

# Chapter 1

## Plant Growth-Promoting Rhizobacteria (PGPR) and Medicinal Plants: The State of the Art

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### 1.1 Introduction

Plant growth-promoting rhizobacteria (PGPR) are bacteria colonizing rhizospheres of plant that enhance plant growth through various mechanisms like nitrogen fixation, solubilization of phosphate, quorum sensing, etc. (Bhattacharya and Jha 2012). PGPR offer various ways to replace chemical fertilizers, pesticides, etc., and thus this quality has significantly led to their increased demand.

Before we start with the current applications and state of the art related to PGPR and medicinal plants, it will really be interesting to know the basic and history behind this wonderful science. Basis of application of plant growth-promoting bacteria may be said to be led days back when Theophrastus (372–287 B.C.) suggested mixing of different soil samples to remove defects of one and add life to soil (Tisdale and Nelson 1975). Certainly the technical approach behind the same only became clear after microscopy came into play. Establishment of legumes on cultivable land was recorded for the first time by Virgil (Chew 2002). Investigation of rhizosphere root colonization in grasses and confirmation of the fact that soil bacteria could convert atmospheric nitrogen into plant-usable forms were reported by Hellriegel and Wilfarth (1888). The term “rhizobacteria” was coined by Kloepper and Schroth (1978), based on their experiments with radishes, and they defined these bacteria as a community that competitively colonizes plant root and enhances their growth and also reduces plant diseases. Few properties strictly

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associated with PGPR are their properties of aggressive colonization and plant growth stimulation and their biocontrol ability (Weller et al. 2002; Vessey 2003). Rhizobacteria show all positive, negative, and neutral interaction with plants (Whipps 2001). PGPR are further classified as extracellular plant growth rhizobacteria or intracellular plant growth rhizobacteria depending upon their intimacy in interaction with plants (Martinez-Viveros et al. 2010). These are designated as ePGPR and iPGPR. The ePGPR is mainly existing in rhizosphere, rhizoplane, or between cells of root cortex include generally bacteria from genera like *Azotobacter*, *Chromobacterium*, *Agrobacterium*, *Caulobacter*, etc. (Gray and Smith 2005). Specialized nodular structures for root cells are home for iPGPR which includes endophytes (*Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, etc.) and *Frankia* species (Verma et al. 2010; Wang and Martinez-Romero 2000).

Studies have reported that application of PGPR increases nodulation and nitrogen fixation in many plants including soybean (*Glycine max* (L.) Merr.) (Zhang et al. 1996). PGPR have both direct and indirect mechanisms to promote growth and yield of crop plants. Rhizosphere colonization accounts for siderophore (Schippers et al. 1988), antibiotic (Weller 1988), and hydrogen cyanide (Stutz et al. 1986) production.

The objective of this chapter is to understand the mechanisms of plant growth promotion by rhizobacteria and to know about the state of the art of this wide area of study.

## 1.2 Plant–Microbe Interaction

The interaction of plants with microbes occurs at three different layers, namely, endosphere, phyllosphere, and rhizosphere. The region of contact between root and soil is rhizosphere. This region is a cloud of microbes which literally surrounds plant roots and is vital for the plant's survival and growth. The term "rhizosphere" was coined by Lorenz Hiltner in 1904. Clark proposed the term "rhizoplane" for the external root surface and closely adhering particles of soil and debris. The influence of root exudates on the proliferation of soil microorganisms around and inside roots (Hartmann et al. 2008) and interactions between soil microorganisms, rhizosphere colonists, and plant hosts (Dennis et al. 2010; Friesen et al. 2011; Berendsen et al. 2012) has been widely studied. In rhizosphere, the microbial population differs both quantitatively and qualitatively from that in the soil. As per the hypothesis, most of the plant roots are surrounded by mycorrhizae. Hence, it is appropriate to use the word mycorrhizosphere instead of rhizosphere (Shrivastava et al. 2014). Amino acids and sugars released as plant exudates are rich sources of energy and nutrition. Plant root interaction in the rhizosphere is a combinatorial effect of root–root interaction, root–microbe interaction, and root–insect interaction.

