseudomonas* bacteria) present high antimicrobial activity and affinity to ions of trivalent iron (Das et al. 2007; Maksimov et al. 2011). Pseudobacin is involved in induced systemic resistance, induction of H_2O_2 local storage, phenol compounds, and strengthening cell wall of rice plants in infection zone. Siderophores may indirectly stimulate the biosynthesis of other antimicrobial compounds by increasing the availability of these minerals to the bacteria. Antibiotics and siderophores may additionally function as stress factors or signal inducing local and systemic host resistance. Biosynthesis of antibiotics and other antifungal compounds is regulated by a cascade of endogenous signals.

12.5 Possible Mechanism of Interaction or Physiology of Interaction

Plant growth promotion can be achieved by the direct interaction between beneficial microbes and their host plant and also indirectly due to their antagonistic activity against plant pathogens. The current status of research, commercial development, and application of PGPR inoculants is to promote plant health and environmental sustainability. In comparison with chemically synthesized pesticides and fertilizers, microbial inoculants have several advantages: they are more safe, show reduced environmental damage and potentially smaller risk to human health, show much more targeted activity, are effective in small quantities, multiply themselves but are controlled by the plant as well as by the indigenous microbial populations, decompose more quickly than conventional chemical pesticides, resistance development is reduced due to several mechanisms, and can be also used in integrated pest management systems (Gabriele 2009; Chadha et al. 2014; Prasad et al. 2014).

The possible mechanisms by which PGPR aid plant growth include suppression of root pathogens through production of siderophores (compounds secreted by microorganisms that bind iron, making it less available to pathogens) or production of antibiotics (Kloepper et al. 1991), fixation of nitrogen (Chanway and Holl 1991), and production of plant hormones (Holl et al. 1988). PGPR are synergistic with mycorrhizae in stimulating plant growth and root colonization. There has been some success with PGPR in agriculture and commercial preparations are likely to become available (Linderman and Paulitz 1990). Major among them are *Rhizobium* symbiosis with legumes and free-living associative rhizosphere soil bacteria—*Azotobacter* and *Azospirillum*. The other group of beneficial microorganisms includes rhizobacteria, mainly *Pseudomonas*, *Erwinia*, *Flavobacterium*, and *Bacilli*, which improve health and productivity of crop plants through a variety of secondary metabolites and involved in promotion of root growth. Members of the bacterial genera *Azospirillum* and *Rhizobium* are well-studied examples for plant growth promotion; *Bacillus*, *Pseudomonas*, *Serratia*, *Stenotrophomonas*, and *Streptomyces* and the fungal genera *Ampelomyces*, *Coniothyrium*, *Piriformospora indica*, and *Trichoderma* are model organisms to demonstrate influence on plant health (Chadha et al. 2014). Another challenge is that plant-associated bacteria especially those from the rhizosphere play an emerging role as opportunistic human pathogens (Berg et al. 2005). Examples are antagonistic species of the genera *Burkholderia*, *Enterobacter*, *Herbaspirillum*, *Ochrobactrum*, *Pseudomonas*, *Serratia*, *Staphylococcus*, and *Stenotrophomonas* that are root-associated bacteria that can enter interactions with plant and human hosts (Ribbeck-Busch et al. 2005; Egamberdieva et al. 2008). Mechanisms involved in the interaction between antagonistic plant-associated bacteria and their host plants are similar to those responsible for the pathogenicity of bacteria to humans (Berg et al. 2005).

For all successful plant–microbe interactions, the competence to root colonize plant habitats is important for beneficial effects on plant growth (Kamilova et al. 2005). Steps of colonization include recognition, adherence, invasion (only endophytes and pathogens), colonization and growth, and several strategies to establish interactions. Plant roots initiate crosstalk with soil microbes by producing signals that are recognized by the microbes, which in turn produce signals that initiate colonization (Bais et al. 2006). To participate and react in this crosstalk, motile organisms are preferred (Lugtenberg et al. 2002). Moreover, there is growing appreciation that the intensity, duration, and outcome of plant–microbe interactions are significantly influenced by the conformation of adherent microbial populations (Danhorn and Fuqua 2004). Bacterial traits, such as pili, outer membrane proteins, and flagella, are involved in the PGPR adherence to plant root surfaces. Not only is the surface of roots colonized but also inner tissues of the

