

Soil beneficial bacteria and their role in plant growth promotion: a review

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Abstract Soil bacteria are very important in biogeochemical cycles and have been used for crop production for decades. Plant–bacterial interactions in the rhizosphere are the determinants of plant health and soil fertility. Free-living soil bacteria beneficial to plant growth, usually referred to as plant growth promoting rhizobacteria (PGPR), are capable of promoting plant growth by colonizing the plant root. PGPR are also termed plant health promoting rhizobacteria (PHPR) or nodule promoting rhizobacteria (NPR). These are associated with the rhizosphere, which is an important soil ecological environment for plant–microbe interactions. Symbiotic nitrogen-fixing bacteria include the cyanobacteria of the genera *Rhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Allorhizobium*, *Sinorhizobium* and *Mesorhizobium*. Free-living nitrogen-fixing bacteria or associative nitrogen fixers, for example bacteria belonging to the species *Azospirillum*, *Enterobacter*, *Klebsiella* and *Pseudomonas*, have been shown to attach to the root and efficiently colonize root surfaces. PGPR have the potential to contribute to sustainable plant growth promotion. Generally, PGPR function in three different ways: synthesizing particular compounds for the plants, facilitating the uptake of certain nutrients from the soil, and lessening or preventing the plants from diseases. Plant growth promotion and development can be facilitated both directly and indirectly. Indirect plant growth promotion

includes the prevention of the deleterious effects of phytopathogenic organisms. This can be achieved by the production of siderophores, i.e. small metal-binding molecules. Biological control of soil-borne plant pathogens and the synthesis of antibiotics have also been reported in several bacterial species. Another mechanism by which PGPR can inhibit phytopathogens is the production of hydrogen cyanide (HCN) and/or fungal cell wall degrading enzymes, e.g., chitinase and β -1,3-glucanase. Direct plant growth promotion includes symbiotic and non-symbiotic PGPR which function through production of plant hormones such as auxins, cytokinins, gibberellins, ethylene and abscisic acid. Production of indole-3-ethanol or indole-3-acetic acid (IAA), the compounds belonging to auxins, have been reported for several bacterial genera. Some PGPR function as a sink for 1-aminocyclopropane-1-carboxylate (ACC), the immediate precursor of ethylene in higher plants, by hydrolyzing it into α -ketobutyrate and ammonia, and in this way promote root growth by lowering indigenous ethylene levels in the micro-rhizo environment. PGPR also help in solubilization of mineral phosphates and other nutrients, enhance resistance to stress, stabilize soil aggregates, and improve soil structure and organic matter content. PGPR retain more soil organic N, and other nutrients in the plant–soil system, thus reducing the need for fertilizer N and P and enhancing release of the nutrients.

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Introduction

Soil bacteria have been used in crop production for decades. The main functions of these bacteria (Davison

1988) are (1) to supply nutrients to crops; (2) to stimulate plant growth, e.g., through the production of plant hormones; (3) to control or inhibit the activity of plant pathogens; (4) to improve soil structure; and (5) bioaccumulation or microbial leaching of inorganics (Brierley 1985; Ehrlich 1990). More recently, bacteria have also been used in soil for the mineralization of organic pollutants, i.e. bioremediation of polluted soils (Middledrop et al. 1990; Burd et al. 2000; Zhuang et al 2007; Zaidi et al. 2008). In the 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. 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 (Sturz et al. 2000; Shoebitz et al. 2009). A variety of symbiotic (*Rhizobium* sp.) and non-symbiotic bacteria (*Azotobacter*, *Azospirillum*, *Bacillus*, and *Klebsiella* sp., etc.) are now being used worldwide with the aim of enhancing plant productivity (Burd et al. 2000; Cocking 2003).

Free-living soil bacteria beneficial to plant growth are usually referred to as plant growth promoting rhizobacteria (PGPR), capable of promoting plant growth by colonizing the plant root (Kloepper and Schroth 1978; Kloepper et al. 1989; Cleyet-Marcel et al. 2001). PGPR are also termed as plant health promoting rhizobacteria (PHPR) or nodule promoting rhizobacteria (NPR) and are associated with the rhizosphere which is an important soil ecological environment for plant–microbe interactions (Burr and Caesar 1984). According to their relationship with the plants, PGPR can be divided into two groups: symbiotic bacteria and free-living rhizobacteria (Khan 2005). PGPR can also be divided into two groups according to their residing sites: iPGPR (i.e., symbiotic bacteria), which live inside the plant cells, produce nodules, and are localized inside the specialized structures; and ePGPR (i.e., free-living rhizobacteria), which live outside the plant cells and do not produce nodules, but still prompt plant growth (Gray and Smith 2005). The best-known iPGPR are *Rhizobia*, which produce nodules in leguminous plants. A variety of bacteria have been used as soil inoculants intended to improve the supply of nutrients to crop plants. Species of *Rhizobium* (*Rhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Allorhizobium* and *Sinorhizobium*) have been successfully used worldwide to permit an effective establishment of the nitrogen-fixing symbiosis with leguminous crop plants (Bottomley and Maggard 1990; Bottomley and Dughri 1989). On the other hand, non-symbiotic nitrogen-

fixing bacteria such as *Azotobacter*, *Azospirillum*, *Bacillus*, and *Klebsiella* sp. are also used to inoculate a large area of arable land in the world with the aim of enhancing plant productivity (Lynch 1983). In addition, phosphate-solubilizing bacteria such as species of *Bacillus* and *Paenibacillus* (formerly *Bacillus*) have been applied to soils to specifically enhance the phosphorus status of plants (Brown 1974).

PGPR have the potential to contribute in the development of sustainable agricultural systems (Schippers et al. 1995). Generally, PGPR function in three different ways (Glick 1995, 2001): synthesizing particular compounds for the plants (Dobbelaere et al. 2003; Zahir et al. 2004), facilitating the uptake of certain nutrients from the soil (Lucas et al. 2004a, b; Çakmakçi et al. 2006), and lessening or preventing the plants from diseases (Guo et al. 2004; Jetiyanon and Kloepper 2002; Raj et al. 2003; Saravankumar et al. 2008). The mechanisms of PGPR-mediated enhancement of plant growth and yield of many crops are not yet fully understood (Dey et al. 2004). However, the possible explanation include (1) the ability to produce a vital enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase to reduce the level of ethylene in the root of developing plants thereby increasing the root length and growth (Li et al. 2000; Penrose and Glick 2001); (2) the ability to produce hormones like auxin, i.e. indole acetic acid (IAA) (Patten and Glick 2002), abscisic acid (ABA) (Dangar and Basu 1987; Dobbelaere et al. 2003), gibberellic acid (GA) and cytokinins (Dey et al. 2004); (3) a symbiotic nitrogen fixation (Kennedy et al. 1997, 2004); (4) antagonism against phytopathogenic bacteria by producing siderophores, β -1, 3-glucanase, chitinases, antibiotic, fluorescent pigment and cyanide (Cattelan et al. 1999; Pal et al. 2001; Glick and Pasternak 2003); (5) solubilization and mineralization of nutrients, particularly mineral phosphates (de Freitas et al. 1997; Richardson 2001; Banerjee and Yasmin 2002); (6) enhanced resistance to drought (Alvarez et al. 1996), salinity, waterlogging (Saleem et al. 2007) and oxidative stress (Stajner et al. 1995, 1997); and (7) production of water-soluble B group vitamins niacin, pantothenic acid, thiamine, riboflavine and biotin (Martinez-Toledo et al. 1996; Sierra et al. 1999; Revillas et al. 2000). The application of PGPR has also been extended to remediate contaminated soils in association with plants (Zhuang et al. 2007). Thus, it is an important need to enhance the efficiency of meager amounts of external inputs by employing the best combinations of beneficial bacteria in sustainable agriculture production systems. This review covers the perspective of soil-beneficial bacteria and the role they are playing in plant growth promotion via direct and indirect mechanisms. The further elucidation of different mechanisms involved will help to make these bacteria a valuable partner in future agriculture.

