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REVIEW

Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture

P. N. Bhattacharyya · D. K. Jha

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Abstract Plant growth-promoting rhizobacteria (PGPR) are the rhizosphere bacteria that can enhance plant growth by a wide variety of mechanisms like phosphate solubilization, siderophore production, biological nitrogen fixation, rhizosphere engineering, production of 1-Aminocyclopropane-1-carboxylate deaminase (ACC), quorum sensing (QS) signal interference and inhibition of biofilm formation, phytohormone production, exhibiting antifungal activity, production of volatile organic compounds (VOCs), induction of systemic resistance, promoting beneficial plant-microbe symbioses, interference with pathogen toxin production etc. The potentiality of PGPR in agriculture is steadily increased as it offers an attractive way to replace the use of chemical fertilizers, pesticides and other supplements. Growth promoting substances are likely to be produced in large quantities by these rhizosphere microorganisms that influence indirectly on the overall morphology of the plants. Recent progress in our understanding on the diversity of PGPR in the rhizosphere along with their colonization ability and mechanism of action should facilitate their application as a reliable component in the management of sustainable agricultural system. The progress to date in using the rhizosphere bacteria in a variety of applications related to agricultural improvement along with their mechanism of action with special reference to plant growth-promoting traits are summarized and discussed in this review.

P. N. Bhattacharyya · D. K. Jha (✉)
Department of Botany,
Microbial Ecology Laboratory,
Gauhati University, Guwahati,
Assam 781014, India
e-mail: dkjha_gu@rediffmail.com

Keywords ACC- deaminase · Colonization ability · Plant-microbe symbiosis · Quorum sensing signal interference · Rhizosphere bacteria · Rhizosphere engineering

Abbreviations

AHLs	N-acyl homoserine lactones
ACC	1-Aminocyclopropane-1-carboxylate
AFM	Anti-fungal metabolite
DAPG	2, 4-diacetylphloroglucinol
BYMV	Bean yellow mosaic potyvirus
CSI	Central insecticide board
ISR	Induced systemic resistance
PO	Peroxidise
PAL	Phenylalanine ammonia-lyase
PGPR	Plant growth-promoting rhizobacteria
PCBs	Polychlorinated biphenyls
PPO	Polyphenol oxidase
QS	Quorum sensing
RFLP	Restriction fragment length polymorphism
RZT	Root zone temperature
VOCs	Volatile organic compounds
YCF1	Yeast cadmium factor protein

Introduction

Although bacteria were not known to exist until the discovery of microscopic animals by Anton von Leeuwenhoek (1683), their utilization to stimulate plant growth has been exploited since ancient times. Theophrastus (372–287 BC) suggested the mixing of different soil samples for remedying defects and adding heart to soil (Tisdale and Nelson 1975). Virgil recorded the establishment of legumes on