Table 12.1 Production of plant growth regulators (PGRs) by PGPR

PGPR	PGRs	Plant	References
Rhizobium leguminosarum	Indole-3-acetic acid	Rice	Biswas et al. (2000)
Azotobacter sp.	Indole-3-acetic acid	Maize	Zahir et al. (2000)
Pseudomonas fluorescens	Siderophores, indole-3-acetic acid	Groundnut	Dey et al. (2004)
Azospirillum brasilense A3, A4, A7, A10, CDJA	Indole-3-acetic acid	Rice	Thakuria et al. (2004)
Azospirillum lipoferum strains 15	Indole-3-acetic acid	Wheat	Muratova et al. (2005)
Pseudomonas denitrificans	Auxin	Wheat, maize	Egamberdieva (2005)
Azotobacter sp.	Indole-3-acetic acid	Sesbania	Ahmad et al. (2005)
Pseudomonas sp.	Indole-3-acetic acid	Wheat	Roesti et al. (2006)
Bacillus cereus RC 18	Indole-3-acetic acid	Wheat, spinach	Çakmakçi et al. (2007)
Mesorhizobium loti MP6	Chrom-azurol, siderophore, hydrocyanic acid, indole-3-acetic acid	*Brassica*	Chandra et al. (2007)
Pseudomonas tolaasii ACC23	Siderophores, indole-3-acetic acid	*Brassica*	Dell'Amico et al. (2008)
Bacillus sp.	Indole-3-acetic acid	Rice	Beneduzi et al. (2008)
Paenibacillus sp.			

plant. Colonization of the rhizosphere by some nonpathogenic microorganisms can protect the plant from a variety of bacterial, fungal, and viral diseases. This is known as induced systemic resistance. Interaction between the plant and root-colonizing microorganisms triggers signaling pathways and the production of specific gene products that enhance the ability of the plant to resist pathogens. Secondary metabolites involved in these pathways include phenolics, flavonoids, alkaloids, and terpenoids (Table 12.1).

In the processes of plant growth, phytohormones, e.g., production of auxin (IAA), cytokinins, and gibberellins, PGPR can increase root surface and length and promote in this way plant development (Kloepper et al. 2007). Several PGPR as well as symbiotic and free-living rhizobacterial species are reported to produce IAA and gibberellins in the rhizospheric soil and thereby play a significant role in increasing the root surface area and number of root tips in many plants (Bhattacharyya and Jha 2012). A greater root surface area enables the plant to access more nutrients from soil and thus contribute to plant growth promotion (Vessey 2003). These hormones can be synthesized by the plant themselves and also by their associated microorganisms. Furthermore, plant-associated bacteria can influence the hormonal balance of the plant. Ethylene is an important example to show that the balance is most important for the effect of hormones: at low levels, it can promote plant growth in several plant species including *Arabidopsis thaliana*, while it is normally considered as an inhibitor of plant growth and known as a senescence hormone (Pierik et al. 2006). Interestingly, bacteria are able to reduce the ethylene level by the following way. The compound 1-aminocyclopropane-1-carboyclic acid (ACC) is a precursor of ethylene in plants. As ACC deaminase-producing bacteria are able to degrade this substance, the uptake by and the level in the root is reduced. Thus, these bacteria can increase root growth by lowering the endogenous ACC levels (Glick 2005). Due to the fact that ethylene has also established as a stress hormone, ACC deaminase-producing bacteria have an additional potential to protect plants against biotic and abiotic stress (Saleem et al. 2007). Another example to explain the intimate plant–microbe interaction regarding phytohormones is the root-associated bacterium *Serratia plymuthica* HRO-C48 in which IAA production is surprisingly negatively regulated by quorum sensing (QS) (Müller et al. 2009). Also, low amounts of IAA induced resistance in the plant while IAA is involved in many bacteria-plant signaling, an important role of auxin signaling for plant growth promotion was also shown for *Trichoderma* spp. (Hartmann et al. 2004; Contreras-Cornejo et al. 2009). Besides these mechanisms, improved nutrient acquisition is involved in direct growth promotion. The most well-known example is bacterial nitrogen fixation. The symbiosis between rhizobia and its legume plants is an important example for PGPR. Bacteria of this group metabolize root exudates (carbohydrates) and in turn provide nitrogen to the plant for amino acid synthesis. The ability to fix nitrogen also occurs in free-living bacteria like *Azospirillum*, *Burkholderia*, and *Stenotrophomonas* (Dobbelaere et al. 2003). Another nutrient is sulfate, which can be provided to the plant via oxidation by bacteria (Banerjee and Yesmin 2002). Bacteria may contribute to plant nutrition by liberating phosphorous from organic compounds such as phytates and thus indirectly promote plant growth (Unno et al. 2005). *Azospirillum* treatment resulted in enhancement of root growth and activities (e.g., acidification of the root surroundings) that increases phosphorous and other macroelements and microelements uptake (Dobbelaere and Okon 2007). Mineral supply is also involved in plant growth promotion and includes synthesis of siderophores and siderophore uptake systems (Katiyar and Goel 2004). Poorly soluble inorganic nutrients can be made available through the solubilization of bacterial siderophores and the secretion of organic acids. Recently, de Werra et al. (2009) showed that the ability of *Pseudomonas fluorescens* CHA0 to acidify its environment and to solubilize mineral phosphate is strongly dependent on its ability to produce gluconic acid. Furthermore, the study provides new evidence for a close association of gluconic acid metabolism with antagonistic activity against plant pathogens. Some bacteria, especially *Bacillus* and *Pseudomonas* sp., depress growth and development of filamentous fungi both in vitro and in vivo by secreting lytic enzymes such as chitinases and glucanase. It has been assumed that applying bacteria producing chitinases to biological protection of crops from pathogens, especially those that contain chitin and glucans within their cell wall structure (Maksimov et al. 2011).