Symbiotic N₂-fixing bacteria

Nitrogen is required for cellular synthesis of enzymes, proteins, chlorophyll, DNA and RNA, and is therefore important in plant growth and production of food and feed. For nodulating legumes, nitrogen is provided through symbiotic fixation of atmospheric N₂ by nitrogenase in rhizobial bacteroids. This process of biological nitrogen fixation (BNF) accounts for 65% of the nitrogen currently utilized in agriculture, and will continue to be important in future sustainable crop production systems (Matiru and Dakora 2004). Important biochemical reactions of BNF occur mainly through symbiotic association of N₂-fixing microorganisms with legumes that converts atmospheric elemental nitrogen (N₂) into ammonia (NH₃) (Shiferaw et al. 2004). *Rhizobia* (species of *Rhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Allorhizobium* and *Sinorhizobium*) form intimate symbiotic relationships with legumes by responding chemotactically to flavonoid molecules released as signals by the legume host. These plant compounds induce the expression of nodulation (nod) genes in *Rhizobia*, which in turn produce lipo-chitooligosaccharide (LCO) signals that trigger mitotic cell division in roots, leading to nodule formation (Dakora 1995, 2003; Lhuissier et al. 2001; Matiru and Dakora 2004). Nodules—the sites for symbiotic nitrogen fixation—are formed as a result of series of interactions between *Rhizobia* and leguminous plants. However, there are number of factors which affect the nodulation on legume roots including host–microsymbiont compatibility, physicochemical conditions of the soil and the presence of both known and unknown bio-molecules such as flavonoides, polysaccharides and hormones (Tisdale et al. 1990; Zafar-ul-Hye et al. 2007). It is a molecular dialogue between the host plant and a compatible strain of *Rhizobium* which serves as an initiate of the development of nodules (Murray et al. 2007). The rhizobial infection begins when the bacteria enters into roots in a host-controlled manner (Limpens et al. 2003). *Rhizobium* becomes trapped in a cavity formed by curling of root hair. The root hair plasma membrane invaginates the cavity, and a tube-like structure is formed by which *Rhizobium* enters the plant and reaches the base of the root hair. Consequently, the infection thread reaches a nodule primordium in the cortex of the root that develops into a nodule upon release of the *Rhizobium* (Limpens et al. 2003). Sometimes, no nodulation occurs in spite of inoculation with certain rhizobial cultures, because the strains used in such cases become exopolysaccharide-deficient due to mutation or any unspecified reason (van Rhijn et al. 2001).

Rhizobium–legume symbiosis has been examined extensively. The N₂ fixed by *Rhizobia* in legumes can also benefit associated non-legumes via direct transfer of biologically fixed N to cereals growing in intercrops (Snapp et al. 1998) or to subsequent crops rotated with symbiotic legumes (Shah

et al. 2003; Hayat 2005; Hayat et al. 2008a, b). In many low input grassland systems, the grasses depend on the N₂ fixed by the legume counterparts for their N nutrition and protein synthesis, which is much needed for forage quality in livestock production (Paynel et al. 2001; Hayat and Ali 2010). In addition to N₂-fixation in legumes, *Rhizobia* such as species of *Rhizobium* and *Bradyrhizobium* produce molecules (auxins, cytokinins, abscisic acids, lumichrome, riboflavin, lipochitooligosaccharides and vitamins) that promote plant growth (Hardarson 1993; Herridge et al. 1993; Keating et al. 1998; Hayat and Ali 2004; Hayat et al. 2008a, b). Their colonization and infection of roots would also be expected to increase plant development and grain yield (Kloepper and Beauchamp 1992; Dakora 2003; Matiru and Dakora 2004). Other PGPR traits of *Rhizobia* and *Bradyrhizobium* include phytohormone production (Chabot et al. 1996a, b; Arshad and Frankenberger 1998), siderophore release (Plessner et al. 1993; Jadhav et al. 1994), solubilization of inorganic phosphorus (Abd-Alla 1994a; Chabot et al. 1996a) and antagonism against plant pathogenic microorganisms (Ehteshamul-Haque and Ghaffar 1993). A number of researchers have experimentally demonstrated the ability of *Rhizobia* to colonize roots of non-legumes and localize themselves internally in tissues, including the xylem (Spencer et al. 1994). Applying *Bradyrhizobium japonicum* to radish significantly increased plant dry matter, by 15% (Antoun et al. 1998). Naturally-occurring *Rhizobia*, isolated from nodules of some tropical legumes, have also been shown to infect roots of many agricultural species such as rice, wheat and maize via cracks made by emerging lateral roots (Webster et al. 1997). In a study with maize, Chabot et al. (1996b) used bioluminescence from *Rhizobium leguminosarum* bv. *phaseoli* strain harboring *lux* genes to visualize in situ colonization of roots by *Rhizobia*, as well as to assess the efficiency with which these bacteria infected maize roots. These observations were consistent with findings on maize root colonization and infection by *Rhizobia* reported by Schloter et al. (1997) and Yanni et al. (2001).

The success of laboratory studies in infected cereal roots with *Rhizobia* led to the hypothesis that during legume–cereal rotations and/or mixed intercropping *Rhizobia* are brought into closer contact with cereal roots, and this probably results in non-legume root infection by native rhizobial populations in the soil. Yanni et al. (1997) isolated *Rhizobium leguminosarum* bv. *trifolii* as a natural endophyte from roots of rice in the Nile delta. Because rice has been grown in rotation with berseem clover for about seven centuries in the Nile delta, this probably promoted closer rhizobial affinity to this cereal as a “host plant”. This hypothesis is re-enforced by the fact that population of clover-nodulating *Rhizobia* isolated from rice could occur up to 2.5×10^7 cell g⁻¹ fresh weight of root,

concentrations similar to those obtained for bacteroids in legume root nodules. Chaintreuil et al. (2000) similarly isolated photosynthetic *Bradyrhizobia* from roots of the African brown rice, *Oryza glaberrima*, which generally grows in the same wetland as *Aeschynomene sensitiva*, a stem-nodulated legume associated with photosynthetic strains of *Bradyrhizobium*. Again, this may well suggest co-evolution of *Aeschynomene*, *Bradyrhizobia* and wild genotype of African brown rice. But whether these *Bradyrhizobia* affect growth of *O. glaberrima* plant has not been determined. Besides rice, *Rhizobia* have also been isolated as natural endophytes from roots of other non-legumes species such as cotton, sweet corn (McInroy and Kloepper 1995), maize (Martinez-Romero et al. 2000), wheat (Biederbeck et al. 2000) and canola (Lupwayi et al. 2000) either grown in rotation with legumes or in a mixed cropping system involving symbiotic legumes. Rhizobial attachment to roots of asparagus (*Asparagus officinalis* L.), oat (*Avena sativa* L.), rice (*Oryza sativa*), and wheat (*Triticum aestivum*) has also been reported by Terouchi and Syono (1990). Wiehe and Hoflich (1995) demonstrated that the strain R39 of *Rhizobium leguminosarum* bv. *trifolii*, multiplied under field conditions in the rhizosphere of host legumes (lupin and pea) as well as non-legumes including corn (*Zea mays*), rape (*Brassica napus* L) and wheat (*Triticum aestivum*). The effect of *Rhizobium leguminosarum* bv. *trifolii* on non-legume plant growth has been reported to be similar to *Pseudomonas fluorescens* as PGPR in its colonization on certain plant roots (Hoflich et al. 1994; 1995; Hoflich 2000). The plant growth promoting ability of *Rhizobia* inoculation varies with soil properties and crop rotation (Hilali et al. 2000; 2001). Inoculation response to *Bradyrhizobium* largely depends on the soil moisture, available N, yield potential of the crop, and the abundance and effectiveness of native *Rhizobia* (Venkateswarlu et al. 1997). In trials conducted in arid areas on legumes like guar (*Cyamopsis tetragonoloba* L. Taub), moth (*Vigna acontifolia*) and mung (*Vigna radiata*), inoculation gave up to 10–25% yield benefits with normal rainfall (Rao 2001). Leelahawonge et al. (2010) isolated root nodule bacteria from the medicinal legume *Indigofera tinctoria* and reported a new legume symbiont related to *Pseudoalteromonas* from the gamma class of proteobacteria. The partial *nifH* gene of *Pseudoalteromonas* (strain DASA 57075) had 96% similarity with *nifH* gene of a member of *Bradyrhizobium*. The partial *nodC* gene of *Pseudoalteromonas* DASA 57075 also had 88% similarity with *nodC* gene of several *Rhizobia* including *Sinorhizobium*, *Bradyrhizobium* and *Mesorhizobium*.