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cultivated land and demonstrated the beneficial effects of legume crops in increasing the fertility of soil (Chew 2002). Hellriegel and Wilfarth (1888) investigated the rhizosphere root colonization in grasses and legumes and suggested the ability of soil bacteria to convert atmospheric N_2 into plant usable forms. Based on their experiments on radishes, Kloepper and Schroth (1978) introduced the term 'rhizobacteria' to the soil bacterial community that competitively colonized plant roots and stimulated growth and thereby reducing the incidence of plant diseases. Kloepper and Schroth (1981) termed these beneficial rhizobacteria as plant growth-promoting rhizobacteria (PGPR). PGPR can be defined as the indispensable part of rhizosphere biota that when grown in association with the host plants can stimulate the growth of the host. PGPR seemed as successful rhizobacteria in getting established in soil ecosystem due to their high adaptability in a wide variety of environments, faster growth rate and biochemical versatility to metabolize a wide range of natural and xenobiotic compounds. Cook (2002) considered PGPR as the significant component in the management of agricultural practices with innate genetic potential. The concept of PGPR has now been confined to the bacterial strains that can fulfil at least two of the three criteria such as aggressive colonization, plant growth stimulation and biocontrol (Weller et al. 2002; Vessey 2003). According to Whipps (2001) there are three basic categories of interactions (neutral, negative or positive) generally exists between the rhizobacteria and growing plants. Most rhizobacteria associated with plants are commensals in which the bacteria establish an innocuous interaction with the host plants exhibiting no visible effect on the growth and overall physiology of the host (Beattie 2006). In negative interactions, the phytopathogenic rhizobacteria produces phytotoxic substances such as hydrogen cyanide or ethylene, thus, negatively influence on the growth and physiology of the plants. Counter to these deleterious bacteria, there are some PGPRs that can exert a positive plant growth by direct mechanisms such as solubilization of nutrients, nitrogen fixation, production of growth regulators, etc., or by indirect mechanisms such as stimulation of mycorrhizae development, competitive exclusion of pathogens or removal of phytotoxic substances (Bashan and de-Bashan 2010). However, in accordance with their degree of association with the plant root cells, PGPRs can be classified into extracellular plant growth promoting rhizobacteria (ePGPR) and intracellular plant growth promoting rhizobacteria (iPGPR) (Martinez-Viveros et al. 2010). The ePGPRs may exist in the rhizosphere, on the rhizoplane or in the spaces between the cells of root cortex; on the other hand, iPGPRs locates generally inside the specialized nodular structures of root cells. The bacterial genera such as *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcous*, *Pseudomonas* and *Serratia* belongs to ePGPR (Gray and Smith 2005). The iPGPR includes the endophytes and *Frankia* species both of which can symbiotically fix atmospheric N_2 with the higher plants (Verma et al. 2010). Endophyte includes a wide range of soil bacterial genera such as *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium* and *Rhizobium* of the family Rhizobiaceae that generally invades the root systems in crop plants to form nodules (Wang and Martinez-Romero 2000) and stimulates growth either directly or indirectly. This group of rhizobacteria is mostly Gram-negative and rod-shaped with a lower proportion being Gram-positive rods, cocci and pleomorphic. Examples can also be cited from *Allorhizobium undicola* (de Lajudie et al. 1998a), *Azorhizobium caulinodans* (Dreyfus et al. 1988), *Bradyrhizobium japonicum* (Guerinot and Chelm 1984), *Mesorhisobium chacoense* (Velazquez et al. 2001), *Mesorhizobium pluriforium* (de Lajudie et al. 1998b), *Rhizobium ciceri* (Nour et al. 1994), *Rhizobium etli* (Segovia et al. 1993), *Rhizobium fredii* (Scholla and Elkan 1984), *Rhizobium galegae* (Lindstrom 1989), *Rhizobium gallicum* (Amarger et al. 1997), *Rhizobium giardinii* (Amarger et al. 1997), *Sinorhizobium arboris* (Nick et al. 1999), *Sinorhizobium fredii* (Chen et al. 1988) and *Sinorhizobium medicae* (Rome et al. 1996). Some of the important plant species forming symbiotic association with these rhizobial species includes *Acacia* sp., *Arachis hypogaea*, *Cajanus cajan*, *Cercis canadensis*, *Cicer arietinum*, *Glycine max*, *Lens culinaris*, *Lotus corniculatus*, *Medicago sativa*, *Phaseolus vulgaris*, *Pisum sativum* and *Trifolium* sp. (Verma et al. 2010). In addition, several actinomycetes, one of the major components of rhizosphere microbial populations are also useful because of their significant ecological roles in soil nutrient cycling (Halder et al. 1991; Elliot and Lynch 1995) as well in plant growth-promoting activities (Merzaeva and Shirokikh 2006). Numbers of reports (Gomes et al. 2000; Sousa et al. 2008) are available on the potential of actinomycetes as plant growth-promoting agent. Actinomycetes strains like *Micromonospora* sp., *Streptomyces* spp., *Streptosporangium* sp., and *Thermobifida* sp., are recorded as best to colonize the plant rhizosphere, showing an immense potentiality as biocontrol agent against a range of root pathogenic fungi (Franco-Correa et al. 2010). Rhizosphere *Streptomycetes* as potential biocontrol agent of *Fusarium* and *Armillaria* pine rot and as PGPR of *Pinus taeda* was reported (de Vasconcellos and Cardoso 2009). Evidences are now available on actinobacteria used in the control of *Rhizoctonia solani* and *Pseudomonas solanacearum* in tomato (Sabaratnam and Traquair 2002) and *Colletotrichum musae* in banana (Taechowisan et al. 2003). Soil actinomycetes are also an important source of diverse antimicrobial metabolites (Terkina et al. 2006). de Vasconcellos et al. (2010) isolated and screened antagonistic actinobacteria of

Araucaria angustifolia rhizosphere for the production of active metabolites. The metabolites, especially, Indole-acetic acid (IAA) and chitinase are recorded as responsible for the degradation of different complex and relatively recalcitrant organic compounds present in soil. Similar antagonistic activity of endophytic *Streptomyces griseorubiginosus* against *Fusarium oxysporu*m f. sp. *cubense* has been recorded by Cao et al. (2004).