Rhizosphere microorganisms, which are able to eliminate or reduce other pathogenic microorganisms, have been defined as biocontrol agents. Important mechanisms of microbial antagonism to plant pathogens are antibiosis, parasitism, and competition for nutrients and/or induced host defense responses (Podile and Kishore 2006). Microbial antagonism include (1) the inhibition of microbial growth by diffusible antibiotics and volatile organic compounds (VOCs), toxins, and biosurfactants (antibiosis); (2) competition for colonization sites and nutrients; (3) competition for minerals, e.g., for iron through production of siderophores or efficient siderophore uptake systems; (4) degradation of pathogenicity factors of the pathogen such as toxins; and (5) parasitism that may involve production of extracellular cell wall-degrading enzymes such as chitinases and β-1,3-glucanase (Whipps 2001; Wheatley 2002; Compant et al. 2005; Haas and Défago 2005; Raaijmakers et al. 2006; Kamal et al. 2008). Plant-associated bacteria can reduce the activity of pathogenic microorganisms not only through microbial antagonisms but also by activating the plant to better defend itself, a phenomenon termed "induced systemic resistance" (Conrath et al. 2002; Van Loon 2007). However, sometimes, the mechanism of ISR elicited by PGPR overlaps partly with that of pathogen-induced systemic acquired resistance (SAR). Both ISR and SAR represent a state of enhanced basal persistence of the plant that depends on the signaling compounds jasmonic acid and salicylic acid (Van Loon 2007). Pathogens are differently sensitive to the resistance activated by these signaling pathways. These interactions are highly specific on each component: the host plant, the pathogen, as well as the PGPR strain. They recognize each other by chemical signaling: root exudates as well as microbial metabolites. The mechanisms of ISR include (1) developmental escape: linked to growth promotion, (2) physiological-tolerance: reduced symptom expression, (3) environmental: associated with microbial antagonisms in the rhizosphere, and (4) biochemical-resistance: induction of cell wall reinforcement, induction of phytoalexins, induction of pathogenesis-related proteins, and "priming" of defense responses (resistance). Substances involved in ISR are partly the same with those involved in microbial antagonisms: siderophores, antibiotics, N-acyl-homoserine lactones, VOCs (e.g., 3-hydroxy-2-butanone (acetoin), and 2, 3-butandiol). Whereas some PGPR activate defense-related gene expression, other examples appear to act solely through priming of effective resistance mechanisms, as reflected by earlier and stronger defense reaction once infection occurs.

PGPR can be used to enhance the growth of plants with natural health products. Pre-inoculation of hosts with PGPR can induce/enhance specific human health promoting compounds in plants; enhance root health; Increase resistance to environmental stress; and increase yield and quality of active ingredient products. Although PGPR have not been used specifically to increase the production of medicinal compounds in plants before, their ability to enhance plant growth and root health has been demonstrated with many crop species (Glick 1995; Van Loon et al. 1998). The use of microbial associations for medicinal plants provides a sustainable approach to improving crop quality and yield and is suitable for use in organic agriculture (Prasad et al. 2008; 2013). It provides the potential to increase production, value, and export of human health-enhancing crops and products. This will open new avenues products and markets for inoculant manufacturers.