Studies based on molecular techniques have estimated about 4,000 microbial species per gram of soil sample (Montesinos 2003). One of the most important communities in rhizosphere microbiota is filamentous actinomycetes (Benizri et al. 2001). Rhizosphere microbial colonies have dynamic association with biogeochemical cycling of nutrients (C, P, N, and S) and production of phytohormones or antibiotics (Cardoso and Freitas 1992). PGPR are well known to colonize plant roots and stimulate plant growth (Andrews and Harris 2000). *Azospirillum* sp., *Bacillus subtilis* sp., and *Pseudomonas* sp. have been well studied as plant rhizosphere-colonizing microorganisms (Steenhoudt and Vanderleyden 2000; Trivedi et al. 2005). Soil microorganisms (free-living, associative, and symbiotic rhizobacteria) belonging to the genera like *Acinetobacter*, *Burkholderia*, *Enterobacter*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Erwinia*, *Flavobacterium*, *Rhizobium*, *Serratia*, *Xanthomonas*, *Proteus*, and *Pseudomonas* are the integral parts of rhizosphere biota (Glick 1995; Kaymak 2011) and exhibit successful rhizosphere colonization. Rhizospheric colonization is a crucial step in the application of microorganisms for beneficial purposes such as biofertilization, phytostimulation, biocontrol, and phytoremediation, although the colonization of rhizosphere by PGPR is not a uniform process.

## 1.3 PGPR in Agriculture

### 1.3.1 PGPR as Biofertilizer

Biofertilizers are the substances prepared from living microorganisms which, when applied to the seeds or plant surfaces adjacent to soil, can colonize rhizosphere or the interior parts of the plants and thereby promote root growth. *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, and *Sinorhizobium* are reported as the potent PGPR strains for their ability to act as biofertilizers (Vessey 2003). In rhizospheric relationship, the PGPR can colonize the rhizosphere, the surface of the root, or even the superficial intercellular spaces of plant roots (McCully 2001). It is only due to the changes in different physicochemical properties of rhizospheric soil such as soil pH, water potential and partial pressure of O<sub>2</sub>, and plant exudation as compared to the bulk soil that in turn can affect the ability of PGPR strains to colonize the rhizosphere (Griffiths et al. 1999). In endophytic relationship, PGPR reside within the apoplastic spaces inside the host plants. There is a direct evidence of existence of endophytes in the apoplastic intercellular spaces of parenchyma tissue (Dong et al. 1997) and xylem vessel (James et al. 2001). The best examples can be cited from legume–rhizobia symbioses in leguminous plants (Vessey 2003).

### **1.3.2 Plant Growth Regulator by PGPR**

PGPR can alter root architecture and promote plant development with the production of different phytohormones like IAA, gibberellic acid, and cytokinins (Kloepper et al. 2007). Several PGPR as well as some pathogenic, symbiotic, and free-living rhizobacterial species are reported to produce IAA and gibberellic acid in the rhizospheric soil and thereby play a significant role in increasing the root surface area and number of root tips in many plants (Han et al. 2005). Recent investigations on auxin synthesizing rhizobacteria (Spaepen et al. 2007) as phytohormone producer demonstrated that the rhizobacteria can synthesize IAA from tryptophan by different pathways, although the general mechanism of auxin synthesis was basically concentrated on the tryptophan-independent pathways.