Non-symbiotic N₂-fixing bacteria

A range of plant growth promoting rhizobacteria (PGPR) participate in interaction with C3 and C4 plants (e.g., rice,

wheat, maize, sugarcane and cotton), and significantly increase their vegetative growth and grain yield (Kennedy et al. 2004). *Azotobacter* species (*Azotobacter vinelandii* and *Azotobacter chroococcum*) are free-living heterotrophic diazotrophs that depend on an adequate supply of reduced C compounds such as sugars for their energy source (Kennedy and Tchan 1992). Their activity in rice culture can be increased by straw application (Kanungo et al. 1997), presumably as a result of microbial breakdown of cellulose into cellobiose and glucose. Yield of rice (Yanni and El-Fattah 1999), cotton (Iruthayaraj 1981; Patil and Patil 1984; Anjum et al. 2007), and wheat (Soliman et al. 1995; Hegazi et al. 1998; Barassi et al. 2000) increased with the application of *Azotobacter*. In contrast to *Azotobacter*, *Clostridia* are obligatory anaerobic heterotrophs only capable of fixing N₂ in the complete absence of oxygen (Kennedy and Tchan 1992; Kennedy et al. 2004). *Clostridia* can usually be isolated from rice soils (Elbadry et al. 1999), and their activity also increased after returning straw to fields, raised the C to N ratio in the soil.

Beneficial effects of inoculation with *Azospirillum* on wheat yields in both greenhouse and field conditions have been reported (Hegazi et al. 1998; El Mohandes 1999; Ganguly et al. 1999). Strains of *Azospirillum*, a nitrogen-fixing organism living in close association with plants in the rhizosphere. *Azospirillum* species are aerobic heterotrophs that fix N₂ under microaerobic conditions (Roper and Ladha 1995) and grow extensively in the rhizosphere of gramineous plants (Kennedy and Tchan 1992; Kennedy et al. 2004). The *Azospirillum*–plant association leads to enhanced development and yield of different host plants (Fallik et al. 1994). This increase in yield is attributed mainly to an improvement in root development by an increase in water and mineral uptake, and to a lesser extent biological N₂-fixation (Okon and Labandera-Gonzalez 1994; Okon and Itzigsohn 1995). *Azospirillum brasilense* shows both chemotaxis and chemokinesis in response to temporal gradient of different chemoeffectors, thereby increasing the chance of root–bacterial interactions. Phytohormones synthesized by *Azospirillum* influence the host root respiration rate, metabolism and root proliferation and hence improve mineral and water uptake in inoculated plants (Okon and Itzigsohn 1995). *Azospirillum lipoferum* and *Azospirillum brasilense* have been isolated from roots and stems of rice and sugar cane plants (Ladha et al. 1982; James et al. 2000; Reis et al. 2000) while *Azospirillum amazonense* has been isolated from the roots of rice (Pereira et al. 1988), and root and stems of sugar cane (Reis et al. 2000). In greenhouse studies, inoculation with *Azospirillum lipoferum* increased rice yield up to 6.7 g plant⁻¹ (Mirza et al. 2000). Balandreau (2002) found in a field experiment that estimated yield increased was around 1.8 t ha⁻¹ due to inoculation with *Azospirillum lipoferum*. Wheat grain yield

was increased by up to 30% (Okon and Labandera-Gonzalez 1994) by inoculation with *Azospirillum brasilense*. Plant inoculation with *Azospirillum brasilense* promoted greater uptake of NO_3^- , K^+ and H_2PO_4 in corn, sorghum and wheat (Zavalin et al. 1998; Saubidet et al. 2000). Inoculation with *Azospirillum brasilense* significantly increases cotton plant height and dry matter under greenhouse conditions (Bashan 1998).

Soil applications with *Azospirillum* can significantly increase cane yield in both plant and ratoon crops in the field (Shankariah and Hunsigi 2001). The PGPR effects also increase N and P uptake in field trials (Galal et al. 2000; Panwar and Singh 2000), presumably by stimulating greater plant root growth. Substantial increases in N uptake by wheat plants and grain were observed in greenhouse trials with inoculation of *Azospirillum brasilense* (Islam et al. 2002). ^{15}N tracer techniques showed that *Azospirillum brasilense* and *Azospirillum lipoferum* contributed 7–12% of wheat plant N by BNF (Malik et al. 2002). Inoculation with *Azospirillum brasilense* significantly increases N contents of cotton up to $0.91 \text{ mg plant}^{-1}$ (Fayez and Daw 1987). Inoculation with *Azospirillum* also significantly increased N content of sugarcane leaves in greenhouse experiments (Muthukumarasamy et al. 1999). *Azospirillum* is also capable of producing antifungal and antibacterial compounds, growth regulators and siderophores (Pandey and Kumar 1989). *Acetobacter (Gluconacetobacter) diazotrophicus* is another acid-tolerant endophyte which grows best on sucrose-rich medium (James et al. 1994; Kennedy et al. 2004). Studies confirmed that up to 60–80% of sugarcane plant N (equivalent to over $200 \text{ kgN ha}^{-1}\text{year}^{-1}$) was derived from BNF and *Azospirillum diazotrophicus* is apparently responsible for much of this BNF (Boddey et al. 1991). The *Acetobacter*-sugarcane system has now become an effective experimental model and the diazotrophic character (nif^+) is important component of this system (Lee et al. 2002). Reinhold-Hurek et al. (1993) studied a strain of the endophytic Gram-negative N_2 -fixing bacterium *Azoarcus* sp. BH72, originally isolated from Kallar grass (*Leptochloa fusa* Kunth) growing in the saline-sodic soils typical of Pakistan. *Azoarcus* spp. also colonise grasses, such as rice, in both laboratory and field conditions (Hurek et al. 1994). In rice roots, the zone behind the meristem was most intensively colonized and response of rice roots to inoculation with *Azoarcus* sp. BH72 in aseptic system was cultivar-dependent (Reinhold-Hurek et al. 2002). The genus *Burkholderia* comprises 67 validly published species, with several of these including *Burkholderia vietnamiensis*, *B. kururiansis*, *B. tuberum* and *B. phynatum* being capable of fixing N_2 (Estrada-delos Station et al. 2001; Vandamme et al. 2002). When *B. vietnamiensis* was used to inoculate rice in a field trial, it increased grain yields significantly up to 8 t ha^{-1} (Tran Van et al. 2000). In field trials, this strain was

found capable of saving $25\text{--}30 \text{ kgN ha}^{-1}$ of fertilizer. The species *B. glumae* causes grain and seedling rot of rice (Nakata 2002). Another species, *B. cepacia*, can be hazardous to human health (Balandreau 2002), so appropriate care and risk-reducing techniques should be employed while isolating and culturing species of *Burkholderia* (Kennedy et al. 2004). *B. brasilensis* is an endophyte of roots, stems and leaves of sugarcane plant while *B. tropicalis* is confined to its roots and stems (Reis et al. 2000). There is also evidence that these organisms can produce substances antagonistic to nematodes (Meyer et al. 2000).