12.6 Ecological Significance of Microbial Interactions

Microorganisms may contribute to the biocontrol of pathogens and improved supply of nutrients, thus maintaining plant health and production. Therefore, understanding of these interactions and the mechanisms could have implications for the progress of sustainable agriculture. Phosphate solubilizing bacteria are widespread in soils and secretion conversion of insoluble forms of phosphorus to plant-available forms (Vessey 2003). The biofertilizer properties of PGPR are frequently attributed to their ability to increase the bioavailability of inorganic and organic phosphorus, and some bacteria have documented synergistically effects on nitrogen fixation and formation of mycorrhizal associations.

PGPR present an alternative to the use of chemicals for plant growth enhancement in many different applications. Extensive research has demonstrated that PGPR could have an important role in agriculture and horticulture in improving crop productivity. In addition, these organisms are also useful in forestry and environmental restoration purposes. Because PGPR, which can fulfill diverse functions in plants, lead to promising solutions for a sustainable, environmentally friendly alternative to chemical fertilizers and pesticides, the use of which is regulated and sometimes forbidden; the market for bioinoculants is still expanding. While inoculants for plant growth promotion and biocontrol already exist, in the future, stress-protecting agents (stress conditions like those generated by salinity, drought, water logging, heavy metals, and pathogenicity) will be of emerging importance not only due to climate change. Furthermore, to improve food quality by PGPR is an important task.

12.7 Conclusions

PGPR are the potential tools for environmentally sustainable approach to increase soil fertility and plant health. PGPR benefit the growth and development of plants directly and indirectly through several mechanisms. The production of secondary metabolites, i.e., plant growth substances, changes root morphology resulting in greater root surface area for the uptake of nutrients, siderophores production, antagonism to soil-borne root pathogens, phosphate solubilization, and di-nitrogen fixation. The root surface area for uptake of nutrients and production of PGPR may help to optimize nutrient cycling in the event of stresses due to unsuitable weather or soil conditions. The beneficial effects of PGPR on plant growth are from changing the root architecture and enhancing nutrient uptake to biocontrol. The application of molecular tools is enhancing our ability to understand and manage the rhizosphere and will lead to new products with improved effectiveness. The discovery of many traits and genes that are involved in the beneficial effects of PGPR has resulted in a better understanding of the performance of bioinoculants in the field and provides the opportunity to enhance the beneficial effects of PGPR strains by genetic modification.

References

Ahmad F, Ahmad I, Khan MS (2005) Indole acetic acid production by the indigenous isolates of *Azotobacter* and fluorescent *Pseudomonas* in the presence and absence of tryptophan. Turk J Biol 29:29–34

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol 57:234–266

Banerjee M, Yesmin L (2002) Sulfur-oxidizing plant growth promoting *Rhizobacteria* for enhanced canola performance. US Patent

Barea JM, Andrade G, Bianciotto V, Dowling D, Lokhrke S, Bonfante P, O'gara F, Azcon-Aguilar C (1998) Impact on arbuscular mycorrhiza formation of *Pseudomonas* strains used as inoculants for biocontrol of soil-borne fungal plant pathogens. Appl Environ Microbiol 64:2304–2307

Barea JM, Azcon R, Azcon-Aguilar C (2004) Mycorrhizal fungi and PGPR. In: Werner D, Hampp R, Varma A, Abbott L (eds) Plant surface microbiology. Springer, Berlin, pp 351–362

Beneduzi A, Peres D, Vargas LK, Bodanese-Zanettini MH, Passaglia LMP (2008) Evaluation of genetic diversity and plant growth promoting activities of nitrogen-fixing Bacilli isolated from rice fields in South Brazil. Appl Soil Ecol 39:311–320

Benizri E, Baudoin E, Guckert A (2001) Root colonization by inoculated plant growth promoting rhizobacteria. Biocontrol Sci Technol 11:557–574

Berg G, Eberl L, Hartmann A (2005) The rhizosphere as a reservoir for opportunistic human pathogenic bacteria. Environ Microbiol 71:4203–4213

Bhattacharyya P, Jha D (2012) Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. World J Microbiol Biotechnol 28:1327–1350

Biswas JC, Ladha JK, Dazzo FB (2000) Rhizobia inoculation improves nutrient uptake and growth of lowland rice. Soil Sci Soc Am J 64:1644–1650