### **1.3.3 PGPR as Phosphorous Solubilizers**

Phosphorus is one of the most essential nutrient requirements in plants. Ironically, soils may have large reservoir of total phosphorus (P) but the amounts available to plants are usually a tiny proportion of this total. This low availability of phosphorus to plants is because of the vast majority of soil P found in insoluble forms, while the plants can only absorb it in two soluble forms, the monobasic ( $\text{H}_2\text{PO}_4^-$ ) and the diabolic ( $\text{HPO}_4^{2-}$ ) ions (Glass 1989). Several phosphate-solubilizing microorganisms (PSMs) are now recorded to convert the insoluble form of phosphorus to soluble form through acidification, secretion of organic acids or protons (Richardson et al. 2009), and chelation and exchange reactions (Hameeda et al. 2008). Saprophytic bacteria and fungi are reported for the chelation-mediated mechanisms (Whitelaw 2000) to solubilize phosphate in soil. Release of plant root exudates such as organic ligands can also alter the concentration of P in soil solution (Hinsinger 2001).

### **1.3.4 PGPR as Producers of Volatile Organic Compounds**

The discovery of rhizobacterial-produced volatile organic compounds (VOCs) constitutes an important mechanism for the elicitation of plant growth by rhizobacteria. Ryu et al. (2003) recorded some PGPR strains, namely, *Bacillus subtilis* GB03, *B. amyloliquefaciens* IN937a, and *Enterobacter cloacae* JM22 that released a blend of volatile components, particularly, 2,3-butanediol and acetoin, which promoted growth of *Arabidopsis thaliana*, suggesting that synthesis of bioactive VOCs is a strain-specific phenomenon. Acetoin-forming enzymes have been identified earlier (Forlani et al. 1999) in certain crops like tobacco, carrot, maize, and rice although their possible functions in plants were not properly

established in that period. It has now been established that the VOCs produced by the rhizobacterial strains can act as signaling molecule to mediate plant–microbe interactions as volatiles produced by PGPR colonizing roots are generated at sufficient concentrations to trigger the plant responses (Ryu et al. 2003). Farmer (2001) identified low molecular weight plant volatiles such as terpenes, jasmonates, and green leaf components as potent signal molecules for living organisms in different trophic levels. However, to acquire a clear appreciation on the mechanisms of VOCs in signaling plants to register plant defense, more investigations into the volatile components in plant–rhizobacteria system should follow.

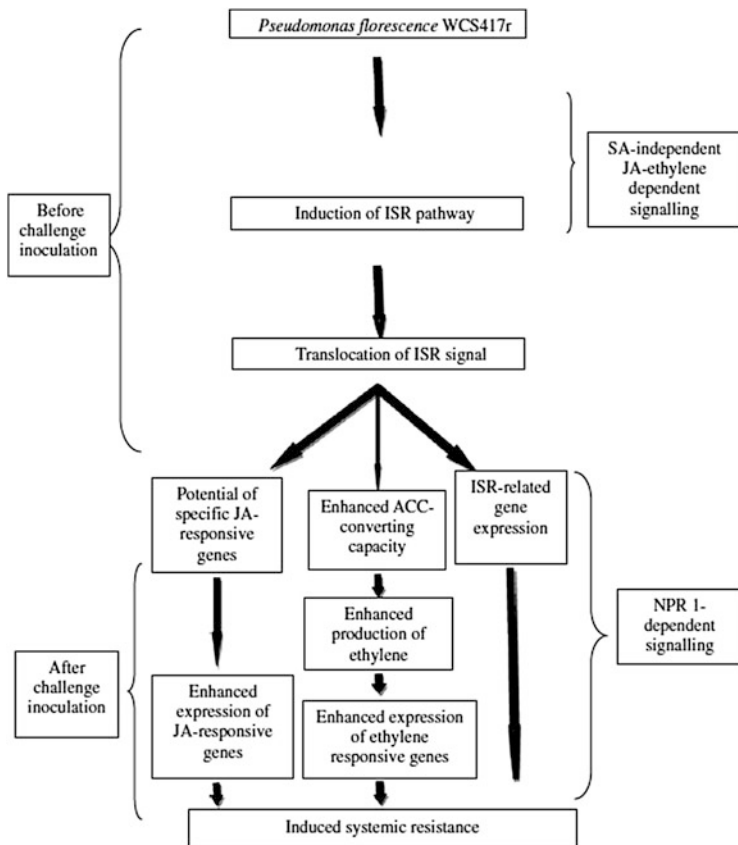
### ***1.3.5 PGPR as Biotic Elicitors***