Several species of family *Enterobacteriaceae* include diazotrophs, particularly those isolated from the rhizosphere of rice. These enteric genera containing some examples of diazotrophs with PGP activity include *Klebsiella*, *Enterobacter*, *Citrobacter*, *Pseudomonas* and probably several others yet unidentified (Kennedy et al. 2004). *Klebsiella pneumoniae*, *Enterobacter cloacae*, *Citrobacter freundii* and *Pseudomonas putida* or *Pseudomonas fluorescens* are also examples of such plant-associated bacteria. *Herbaspirillum* is an endophyte which colonises sugarcane, rice, maize, sorghum and other cereals (James et al. 2000). It can fix 31–45% of total plant N in rice (30-day-old rice seedling) N from the atmosphere (Baldani et al. 2000). The estimated N fixation by *Herbaspirillum* was $33\text{--}58 \text{ mg tube}^{-1}$ under aseptic conditions (Reis et al. 2000). In a greenhouse study, inoculation with *Herbaspirillum* increased rice yield significantly up to 7.5 g plant^{-1} (Mirza et al. 2000). These authors quantified BNF by different strains of *Herbaspirillum* in both basmati and super basmati rice. The %N (N derived from the atmosphere) values were 19.5–38.7, and 38.1–58.2 in basmati and super basmati, respectively. *Herbaspirillum seropedicae* also acts as an endophytic diazotroph of wheat plants (Kennedy and Islam 2001), colonizing wheat roots internally between the cells. *Herbaspirillum seropedicae* is also found in roots and stems of sugarcane plant while *Herbaspirillum rubrisubalbicans* is an obligate endophyte of roots, stems and leaves (Reis et al. 2000). *Herbaspirillum* can also colonize maize plants endophytically and fix N_2 , in addition to sugarcane and wheat (James et al. 2000).

Phosphorus-solubilizing bacteria

Phosphorus (P) is one of the major essential macronutrients for plant growth and development (Ehrlich 1990). It is present at levels of $400\text{--}1,200 \text{ mg kg}^{-1}$ of soil. Phosphorus exists in two forms in soil, as organic and inorganic phosphates. To convert insoluble phosphates (both organic and inorganic) compounds in a form accessible to the plant is an important trait for a PGPR in increasing plant yields (Igual et al. 2001; Rodriguez et al. 2006). The concentration

of soluble P in soil is usually very low, normally at levels of 1 ppm or less (Goldstein 1994). The plant takes up several P forms but major part is absorbed in the forms of HPO_4^{2-} or $\text{H}_2\text{PO}_4^{-1}$. The phenomenon of P fixation and precipitation in soil is generally highly dependent on pH and soil type. Several reports have documented microbial P release from organic P sources (McGrath et al. 1995; Ohtake et al. 1996; McGrath et al. 1998; Rodríguez and Fraga 1999). Bacterial strains belonging to genera *Pseudomonas*, *Bacillus*, *Rhizobium*, *Burkholderia*, *Achromobacter*, *Agrobacterium*, *Micrococcus*, *Aerobacter*, *Flavobacterium* and *Erwinia* have the ability to solubilize insoluble inorganic phosphate (mineral phosphate) compounds such as tricalcium phosphate, dicalcium phosphate, hydroxyl apatite and rock phosphate (Goldstein 1986; Rodríguez and Fraga 1999; Rodríguez et al. 2006). Strains from genera *Pseudomonas*, *Bacillus* and *Rhizobium* are among the most powerful phosphate solubilizers, while tricalcium phosphate and hydroxyl apatite seem to be more degradable substrates than rock phosphate (Arora and Gaur 1979; Illmer and Schinner 1992; Halder and Chakrabarty 1993; Rodríguez and Fraga 1999; Banerjee et al. 2006). The production of organic acids especially gluconic acid seems to be the most frequent agent of mineral phosphate solubilization by bacteria such as *Pseudomonas* sp., *Erwinia herbicola*, *Pseudomonas cepacia* and *Burkholderia cepacia* (Rodríguez and Fraga 1999). Another organic acid identified in strains with phosphate-solubilizing ability is 2-ketogluconic acid, which is present in *Rhizobium leguminosarum* (Halder et al. 1990), *Rhizobium meliloti* (Halder and Chakrabarty 1993), *Bacillus firmus* (Banik and Dey 1982), and other unidentified soil bacteria (Duff and Webley 1959). Strains of *Bacillus licheniformis* and *B. amyloliquefaciens* were found to produce mixtures of lactic, isovaleric, isobutyric, and acetic acids. Other organic acids, such as glycolic acid, oxalic acid, malonic acid, succinic acid, citric acid and propionic acid, have also been identified among phosphate solubilizers (Illmer and Schinner 1992; Banik and Dey 1982; Chen et al. 2006). Goldstein (1994, 1995) has proposed that the direct periplasmic oxidation of glucose to gluconic acid, and often 2-ketogluconic acid, forms metabolic basis of the mineral phosphate solubilization phenotype in some Gram-negative bacteria. Alternative possibilities other than organic acids include the release of H^+ to the outer surface in exchange for cation uptake or ATPase which can constitute alternative ways, with the help of H^+ translocation, for solubilization of mineral phosphates (Rodríguez and Fraga 1999).

Soil also contains a wide range of organic substrates, which can be a source of P for plant growth. To make this form of P available for plant nutrition, it must be hydrolyzed to inorganic P. Mineralization of most organic phosphorous compounds is carried out by means of enzymes like phosphatase (phosphohydrolases) (Gügi et

al. 1991; Rodríguez and Fraga 1999), phytase (Richardson and Hadobas 1997), phosphonoacetate hydrolase (McGrath et al. 1998), D- α -glycerophosphatase (Skrary and Cameron 1998) and C-P lyase (Ohtake et al. 1996). Activity of various phosphatases in the rhizosphere of maize, barley, and wheat showed that phosphatase activity was considerable in the inner rhizosphere at acidic and neutral soil pH (Burns 1983). Soil bacteria expressing a significant level of acid phosphatases include strains from the genus *Rhizobium* (Abd-Alla 1994a, b), *Enterobacter*, *Serratia*, *Citrobacter*, *Proteus* and *Klebsiella* (Thaller et al. 1995a), as well as *Pseudomonas* (Gügi et al. 1991) and *Bacillus* (Skrary and Cameron 1998). Four strains, namely *Arthrobacter ureafaciens*, *Phyllobacterium myrsinacearum*, *Rhodococcus erythropolis* and *Delftia* sp. have been reported for the first time by Chen et al. (2006) as phosphate-solubilizing bacteria (PSB) after confirming their capacity to solubilize considerable amounts of tricalcium phosphate in the medium by secreting organic acids. There are also more reports on phosphate solubilization by *Rhizobium* (Halder et al. 1990, 1991; Abd-Alla 1994a, b; Chabot et al. 1996a, b) and the non-symbiotic nitrogen fixer, *Azotobacter* (Kumar et al. 2001). The efficacy of a strain of *Mesorhizobium mediterraneum* to enhance the growth and phosphorous content in chickpea and barley plants was assessed in a soil with and without addition of phosphates in a growth chamber (Peix et al. 2001). The results show that strain PECA21 was able to mobilize phosphorous efficiently in plants when tricalcium phosphate was added to soil. The effectiveness of strains of *Rhizobia* used in inoculation of a soil should not be based only on their fixation potential, since these bacteria can also increase plant growth by means of other mechanisms including the phosphate solubilization (Peix et al. 2001). The phosphate-solubilizing activity of *Rhizobium* (e.g., *Rhizobium/bradyrhizobium*), was associated with the production of 2-ketogluconic acid which was abolished by the addition of NaOH, indicating that the phosphate-solubilizing activity of this organism was entirely due to its ability to reduce pH of the medium (Halder and Chakrabarty 1993). However, detailed biochemical and molecular mechanisms of phosphate solubilization of symbiotic nodule bacteria need to be investigated. De Freitas et al. (1997) isolated 111 strains from plant rhizospheric soil, and a collection of nine bacteria (PGPR) were screened for P-solubilization in vitro. The P-solubilizing isolates were identified as two *Bacillus brevis* strains, *Bacillus megaterium*, *B. polymyxa*, *B. sphaericus*, *B. thuringiensis* and *Xanthomonas maltophilia* (PGPR strains R85). In addition, phosphate (P)-solubilizing bacteria such as *Bacillus* and *Paenibacillus* (formerly *Bacillus*) sp. have been applied to soils to enhance the phosphorus status of plant (Van Veen et al. 1997). The beneficial effects of PSB on plant growth varied significantly depending on environmental conditions,