Bloemberg GV, Lugtenberg BJJ (2001) Molecular basis of plant growth promotion and biocontrol by rhizobacteria. Curr Opin Plant Biol 4:343–350

Çakmakçi R, Erat M, Erdoğan ÜG, Dönmez MF (2007) The influence of PGPR on growth parameters, antioxidant and pentose phosphate oxidative cycle enzymes in wheat and spinach plants. J Plant Nutr Soil Sci 170:288–295

Chadha N, Mishra M, Prasad R, Varma A (2014) Root endophytic fungi: research update. J Biol Life Sci USA 5:135–158. doi:10.5296/jblsjbls.v5i2.59605960

Chandra S, Choure K, Dubey RC, Maheshwari DK (2007) Rhizosphere competent Mesorhizobium loti MP6 induces root hair curling, inhibits *Sclerotinia sclerotiorum* and enhances growth of Indian mustard (*Brassica campestris*). Braz J Microbiol 38:124–130

Chanway CP, Holl FB (1991) Biomass increase and associative nitrogen fixation of mycorrhizal *Pinus contorta* seedlings inoculated with a plant growth promoting *Bacillus* strain. Can J Bot 69:507–511

Cocking EC (2003) Endophytic colonization of plant roots by nitrogen-fixing bacteria. Plant Soil 252:169–175

Compant S, Duffy B, Nowak J, Clement C, Barka EA (2005) Use of plant growth-promoting bacteria for biocontrol of plant diseases: principles, mechanisms of action, and future prospects. Appl Environ Microbiol 71:4951–4959

Conrath U, Pieterse CMJ, Mauch-Mani B (2002) Priming in plant-pathogen interactions. Trends Plant Sci 7:210–216

Contreras-Cornejo HA, Macías-Rodríguez L, Cortés-Penagos C, López-Bucio J (2009) *Trichoderma virens*, a plant beneficial fungus, enhances biomass production and promotes lateral root growth through an auxin-dependent mechanism in *Arabidopsis*. Plant Physiol 149:1579–1592

Danhorn T, Fuqua C (2004) Biofilm formation by plant-associated bacteria. Annu Rev Microbiol 61:401–422

Das A, Prasad R, Srivastava A, Giang PH, Bhatnagar K, Varma A (2007) Fungal siderophores: structure, functions and regulations. In: Varma A, Chincholkar S (eds) Microbial siderophores, vol 12. Springer, Germany, pp 1–42

De Werra P, Péchy-Tarr M, Keel C, Maurhofer M (2009) Role of gluconic acid production in the regulation of biocontrol traits of *Pseudomonas fluorescens* CHA0. Appl Environ Microbiol 75:4162–4174

Dell'Amico E, Cavalca L, Andreoni V (2008) Improvement of *Brassica napus* growth under cadmium stress by cadmium-resistant rhizobacteria. Soil Biol Biochem 40:74–84

Dey R, Pal KK, Bhatt DM, Chauhan SM (2004) Growth promotion and yield enhancement of peanut (*Arachis hypogaea* L) by application of plant growth promoting rhizobacteria. Microbiol Res 159:371–394

Dobbelaere S, Okon Y (2007) The plant growth promoting effects and plant responses. In: Elmerich C, Newton WE (eds) Nitrogen fixation: origins, applications and research progress, vol V, Associative and endophytic nitrogen-fixing bacteria and cyanobacterial associations. Springer, Heidelberg, pp 145–170

Dobbelaere S, Vanderleyden J, Okon Y (2003) Plant growth promoting effects of diazotrophs in the rhizosphere. CRC Crit Rev Plant Sci 22:107–149

Egamberdieva D (2005) Plant growth promoting rhizobacteria isolated from a calsisol in semi arid region of Uzbekistan: biochemical characterization and effectiveness. J Plant Nutr Soil Sci 168:94–99

Egamberdieva D, Kamilova F, Validov S, Gafurova L, Kucharova Z, Lugtenberg B (2008) High incidence of plant growth-stimulating bacteria associated with the rhizosphere of wheat grown on salinated soil in Uzbekistan. Environ Microbiol 10:1–9

Gabriele B (2009) Plant microbe interactions promoting plant growth and health: perspectives for controlled use of microorganisms in agriculture. Appl Microbiol Biotechnol 84:11–18

Garbaye J (1994) Helper bacteria: a new dimension to the mycorrhiza symbiosis. New Phytol 128:197–200