Elicitors are chemicals or biofactors of various sources that can trigger physiological and morphological responses and phytoalexin accumulation in plants. It may be abiotic elicitors such as metal ions or inorganic compounds and biotic elicitors, basically derived from fungi, bacteria, viruses, plant cell wall components, and chemicals that are released due to antagonistic reaction of plants against phytopathogens or herbivore attack. It has now been observed that the treatment of plants with biotic elicitors can cause an array of defense reactions including the accumulation of a range of plant defensive bioactive molecules such as phytoalexins in the intact plants. Thus, elicitation is being used to induce the expression of genes responsible for the synthesis of antimicrobial metabolites. Rhizosphere microbes are best known to act as biotic elicitors, which can induce the synthesis of secondary products in plants (Sekar and Kandavel 2010). Signal perception is the first committed step toward the biotic elicitor signal transduction pathway in plants. Jasmonic acid and its methyl ester are the signal transducers in a wide range of plant cell cultures that could accumulate rapidly when the suspension cultures of *Rauvolfia canescens* L. and *Eschscholzia californica* Cham. are treated with a yeast elicitor (Roberts and Shuler 1997). Ajmalicine, serpentine, picrocrocine, crocetin, hyoscyamine and scopolamine, safranal compounds, and tanshinone are recorded as the important metabolites produced by PGPR species in eliciting the physiological and morphological responses in crop plants.

### ***1.3.6 Induction of Systemic Disease Resistance by PGPR***

Application of mixtures of different PGPR strains to the seeds or seedlings of certain plants has resulted in increased efficiency of induced systemic resistance (ISR) against several pathogens (Ramamoorthy et al. 2001). Various nonpathogenic PGPR strains have the ability to induce systemic disease resistance in plants against broad-spectrum phytopathogens (Kloepper et al. 2004; Elbadry et al. 2006). Induction of systemic disease resistance in faba bean (*Vicia faba* L.) against bean yellow

mosaic virus (BYMV) via seed bacterization with *Pseudomonas fluorescens* and *Rhizobium leguminosarum* has been investigated by Elbadry et al. (2006). They isolated PGPR strains from the roots of faba bean and examined singly or in combination for the induction of resistance in faba bean against BYMV. The results established a pronounced and significant reduction in percent disease incidence (PDI) as well as in virus concentration (ELISA) in plants treated with *Pseudomonas fluorescens* and *Rhizobium leguminosarum* as compared to the non-bacterized plants. Similarly, induction of systemic resistance by *Pseudomonas putida* strain 89B-27 and *Serratia marcescens* strain 90-166 against *Fusarium* wilt of cucumber incited by *Fusarium oxysporum* f. sp. *cucumerinum* has been investigated by Liu et al. (1995). Alstroem (1991) observed induced systemic protection of PGPR against the bacterial diseases. He reported that the bean seeds when treated with *Pseudomonas fluorescens* protected the plant against the halo blight disease caused by *Pseudomonas syringae* pv. *phaseolicola*. Kloepper et al. (1993) treated cucumber seeds with rhizobacterial strains like *Pseudomonas putida* 89 B-27 and *Serratia marcescens* 90-166 and recorded a significant decrease in incidence of bacterial wilt. Similar investigations on the treatment of cucumber seeds against angular leaf spot disease caused by *Pseudomonas syringae* pv. *lachrymans*, with a large number of PGPR strains such as *Pseudomonas putida* 89B-27, *Flavimonas oryzihabitans* INR-5, *Serratia marcescens* 90-166, and *Bacillus pumilus* INR-7, have been made by Wei et al. (1996). They observed more systemic protection in the plants (indicated by the reduction of total lesion diameter) whose seeds are inoculated with the strains of PGPR as compared to the uninoculated plants. Pieterse et al. (2001) studied rhizobacterial strain *Pseudomonas fluorescens* to enhance the defensive capacity in plants against broad-spectrum foliar pathogens (Fig. 1.1). Based on their experiments they concluded that *Pseudomonas fluorescens* strain WCS417r could elicit systemic disease resistance in plants through a variety of signal translocation pathways like SA-independent JA-ethylene-dependent signaling, ISR-related gene expression, NPR 1-dependent signaling, etc. Recently, interactions between *Bacillus* spp. and plants with special reference to induced systemic disease resistance have been elicited by Choudhary and Johri (2009). Several strains of *Bacillus* like *B. amyloliquefaciens*, *B. subtilis*, *B. pasteurii*, *B. cereus*, *B. pumilus*, *B. mycoides*, and *B. sphaericus* (Ryu et al. 2004) are presently recorded to elicit significant reduction in disease incidence on diversity of hosts. Elicitation of resistance by the strains has been demonstrated both in greenhouse and field trials on tomato, bell pepper, muskmelon, watermelon, sugar beet, tobacco, and cucumber. Through the activation of various defense-related enzymes like chitinases,  $\beta$ -1, 3-glucanase, peroxidase (PO), phenylalanine ammonia-lyase (PAL), and polyphenol oxidase (PPO), PGPR strains can induce this type of systemic resistance in plants (Bharathi 2004).