bacterial strain, host plant and soil conditions (Şahin et al. 2004; Çakmakçı et al. 2006). The most common mechanism used by microorganisms for solubilizing tri-calcium phosphates seems to be acidification of the medium via biosynthesis and release of a wide variety of organic acids (Rodríguez and Fraga 1999; Igual et al. 2001; Goldstein and Krishnaraj 2007; Goldstein 2007; Delvasto et al. 2008).

Genetic manipulation of phosphate-solubilizing bacteria is another way to enhance their ability for plant growth improvement (Rodríguez and Fraga 1999; Rodríguez et al. 2006). This may include cloning gene(s) involved in both mineral and organic phosphate solubilization, followed by their expression in selected rhizobacterial strains (Rodríguez et al. 2006). Several attempts have been made to identify and characterize the genes involved for P uptake and its transportation (Rossolini et al. 1998; Shenoy and Kalagudi 2005). Apart from genes, quantitative trait loci (QTL) governing maize and barley yield under P-deficient conditions have also been identified (Kajar and Jensen 1995). Goldstein and Liu (1987) were the first to clone a gene involved in mineral phosphate solubilization from the Gram-negative bacteria *Erwinia herbicola*. Expression of this gene allowed production of GA in *Escherichia coli* HB101 and conferred the ability to solubilize hydroxyl apatite. Another type of gene (gabY) involved in GA production and mineral phosphate solubilization was cloned from *Pseudomonas cepacia* (Babu-Khan et al. 1995). Genes for four major P metabolic enzymes have been investigated (Valverde et al. 1999). The cytosolic GAPDH is coded by the nuclear gene GapC, whereas the chloroplastic GAPDH is encoded by the nuclear genes GapA and GapB. The nuclear GapN encodes the cytosolic GAPDH. The PGK is coded by nuclear gene pgk (Serrano et al. 1993). These cloned genes are an important source of material for genetic manipulation of PGPR strains for this trait. Some of them code for acid phosphatase enzymes that are capable of performing well in soil. For example, acpA gene isolated from *Francisella tularensis* expresses an acid phosphatase with optimum activity at pH 6, with a wide range of substrate specificity (Reilly et al. 1996). Also, genes encoding nonspecific acid phosphatases class A (PhoC) and class B (NapA) isolated from *Morganella morganii* are very promising (Thaller et al. 1994; 1995b). Among rhizobacteria, a gene from *Burkholderia cepacia* that facilitates phosphatase activity has been isolated (Rodríguez et al. 2000). This gene codes for an outer membrane protein that enhances synthesis in the absence of soluble phosphates in the medium, and could be involved in P transport to the cell. Besides, cloning of two nonspecific periplasmic acid phosphatase genes (napD and napE) from *Rhizobium* (*Sinorhizobium*) *meliloti* has been accomplished (Deng et al. 1998, 2001). The napA phosphatase gene from the soil bacterium *Morganella morganii* was transferred to *Burkholderia cepacia* IS-16, a strain used as a biofertilizer,

using the broad-host range vector pRK293 (Fraga et al. 2001). An increase in extracellular phosphatase activity of the recombinant strain was achieved. The ability of plants to obtain phosphorus directly from phytate (the primary source of inositol and the major stored form of phosphate in plant seeds and pollen) is very limited. However, the growth and phosphorus nutrition of *Arabidopsis* plants supplied with phytate was improved significantly when they were genetically transformed with the phytase gene. Thermally stable phytase genes (phy) from *Bacillus* sp. DS11 (Kim et al. 1998) and from *Bacillus subtilis* VTT E-68013 (Kerovuo et al. 1998) have been cloned. Acid phosphatase/phytase genes from *Escherichia coli* (appA and appA2 genes) have also been isolated and characterized (Golovan et al. 2000; Rodríguez et al. 1999). Neutral phytase genes have been recently cloned from *Bacillus licheniformis* (Tye et al. 2002). A phyA gene has been cloned from the FZB45 strain of *Bacillus amyloliquefaciens* isolated from a group of several *Bacillus* having plant growth promoting activity (Idriss et al. 2002).

Other mechanisms of plant growth promotion

Rhizosphere bacteria may improve the uptake of nutrients to plants and/or produce plant growth promoting compounds. They also protect plant root surfaces from colonization by pathogenic microbes through direct competitive effects and production of antimicrobial agents. These bacteria can indirectly or directly affect plant growth (Kloepper et al. 1989; Kloepper 1993, 1994; Glick 1995; Mantelin and Touraine 2004).

Symbiotic and non-symbiotic bacteria may promote plant growth directly through production of plant hormones (Dangar and Basu 1987; Lynch 1990; Arshad and Frankenberger 1991, 1993; Glick 1995; García de Salamone et al. 2001; Gutiérrez-Mañero et al. 2001; Persello-Cartieaux et al. 2003; Dobbelaere et al. 2003; Vivas et al. 2005) and other PGP activities (Dobbelaere et al. 2003). Plant growth promoting rhizobacteria (PGPR) synthesizes and exports phytohormones which are called plant growth regulators (PGRs). These PGRs may play regulatory role in plant growth and development. PGRs are organic substances that influence physiological processes of plants at extremely low concentrations (Dobbelaere et al. 2003). Bacteria known to produce PGRs are listed in Table 1. There are five classes of well-known PGRs, namely auxins, gibberellins, cytokinins, ethylene and abscisic acid (Zahir et al. 2004). Much attention has been given on the role of phytohormone auxin. The physiologically most active auxin in plants is indole-3-acetic acid (IAA), which is known to stimulate both rapid (e.g., increases in cell elongation) and long-term (e.g., cell division and differentiation) responses in

Table 1 Production of plant growth regulators (PGRs) by rhizobacteria and crop responses