Glick BR (1995) The enhancement of plant growth by free-living bacteria. Can J Microbiol 41:109–117

Glick BR (2005) Modulation of plant ethylene levels by the enzyme ACC deaminase. FEMS Microbiol Lett 251:1–7

Haas D, Défago G (2005) Biological control of soil-borne pathogens by fluorescent *Pseudomonads*. Nat Rev Microbiol 3:307–319

Hartmann A, Gantner S, Schuhegger R, Steidle A, Dürr C, Schmid M, Langebartels C, Dazzo FB, Eberl L (2004) N-acyl homoserine lactones of rhizosphere bacteria trigger systemic resistance in tomato plants. In: Lugtenberg B, Tikhonovich I, Provorov N (eds) Biology of molecular plant–microbe interactions, vol 4. APS, St. Paul, pp 554–556

Hartmann A, Rothballer M, Schmid M (2008) Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. Plant Soil 312:7–14

Hiltner L (1904) Uber neuere Erfahrungen und Probleme auf dem Gebiete der Bodenbakteriologie unter bessonderer Berücksichtigung der Gründung und Brache. Arb Dtsch Landwirtsch Ges Berl 98:59–78

Holl FB, Chanway CP, Turkington R, Radley RA (1988) Response of crested wheatgrass *Agropyron cristatum* L. perennial ryegrass *Lolium perenne* and white clover *Trifolium repens* L. to inoculation with *Bacillus polymyxa*. Soil Biol Biochem 20:19–24

Kamal S, Prasad R, Varma A (2009) Soil microbial diversity in relation to heavy metals. In: Sherameti I, Varma A (eds) Soil heavy metals. Springer, Heidelberg, pp 31–64

Kamilova F, Validov S, Azarova T, Mulders I, Lugtenberg B (2005) Enrichment for enhanced competitive plant root tip colonizers selects for a new class of biocontrol bacteria. Environ Microbiol 7:1809–1817

Katiyar V, Goel R (2004) Siderophore mediated plant growth promotion at low temperature by mutant of fluorescent *Pseudomonad*. Plant Growth Regul 42:239–244

Kloepper JW (1993) Plant growth-promoting rhizobacteria as biological control agents. In: Metting FB (ed) Soil microbial ecology: applications in agricultural and environmental management. Dekker, New York, pp 255–274

Kloepper JW, Schroth MN (1978) Plant growth promoting rhizobacteria on radishes. In: Station de Pathologic Vegetal et Phytobacteriologic (ed) Proceedings of the 4th international conference on plant pathogenic bacteria, vol 2. Gilbert-Clarey, Angers, pp 879–882

Kloepper JW, Zablotowicz RM, Tipping EM, Lifshitz R (1991) Plant growth promotion mediated by bacterial rhizosphere colonizers. In: Keister DL, Cregan P (eds) The rhizosphere and plant growth Beltsville symposia in agricultural research, vol 14. Kluwer, Dordrecht, pp 315–326

Kloepper JW, Gutiérrez-Estrada A, McInroy JA (2007) Photoperiod regulates elicitation of growth promotion but not induced resistance by plant growth-promoting rhizobacteria. Can J Microbiol 53:159–167

Linderman RG, Paulitz TC (1990) Mycorrhizal rhizobacterial interactions. In: Hornby D (ed) Biological control of soil borne plant pathogens. CAB International, Wallingford, pp 261–283

Loper JE, Hankels MD (1997) Availability of iron to *Pseudomonas fluorescens* in rhizosphere and bulk soil evaluated with an ice nucleation reported gene. Appl Environ Microbiol 63:99–105

Lucy M, Reed E, Glick BR (2004) Applications of free living plant growth-promoting rhizobacteria. Antonie Van Leeuwenhoek 86:1–25

Lugtenberg BJJ, Dekkers L, Bloemberg GV (2001) Molecular determinants of rhizosphere colonization by *Pseudomonas*. Ann Rev Phytopathol 38:461–490

Lugtenberg BJJ, Chin-A-Woeng TFC, Bloemberg GV (2002) Microbe-plant interactions: principles and mechanisms. Antonie Van Leeuwenhoek 81:373–383

Maksimov IV, Abizgil'dina RR, Pusenkova LI (2011) Plant growth promoting rhizobacteria as alternative to chemical crop protectors from pathogens (Review). Appl Biochem Microbiol 47:333–345