**Fig. 1.1** Possible involvement of jasmonic acid and ethylene in *Pseudomonas fluorescens* WCS417r-mediated induced systemic resistance in *Arabidopsis* (Adapted from Pieterse et al. 2001)

### 1.3.7 Nitrogen Fixation

Nitrogen is a principal plant nutrient. Apart from being the most important, it is also a limiting factor in the agricultural ecosystem due to its loss by rainfall and mineral leaching. PGPR strains such as *Klebsiella pneumoniae*, *Pantoea agglomerans*, and *Rhizobium* sp. are reported to fix atmospheric N<sub>2</sub> in soil and avail it to plants (Antoun et al. 1998; Riggs et al. 2001). Fluorescent *Pseudomonades* and *Pseudomonas fluorescens* have been reported to promote nodulation in chickpea (Parmar and Dadarwal 1999) and tomatoes (Minorsky 2008). They promote enhanced plant height and increased fruiting and flowering capability. Ability of microorganisms to fix nitrogen symbiotically or nonsymbiotically in soil and enhance crop yield could replace the use of nitrogen fertilizers (Vessey 2003). Symbiotic N<sub>2</sub> fixation to legume crops with the inoculation of effective PGPR is well known (Dobereiner

1997; Barea et al. 2005; Esitken et al. 2006). Symbiotic N<sub>2</sub> fixation is mostly done by *Azotobacter* spp., *Bacillus* spp., *Beijerinckia* spp., etc. and is limited to leguminous plants, trees, and shrubs that form actinorhizal roots with *Frankia*, whereas nonsymbiotic nitrogen fixation is carried out by free-living diazotrophs like *Azospirillum* (Bashan and de-Bashan 2010), *Burkholderia* (Estrada de los Santos et al. 2001), *Azoarcus* (Reinhold-Hurek et al. 1993), *Gluconacetobacter* (Fuentes-Ramirez et al. 2001), and *Pseudomonas* (Mirza et al. 2006). Researchers have also studied the effect of combined inoculation of symbiotic and nonsymbiotic microorganisms on plant growth enhancement. Combined inoculations of *Bradyrhizobium* sp. with *Pseudomonas striata* have established enhanced nodule occupancy in soybean resulting in more biological N<sub>2</sub> fixation (Dubey 1996).