PGPR	PGRs	Crops	Responses	Reference
<i>Kluyvera ascorbata</i> SUD 165	Siderophores, indole-3-acetic acid	Canola, tomato	Both strains decreased some plant growth inhibition by heavy metals (nickel, lead, zinc)	Burd et al. (2000)
<i>Rhizobium leguminosarum</i>	Indole-3-acetic acid	Rice	Inoculation with <i>R. leguminosarum</i> had significant growth promoting effects on rice seedlings.	Biswas et al. (2000)
<i>Rhizobium leguminosarum</i>	Indole-3-acetic acid	Rice	Growth promoting effects upon inoculation on axenically grown rice seedlings were observed	Dazzo et al. (2000)
<i>Azotobacter</i> sp.	Indole-3-acetic acid	Maize	Inoculation with strain efficient in IAA production had significant growth promoting effects on maize seedlings.	Zahir et al. (2000)
Rhizobacterial isolates	Auxins	Wheat, rice	Inoculation with rhizobacterial isolates had significant growth promoting effects on wheat and rice	Khalid et al. (2001)
Rhizobacteria (unidentified)	Indole-3-acetic acid	Brassica	Significant correlation between auxin production by PGPR in vitro and growth promotion of inoculated rapeseed seedlings in the modified jar experiments were observed	Asghar et al. (2002)
Rhizobacteria (unidentified)	Indole-3-acetic acid	Wheat, rice	Rhizobacterial strains active in IAA production had relatively more positive effects on inoculated seedlings.	Khalid et al. (2001)
<i>Pseudomonas fluorescens</i>	Siderophores, indole-3-acetic acid	Groundnut	Involvement of ACC deaminase and siderophore production promoted nodulation and yield of groundnut	Dey et al. (2004)
Rhizobacteria (Unidentified)	Auxin, indole-3-acetic acid, acetamide	Wheat	Strain produced highest amount of auxin in non-sterilized soil and caused maximum increase in growth yield	Khalid et al. (2003, 2004)
<i>Azospirillum brasilense</i> A3, A4, A7, A10, CDJA <i>Bacillus circulans</i> P2, <i>Bacillus</i> sp. P3, <i>Bacillus magaterium</i> P5, <i>Bacillus</i> . Sp. Psd7 <i>Streptomyces anthocynicus</i> <i>Pseudomonas aeruginosa</i> Psd5 <i>Pseudomonas pieketti</i> Psd6, <i>Pseudomonas fluorescens</i> MTCC103, <i>Azospirillum lipoferum</i> strains 15	Indole-3-acetic acid,	Rice	All the bacterial strains increased rice grain yield over uninoculated control	Thakuria et al. (2004)
<i>Pseudomonas denitrificans</i> <i>Pseudomonas rathonis</i>	Auxin	Wheat, maize	Promoted development of wheat root system even under crude oil contamination in pot experiment in growth chamber All the bacterial strains had been found to increase plant growth of wheat and maize in pot experiments	Muratova et al. (2005) Egamberdiyeva (2005)
<i>Azotobacter</i> sp. <i>Pseudomonas</i> sp.	Indole-3-acetic acid	Sesbenia, mung bean	Increasing the concentration of tryptophane from 1 mgml ⁻¹ to 5 mgml ⁻¹ resulted in decreased growth in both crops	Ahmad et al. (2005)
<i>Pseudomonas</i> sp.	Indole-3-acetic acid	Wheat	A combined bio-inoculation of diacetyl-phloreoglucinol producing PGPR and AMF and improved the nutritional quality of wheat grain	Roesti et al. (2006)
<i>Bacillus cereus</i> RC 18, <i>Bacillus licheniformis</i> RC08, <i>Bacillus megaterium</i> RC07, <i>Bacillus subtilis</i> RC11, <i>Bacillus</i> . OSU-142, <i>Bacillus</i> M-13, <i>Pseudomonas putida</i> RC06, <i>Paenibacillus polymyxa</i> RC05 and RC14	Indole-3-acetic acid	Wheat, spinach	All bacterial strains were efficient in indole acetic acid (IAA) production and significantly increased growth of wheat and spinach	Çakmakçi et al. (2007b)
<i>Mesorhizobium loti</i> MP6,	Chrom-azurol, siderophore (CAS), hydrocyanic acid (HCN), indole-3-acetic acid	Brassica	<i>Mesorhizobium loti</i> MP6-coated seeds enhanced seed germination, early vegetative growth and grain yield as compared to control	Chandra et al. (2007)
<i>Pseudomonas tolaasii</i> ACC23, <i>Pseudomonas fluorescens</i> ACC9, <i>Alcaligenes</i> sp. ZN4, <i>Mycobacterium</i> sp. ACC14, <i>Bacillus</i> sp. <i>Paenibacillus</i> sp.	Siderophores, Indole-3-acetic acid	Brassica	PGPR strains protect canola plant against the inhibitory effects of cadmium	Dell'Amico et al. (2008)
<i>Streptomyces acidiscabies</i> E13	Hydroxamate siderophores	Cowpea	The isolate SVPR 30, i.e. strain of <i>Bacillus</i> sp., proved to be efficient in promoting a significant increase in the root and shoot parts of rice plants <i>S. acidiscabies</i> promoted cowpea growth under nickel stress	Beneduzi et al. (2008) Dimkpa et al. (2008)

plants (Cleland 1990; Hagen 1990). IAA is the most common and best characterized phytohormone. It has been estimated that 80% of bacteria isolated from the rhizosphere can produce plant growth regulator IAA (Patten and Glick 1996). In addition to IAA, bacteria such as *Paenibacillus polymyxa* and *Azospirilla* also release other compounds in the rhizosphere, like indole-3-butyric acid (IBA), Trp and tryptophol or indole-3-ethanol (TOL) that can indirectly contribute to plant growth promotion (Lebuhn et al. 1997; El-Khawas and Adachi 1999). Cytokinins are other important phytohormones usually present in small amounts in biological samples, and their identification and quantification is difficult. Nieto and Frankenberger (1990b) reported on cytokinin by using bioassays. The most noticeable effect of cytokinin on plants is enhanced cell division: however, root development and root hair formation is also reported (Frankenberger and Arshad 1995). Plants and plant-associated microorganisms have been found to contain over 30 growth promoting compounds of the cytokinin group. It has been found that as many as 90% of microorganisms found in the rhizosphere are capable of releasing cytokinins when cultured in vitro (Barea et al. 1976). Nieto and Frankenberger (1990a, 1991) studied the effect of the cytokinin precursor's adenine (ADE) and isopentyl alcohol (IA) and cytokinin-producing bacteria *Azotobacter chroococcum* on the morphology and growth of radish and maize under in vitro, greenhouse and field conditions. They found improvement in plant growth. A number of articles have reported that PGPR also produced gibberellins (GAs). Dobbelaere et al. (2003) reported that over 89 GAs are known to date and are numbered GA1 through GA89 in approximate order of their discovery (Frankenberger and Arshad 1995; Arshad and Frankenberger 1998). The most widely recognized gibberellin is GA3 (gibberellic acid), the most active GA in plants is GA1, which is primarily responsible for stem elongation (Davies 1995). In addition abscisic acid (ABA) has also been detected by radio-immunoassay or TLC in supernatants of *Azospirillum* and *Rhizobium* sp. cultures (Kolb and Martin 1985; Dangar and Basu 1987; Dobbelaere et al. 2003). Primary role of ABA in stomatal closure is well established, as well as its uptake by and transport in plant, its presence in the rhizosphere could be extremely important for plant growth under a water-stressed environment, such as is found in arid and semiarid climates (Frankenberger and Arshad 1995).