Marschner H (1995) Mineral nutrition of higher plants, 2nd edn. Academic, London

Müller H, Westendorf C, Leitner E, Chernin L, Riedel K, Schmidt S, Eberl L, Berg G (2009) Quorum-sensing effects in the antagonistic rhizosphere bacterium Serratia plymuthica HRO-C48. FEMS Microbiol Ecol 67:468–478

Muratova AY, Turkovskaya OV, Antonyuk LP, Makarov OE, Pozdnyakova LI, Ignatov VV (2005) Oil-oxidizing potential of associative rhizobacteria of the genus *Azospirillum*. Microbiology 74:210–215

Pierik R, Tholen D, Poorter H, Visser EJW, Voesenek LACJ (2006) The Janus face of ethylene: growth inhibition and stimulation. Trends Plant Sci 11:176–183

Podile AR, Kishore GK (2006) Plant growth-promoting rhizobacteria. In: Gnanamanickam SS (ed) Plant-associated bacteria. Springer, The Netherlands, pp 195–230

Prasad R, Sharma M, Kamal S, Rai MK, Rawat AKS, Pushpangdan P, Varma A (2008) Interaction of *Piriformospora indica* with medicinal plants. In: Varma A (ed) Mycorrhiza, 3rd edn. Springer, Heidelberg, pp 655–678

Prasad R, Kamal S, Sharma PK, Oelmueller R, Varma A (2013) Root endophyte *Piriformospora indica* DSM 11827 alters plants morphology, enhances biomass and antioxidant activity of medicinal plant *Bacopa monniera*. J Basic Microbiol 53(12):1016–1024

Prasad R, Kumar V, Prasad KS (2014) Nanotechnology in sustainable agriculture: present concerns and future aspects. Afr J Biotechnol 13:705–713

Raaijmakers JM, de Bruijn I, de Kock MJ (2006) Cyclic lipopeptide production by plant-associated *Pseudomonas* spp.: diversity, activity, biosynthesis, and regulation. Mol Plant Microbe Interact 19:699–710

Ribbeck-Busch K, Roder A, Hasse D, de Boer W, Martínez JL, Hagemann M, Berg G (2005) A molecular biological protocol to distinguish potentially human pathogenic *Stenotrophomonas maltophilia* from plant-associated *Stenotrophomonas rhizophila*. Environ Microbiol 7:1853–1858

Roesti D, Guar R, Johri BN, Imfeld G, Sharma S, Kawaljeet K, Aragno M (2006) Plant growth stage, fertilizer management and bioinoculation of arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria affect the rhizobacterial community structure in rain-fed wheat field. Soil Biol Biochem 38:1111–1120

Saleem M, Arshad M, Hussain S, Bhatti AS (2007) Perspective of plant growth promoting Rhizobacteria (PGPR) containing ACC deaminase in stress agriculture. J Ind Microbiol Biotechnol 34:635–648

Shrivastava S, Prasad R, Varma A (2014) Anatomy of root from eyes of a microbiologist. In: Morte A, Varma A (eds) Root engineering. Springer, Berlin, pp 3–22

Thakuria D, Taleekdar NC, Goswami C, Hazarika S, Boro RC, Khan MR (2004) Characterization and screening of bacteria from rhizosphere of rice grown in acidic soils of Assam. Curr Sci 86:978–985

Unno Y, Okubo K, Wasaki J, Shinano T, Osaki M (2005) Plant growth promotion abilities and microscale bacterial dynamics in the rhizosphere of lupin analysed by phytate utilization ability. Environ Microbiol 7:396–404

Van Loon LC (2007) Plant responses to plant growth promoting bacteria. Eur J Plant Pathol 119:243–254

Van Loon LC, Bakker PAH, Pietesse CMJ (1998) Systemic resistance induced by rhizosphere bacteria. Annu Rev Phytopathol 36:453–483

Vessey JK (2003) Plant growth promoting rhizobacteria as biofertilizers. Plant Soil 255:571–586

Wheatley RE (2002) The consequences of volatile organic compound mediated bacterial and fungal interactions. Antonie Van Leeuwenhoek 81:357–364

Whipps J (2001) Microbial interactions, biocontrol in the rhizosphere. J Exp Bot 52:487–511

Zahir ZA, Abbas SA, Khalid M, Arshad M (2000) Substrate dependent microbially derived plant hormones for improving growth of maize seedlings. Pak J Biol Sci 3:289–291