### 1.3.8 PGPR as Plant Growth Enhancement

Enormous PGPR are known to promote plant growth, crop yield, seed emergence, etc., thus promoting agriculture (Minorsky 2008). Plant properties like leaf area, chlorophyll content, total biomass, etc. are enhanced by inoculation of PGPR (Baset Mia et al. 2010). They also studied the effect of PGPR on external layers of root cortex of maize and wheat seedlings. Increasing demand for food and improving environmental quality have focused on the importance of PGPR in agriculture. Dobbelaere et al. (2001) assessed the inoculation effect of *Azospirillum* sp. on the development of agriculturally important plants and observed a noteworthy boost in the dry weight of both the root system and aerial parts of the PGPR-inoculated plants, resulting in better progress and flowering. Foliar applications of rhizobacterial microbes in mulberry and apricot and their better development in leaf area and chlorophyll production were investigated by Esitken et al. (2003). *Bacillus subtilis*, *B. licheniformis*, *Achromobacter xylosoxidans*, *B. pumilus*, *Brevibacterium halotolerans*, and *Pseudomonas putida* are identified as having critical roles in cell elongation, escalating ACC deaminase activity, and plant growth promotion (Sgroy et al. 2009). The effect of *Pseudomonas fluorescens* on tomato and cucumber roots was studied by Saravanakumar and Samiyappan (2007). Seeds of various crops and ornamental plants bacterized with a mixture of PGPR and rhizobia before planting resulted in enhanced growth and disease resistance (Zehnder et al. 2001). Growth responses in wheat after the inoculation with rhizobacteria basically depends on various factors like plant genotype, nature of PGPR inoculants, as well as environmental conditions as observed by Khalid et al. (2004). The root inoculation of apple tree with *Bacillus* M3 and *Microbacterium* FS01 (Karlidag et al. 2007) and the effect of arbuscular mycorrhizal (AM) fungi and PGPR in soils differing in nitrogen concentration (Ahanthem and Jha 2007) are few other important studies in this field. It was found that enhancing apple tree growth in the study might be due to enhanced production of plant growth regulators and mobilization of available nutrients by PGPR.



Ahanthem and Jha (2008) also studied the interactions between *Acaulospora* and *Azospirillum* and their synergistic effect on rice growth at different sources.

### **1.3.9 Maintenance of Soil Fertility and Nutrient Uptake by PGPR**

Plant physiology and nutritional and physical properties of rhizospheric soil are all altered by PGPR. Rhizobacteria are reported to increase uptake of nutrient elements like Ca, K, Fe, Cu, Mn, and Zn through proton pump ATPase (Mantelin and Touraine 2004). *Bacillus* and *Microbacterium* inoculants improve uptake of mineral elements by crop plants (Karlidag et al. 2007). The importance of rhizobacterial activities on maintaining soil fertility is well studied by many scientists (Phillips 1980; Forde 2000; Glass et al. 2002). Rhizobacteria also help in solubilizing unavailable forms of nutrients and facilitating its transport in plants (Glick 1995).

#### **1.3.10 Enhancement of Resistance to Water Stress**

PGPR are beneficial to the wide variety of plants growing in water-stressed conditions (Aroca and Ruiz-Lozano 2009). Drought stress causes limitation to the plant growth and productivity of agricultural crops particularly in arid and semiarid areas. Figueiredo et al. (2008) suggested that inoculation of plants with PGPR can enhance the drought tolerance that might be due to the production of IAA, cytokinins, antioxidants, and ACC deaminase and inoculation of seeds of *Phragmites australis* with *Pseudomonas asplenii* improved germination and protects the plants from growth inhibition (Bashan et al. 2008).

## **1.4 Commercialization of PGPR**

Commercialization of PGPR is important for its beneficial usage and this very aspect requires a proper tuning between scientific organization and industries. Different stages in the process of commercialization include isolation of antagonist strains, screening, pot tests and field efficacy, mass production and formulation development, fermentation methods, formulation viability, toxicology, industrial linkages, and quality control (Nandakumar et al. 2001). Isolation of effective strain is the prime criteria for better agricultural development (Nakkeeran et al. 2005), and then selection of the best antagonistic strain can be carried out by screening for antimicrobial action against soilborne pathogens. The next stage of study is when

the plant, pathogen, and antagonists are tested for their efficacy in field trials along with recommended fungicides (Pengnoo et al. 2000). Mass production is achieved through liquid (Manjula and Podile 2001), semisolid, and solid fermentation requirement for entrepreneurship requires a patent application of the identified strain.