Ethylene is synthesized by many and perhaps all species of bacteria (Primrose 1979). Ethylene is a potent plant growth regulator that affects many aspects of plant growth, development, and senescence (Reid 1987). In addition to its recognition as a ripening hormone, ethylene promotes formation of adventitious root and root hair, stimulates germination, and breaks dormancy of seeds (Esashi 1991). However, if ethylene concentration remains high after

germination, root elongation (as well as symbiotic N₂ fixation in leguminous plants) is inhibited (Jackson 1991). It has been proposed that many plant growth promoting bacteria may promote plant growth by lowering the levels of ethylene in plants. This is attributed to the activity of enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, which hydrolyzes ACC, the immediate biosynthesis precursor of ethylene in plants (Yang and Hoffman 1984). The products of this hydrolysis, ammonia and α ketobutyrate, can be used by the bacterium as a source of nitrogen and carbon for growth (Klee et al. 1991). In this way, the bacterium acts as a sink for ACC and thus lowers ethylene level in plants, preventing some of the potentially deleterious consequences of high ethylene concentrations (Glick et al. 1998; Steenhooudt and Vanderleyden 2000; Saleem et al. 2007). PGPR with ACC-deaminase trait usually give very consistent results in improving plant growth and yield, and thus are good candidates for bio-fertilizer formulation (Shaharoon et al. 2006a, 2006b). The role of PGPR in production of phosphatases, β -glucuronase, dehydrogenase, antibiotic (Hass and Keel 2003) solubilization of mineral phosphates and other nutrients, stabilization of soil aggregates, improved soil structure and organic matter contents (Miller and Jastrow 2000) has been recognized. The mechanisms involved have a significant plant growth promoting potential, retaining more soil organic N and other nutrients in plant–soil systems, thus reducing the need of N and P fertilizers (Kennedy et al. 2004) and enhancing the release of nutrients (Lynch 1990; Nautiyal et al. 2000; Walsh et al. 2001; Dobbelaere et al. 2003; Ladha and Reddy 2003).

PGPR has also been used to remediate contaminated soils (Zhuang et al. 2007; Huang et al. 2004, 2005; Narasimhan et al. 2003) and mineralize organic compounds in association with plants (Saleh et al. 2004). The combined use of PGPR and specific contaminant-degrading bacteria can successfully remove complex contaminants (Huang et al. 2005). The application of certain rhizobacteria can increase the uptake of Ni from soils by changing its phase (Abou-Shanab et al. 2006). Important genera of bacteria used in natural and man-created bioremediation includes *Bacillus*, *Pseudomonads*, *Methanobacteria*, *Ralstonia* and *Deinococcus*, etc. (Milton 2007). *Rhodobacter* can fix carbon and nitrogen from air to make biodegradable plastics (Sasikala and Ramana 1995). Bacteria *Ralstonia metallidurans* (Goris et al. 2001) and *Deinococcus radiodurans* (Callegan et al. 2008) can tolerate high levels of toxic metals and radioactivity, respectively. These bacteria can also be used to clean up pollutants in iron, copper, silver and uranium mines. Specific bacteria facilitate the removal of carbon, nitrogen and phosphorus compounds while others remove toxic metals, aromatic compounds, herbicides, pesticides and xenobiotics in multi-step processes involving both aerobic and anaerobic metabolism (Milton

2007). The bacterium *Accumulibacter phosphatis* has been responsible for the removal of phosphates (Hesselmann et al. 1999; Zhang et al. 2003).

Indirect plant growth promotion includes the prevention of deleterious effects of phytopathogenic organisms (Schippers et al. 1987; Dobbelaere et al. 2003; Glick and Pasternak 2003). This can be achieved by the production of siderophores, i.e. small iron-binding molecules. In soils, iron is found predominately as ferric ions, a form that cannot be directly assimilated by microorganisms. Siderophore production enables bacteria to compete with pathogens by removing iron from the environment (O'Sullivan and O'Gara 1992; Persello-Cartieaux et al. 2003). Siderophore production is very common among *Pseudomonas* (O'Sullivan and O'Gara 1992), *Frankia* (Boyer et al. 1999) and *Streptomyces* sp. (Loper and Buyer 1991) have also been shown to produce iron-chelating compounds. Biological control of soil-borne plant pathogens (Sutton and Peng 1993; Idriss et al. 2002; Chin-A-Woeng et al. 2003; Picard et al. 2004) and the synthesis of antibiotics have also been reported in several bacterial species (O'Sullivan and O'Gara 1992; Haansuu et al. 1999). Another mechanism by which rhizobacteria can inhibit phytopathogens is the production of hydrogen cyanide (HCN) and/or fungal cell wall-degrading enzymes e.g., chitinase and β -1, 3-glucanase (Friedlander et al. 1993; Bloemberg and Lugtenberg 2001; Persello-Cartieaux et al. 2003). Although pectinolytic capability is usually associated with phytopathogenic bacteria, nonphytopathogenic species such as *Rhizobium* (Angle 1986), *Azospirillum* (Umali-Garcia et al. 1980; Tien et al. 1981), some strains of *Klebsiella pneumoniae* and *Yersinia* (Chatterjee et al. 1978), and *Frankia* (Séguin and Lalonde 1989) are also able to degrade pectin. In general, pectinolytic enzymes play an important role in root invasion by bacteria. While PGPR have been identified within many different bacterial taxa, most commercially developed PGPR are species of *Bacillus* which come from endospores that confer population stability during formulation and storage of products. Among bacilli, strains of *Bacillus subtilis* are the most widely used PGPR due to their disease-reducing and antibiotic-producing capabilities when applied as seed treatments (Brannen and Backman 1994; Kokalis-Burelle et al. 2006). Specific mechanisms involved in pathogen suppression by PGPR vary and include antibiotic production, substrate competition, and induced systemic resistance in the host (Van Loon et al. 1998). Fluorescent pseudomonads are known to suppress soil-borne fungal pathogens by producing antifungal metabolites and by sequestering iron in the rhizosphere through release of iron-chelating siderophores, and thus rendering it unavailable to other organisms (Dwivedi and Johri 2003). Ryu et al. (2004) have identified several volatile organic compounds pro-

duced by various bacteria that promote plant growth and induce systemic resistance in *Arabidopsis thaliana*.

Previous research has shown the practicality of introducing PGPR into commercial peat-based substrates for vegetable production in order to increase plant vigor, control root diseases and increase yields (Kokalis-Burelle 2003; Kokalis-Burelle et al. 2002a, 2002b, 2003, 2006; Kloepper et al. 2004). Trials conducted on muskmelon (*Cucumis melo*) and water melon (*Citrullus lanatus*) resulted in reduction of root knot nematode disease severity with several PGPR formulations (Kokalis-Burelle et al. 2003). Kokalis-Burelle et al. (2006) conducted field trials in Florida on bell pepper (*Capsicum annuum*) to monitor the population dynamics of two plant growth-promoting rhizobacteria (PGPR) strains (*Bacillus subtilis* strain GBO3 and *Bacillus amyloliquefaciens* strain IN937a) applied in the potting media at seedling stage and at various times after transplanting to the field during the growing season. Most treatments reduced disease incidence in a detached leaf assay compared to control, indicating that systemic resistance was induced by PGPR treatments. Application of PGPR strains did not adversely affect populations of beneficial indigenous rhizosphere bacteria including fluorescent pseudomonads and siderophore-producing bacterial strains. Treatment with PGPR increased populations of fungi in the rhizosphere but did not result in increased root disease incidence. This fungal response to PGPR products was likely due to an increase in nonpathogenic chitinolytic fungal strains resulting from application of chitosan, which is a component of the PGPR formulation applied to the potting media. Table 2 cites important studies of biological control by PGPR against certain diseases, pathogens and insects in different crops.

Inoculation of *Pseudomonas fluorescens* isolates PGPR1, PGPR2 and PGPR4 reduced the seedling mortality caused by *Aspergillus niger* (Dey et al. 2004). Inoculation of *Pseudomonas fluorescens* isolates PGPR4 and PGPR5 showed strong inhibition to *Sclerotium rolfsii*, and reduced the incidence of stem rot severity. Several *Pseudomonas fluorescens* isolates, viz. PGPR1, PGPR2 and PGPR4, also produced siderophores and antifungal metabolites. Production of antifungal metabolites by fluorescent pseudomonads has also been found to suppress soil-borne fungal pathogens on many occasions (Pal et al. 2001; Dey et al. 2004). There are some cases where PGPR promoted plant growth in non-sterile soil by controlling fungal diseases (Cattelan et al. 1999). The addition of siderophores-producing *Pseudomonas putida* converted a fusarium-conducive soil into a fusarium-suppressive soil for growth of different plants (Dey et al. 2004). Improvement in plant growth and disease resistance to a broad array of plant pests can be accomplished using PGPR (Kloepper et al. 2004). The concept of

Table 2 Biological control by PGPR against diseases, pathogens and insects in different crops

PGPR	Crops	Disease/pathogen/insect	Reference
<i>Bacillus amyloliquefaciens</i> strain 1 N 937a <i>Bacillus subtilis</i> 1 N 937b	Tomato	Tomato mottle virus	Murphy et al. (2000)
<i>Pseudomonas fluorescens</i> and unidentified PGPR	Tobacco	Tobacco necrosis virus, wild fire (<i>Ps. syringae</i> , <i>Pv. tabaci</i>)	Park and Kloepper (2000)
<i>Pseudomonas aeruginosa</i> , <i>Bacillus subtilis</i>	Mung bean	Root rot, root knot	Siddiqui et al. (2001)
<i>Streptomyces marcescens</i> 90-116, <i>Bacillus pumilus</i> SE 34, <i>Pseudomonas fluorescens</i> 89B-61, <i>Bacillus pumilus</i> T4, <i>Bacillus pasteurii</i> C-9	Tobacco	Blue mold	Zhang et al. (2003)
<i>Pseudomonas</i> sp.	White clover <i>Medicago</i>	Blue green aphids <i>Acyrtosiphon kondoi</i> Shinji	Kempster et al. (2002)
<i>Bacillus</i> sp.	Cucumber	Cotton aphids <i>Aphis gossypii</i> Glover	Stout et al. (2002)
<i>Bacillus amyloliquefaciens</i> strain 1 N 937a <i>Bacillus subtilis</i> G803	Pepper	<i>Myzus persicae</i>	Kokalis-Burelle et al. (2002b)
<i>Pseudomonas</i> sp.	Groundnut	Charcoal rot caused by <i>Rhizoctonia bataticola</i>	Gupta et al. (2002)
<i>Azotobacter</i> sp., <i>Pseudomonas</i> sp.	Wheat	Fungal biocontrol	Wachowaska (2004)
<i>Bacillus licheniformis</i>	Tomato, pepper	<i>Myzus persicae</i>	Lucas et al. (2004b)
<i>Pseudomonas fluorescens</i>	Pea nut	Collar rot caused by <i>Aspergillus niger</i> , <i>Aspergillus flavus</i> and stem rot caused by <i>Sclerotium rolfsii</i>	Dey et al. (2004)
<i>Glomus mosseae</i> , <i>Bacillus subtilis</i> , <i>Pseudomonas fluorescens</i> <i>Trichoderma harzianum</i> , <i>Gliocladium catenulatum</i>	Strawberry	Crown rot caused by <i>Phytophthora cactorum</i> and red steel caused by <i>Phytophthora fragari</i>	Vestberg et al. (2004)
<i>Bacillus cereus</i> MJ-1	Red pepper	<i>Myzus persicae</i>	Joo et al. (2005)
<i>Paenibacillus polymyxa</i> E681	Sesame	Fungal disease	Ryu et al. (2006)
<i>Mesorhizobium loti</i> MP6,	Mustard <i>Brassica campestris</i>	White rot <i>Sclerotinia sclerotiorum</i>	Chandra et al. (2007)
<i>Bacillus amyloliquefaciens</i> , <i>Bacillus subtilis</i>	Bell pepper	<i>Green peach aphids</i> , <i>Myzus persicae</i> Sluzer	Herman et al. (2008)
<i>Azospirillum brasilense</i> Sp245	<i>Prunus cerasifera</i> L. clone Mr. 2/5	Rhizosphere fungi <i>Rhizoctonia</i> sp.	Russo et al. (2008)
<i>Bacillus cereus</i> BS 03, <i>Pseudomonas aeruginosa</i> RRLJ04 <i>Rhizobia</i>	Pigeonpea	<i>Fusarial wilt</i> , <i>Fusarium udum</i>	Dutta et al. (2008)
Pseudomonadaceae family.	Pea, entil and chickpea	<i>Pythium</i> sp. <i>Fusarium avenaceum</i>	Hynes et al. (2008)
Enterobacteriaceae family		<i>Rhizoctonia solani</i> CKP7	

introducing PGPR into the rhizosphere using the transplant plug is based on the hypothesis that their establishment in the relatively clean environment of planting media would afford them an opportunity to develop stable populations in the seedling rhizosphere, and that these populations would then persist in the field. It was also hypothesized that early exposure to PGPR might precondition young plants to resist pathogen attack after transplanting in the field. It is well recognized that PGPR can influence plant growth and resistance to pathogens (Cleyet-Marcel et al. 2001). However, it is necessary to establish a greater understanding of the dynamics of applied beneficial organisms under field conditions in order to optimize their application method and timing. It is also important to understand the effects of applied biocontrol strains on populations of indigenous beneficial bacteria including fluorescent pseudomonads, which commonly occur in the rhizosphere, and are known to suppress pathogen

establishment and disease (Dwivedi and Johri 2003). Because typical disease control levels observed with PGPR are less than those achieved with chemicals, it is feasible to utilize PGPR as components in integrated management systems that include reduced rates of chemicals and cultural control practices (Kokalis-Burelle et al. 2006). Attempts to identify methyl bromide, a soil fumigant alternative for vegetable production, has led to re-examination of existing soil fumigants (Gilreath et al. 2001), such as 1,3-D, metam sodium and chloropicrin, and development of new broad-spectrum biocides, such as methyl iodide and propargyl bromide (Ohr et al. 1996; Noling and Gilreath 2001), as well as increasing interest in non-chemical approaches. PGPR have attracted much attention in their role in reducing plant diseases. Although their full potential has not yet been reached, the work to date is very promising. Some PGPR, especially if they are inoculated on seeds before planting, are able to establish

themselves on crop roots. They use scarce resources, and thereby prevent or limit the growth of pathogenic microorganisms. This is a common way in which PGPR reduce the severity of damping-off (*Pythium ultimum*) in many crops. Even if nutrients are not limiting, establishment of beneficial organisms on roots limits the chance that a pathogenic organism that arrives later will find space to become established. Numerous rhizosphere organisms are capable of producing compounds that are toxic to pathogens (plant diseases). *Bacillus subtilis* is one such commercialized PGPR organism, and it acts against a wide variety of pathogenic fungi (Banerjee et al. 2006).

Conclusion

Soil bacteria transform atmospheric N₂ into ammonia and are central to soil and plant health. They play a pivotal role in cycling of nutrients within the soil. The soil contains numerous genera of bacteria, many of which not only have important roles in nutrient cycling but also protect crops against diseases. Plant growth promoting rhizobacteria (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. Biological inoculums for legumes have attracted much attention throughout the world. Other PGPR inoculants (*Azospirillum*, *Azotobacter*, *Bacillus*, *Pseudomonas*, etc.) are also available for a variety of crops, used alone or co-inoculating with *Rhizobium* sp. These technologies have resulted in positive responses under controlled (laboratory and greenhouse) conditions; however, natural variations make it difficult to predict how PGPR may respond when applied to field conditions. PGPR must be propagated artificially to optimize their viability and biological activity under field applications. It is also suggested that PGPR need to be reinoculated every year/season as they will not live forever in the soil.

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