The next crucial step to retain the confidence of farmers on efficacy of antagonistic strain is quality control. The first commercial product of *Bacillus subtilis* was developed in 1985 in the USA. 60–75% of cotton, peanut, soybean, corn, vegetables, and small grain crops raised in the USA are now treated with commercial product of *B. subtilis*, which become effective against soilborne pathogens such as *Fusarium* and *Rhizoctonia* (Nakkeeran et al. 2005). The potential of *Bacillus* spp. has also been widely studied by Backman et al. (1997). Besides *Bacillus* spp., certain other PGPR strains belonging to the genera such as *Agrobacterium*, *Azospirillum*, *Burkholderia*, *Pseudomonas*, and *Streptomyces* are also used for the production of several commercial products, which are generally being applied against several target pathogens like *Botrytis cinerea*, *Penicillium* spp., *Pythium* sp., *Geotrichum candidum*, *Mucor piriformis*, *Erwinia amylovora*, russet-inducing bacteria, *Fusarium* sp., *Rhizoctonia* sp., *Fusarium* sp., *Phytophthora* sp., and *P. tolaasii* (Nakkeeran et al. 2005).

Chet and Chernin (2002) studied a wide variety of PGPR and have also been successful in developing formulations for commercialization of products.

## 1.5 Future Prospects and Challenges

PGPR inoculants can fulfill diverse beneficial interactions in plants. Applications of rhizosphere soil with desirable bacterial populations have established considerable promises in both the laboratory and greenhouse experiments. Combined applications of transgenic plants with PGPR have proved another promising future (Ali and Hj 2010) in advancing rhizoremediation technologies. Rationalizing the understanding of PGPR may promote plant growth, leading to its use as biofertilizer at a wide level. Denton (2007) worked on the use of PGPR to remediate complex contaminated soil which could result in increased crop yield. The rhizobacterial community can be specifically engineered to target various pollutants at co-contaminated sites to provide customized rhizoremediation system (Wu et al. 2006). Production of transgenic plants and then inoculating it with PGPR has also increased efficiency (Zhuang et al. 2007; Farwell et al. 2007). Modern technology based on the transformations of 1-aminocyclopropane-1-carboxylic acid deaminase gene, which directly stimulates plant growth by cleaving the immediate precursor of plant ethylene into *Pseudomonas fluorescens* CHAO, not only increased the plant growth but also accelerated biocontrol properties of PGPR species (Holguin and Glick 2001). Genomic tinkering of naturally occurring PGPR strains with effective genes (Nakkeeran et al. 2005) could lead to accentuated expression of genomic products, thereby alleviating the attack of both pests

and diseases on field crops that would further facilitate for better introduction of a single bacterium with multiple modes of action to benefit the growers.

## 1.6 Conclusions

PGPR enhance plant growth by direct and indirect means, but the specific mechanisms involved have not all been well characterized. The present review indicates the advances and formulations of PGPR in biological promotion of different characteristics of plant growth. Most PGPR isolates significantly increase plant height, root length, and dry matter production in various agricultural crops like potato, tomato, maize, wheat, etc. One of the promising approaches of replacing the use of chemical fertilizers is developing stable formulation of antagonistic PGPR in sustainable agricultural systems. Another approach is through activation of octadecanoid, shikimate, and terpenoid pathways which in turn assists the plant growth promotion. Plenty of research in this field is going on and various are fruitful too. It can be concluded that vigilantly controlled field trials of crop plants inoculated along with rhizobacteria are necessary for utmost commercial exploitation of PGPR strains.

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