Potential role of PGPRs in conferring resistance to water stress in tomatoes and peppers has been investigated (Mayak et al. 2004). Fluorescent pseudomonads and species of *Bacillus* were reported with very high efficiency in host root colonization and production of growth metabolites resulting in improved strategic crop yield (Khalid et al. 2004). The various modes of action of a *Bacillus subtilis* strain, FZB24 against phytopathogens are examined by Kilian et al. (2000) suggesting the role of the bacterium in plant vitality (Fig. 1). According to Cakmakci et al. (2006) soil rhizobacterial populations are capable of exerting beneficial effects on many plants like wheat, potato, maize, grasses, pea and cucumber by colonizing rhizosphere. Applications of PGPR increased the nodulation and nitrogen fixation of soya bean (*Glycine max* (L.) Merr.) over a wide range of root zone temperatures (RZTs) (Zhang et al. 1996). Thus, it has been established that the inoculation of PGPRs can increase nodulation, nitrogen uptake, growth and yield response of crop plants. In addition to this, employing microorganisms as co-culture in biotization is also another important area of research (Sekar and Kandavel 2010) in recent decade. Biotization is a metabolic response of in vitro grown plant material to microbial inoculants leading to developmental and physiological changes of the derived propagules, causing enhancement in the biotic and abiotic stress resistance in plants. Here, plantlets are usually co-cultured with PGPR to produce more biomass and secondary metabolites. For instances, *Origanum vulgare* L. plantlets when co-cultured with *Pseudomonas* spp., produced more phenolics and chlorophyll than non-bacterized control (Nowak 1998). Besides, importance of PGPRs in maintaining root health, nutrient uptake and tolerance to environmental stress are also well recognized (Malhotra and Srivastava 2009) although, specific traits of promoting plant growth and development are limited at a given environment of plant–microbe interactions. Several PGPR formulations are currently available as commercial products for agricultural production of beneficial crops. Our understanding on PGPR is now advancing at cellular, genomic and proteomic level. Large numbers of PGPR strains of different bacterial classes and genera with multifunctional traits have, therefore, been described for their potent application in boosting plant activities in modern agriculture. However, it is equally important to study in detail the potentiality of this group of rhizospheric microbiota along with their mechanism of action involved in sustainable crop production. We also need to improve our knowledge for the selection of potent microbial strains colonizing rhizosphere of growing plants for specific restoration programmes. PGPR can promote growth and yield of crop plants by direct and indirect mechanisms. In some PGPR species, plant growth promotion dominates with nitrogen fixation, phosphate solubilization and production of phytohormones like auxin and cytokinin and volatile growth stimulants such as ethylene and 2, 3-butanediol (Ryu et al. 2003; Vessey 2003).

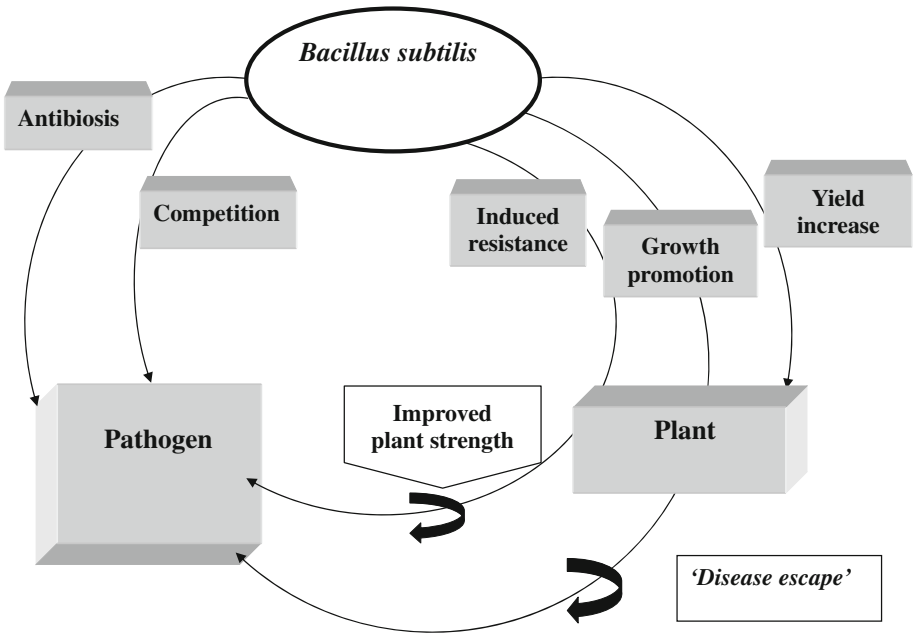

Fig. 1 Modes of action of *Bacillus subtilis* strain, FZB24 promting plant growth (Adapted from Kilian et al. 2000)

Siderophore production for rhizosphere colonization has also been recorded as one of the important mechanism by certain PGPRs (*Bradyrhizobium japonicum*, *Rhizobium leguminosarum* and *Sinorhizobium meliloti*) (Carson et al. 2000; El-Tarabily and Sivasithamparam 2006) with plant growth promoting activity. Besides, iron-chelating siderophores (Schippers et al. 1988), antibiotics (Weller 1988) and hydrogen cyanides (Stutz et al. 1986) are also likely to be produced by PGPR strains, participating tremendously in the reduction of phytopathogens and deleterious rhizobacteria with a corresponding improvement in plant health. However, regardless of the mechanism of plant growth promotion, PGPR must colonize the rhizosphere or root itself (Glick 1995). The objective of this review will be to examine our current understandings on the known, putative and speculative mechanism of plant-growth promotion by the rhizobacteria along with their potential emergence on overall plant growth and development in agriculture.

The rhizosphere and plant–microbe interactions

Plant–microbe interactions may occur at phyllosphere, endosphere and rhizosphere. Phyllosphere is related with the aerial parts of the plants and endosphere with internal transport system. Rhizosphere, the term, can be defined as any volume of soil specially influenced by the plant roots or in association with the roots and plant-produced material. According to Bringhurst et al. (2001) rhizosphere includes the region of soil bound by plant roots, often extending a few mm from the root surface. This region of soil is much richer in bacteria than the surrounding bulk soil (Hiltner 1904). Studies based on molecular techniques have estimated more than 4,000 microbial species per gram of soil (Montesinos 2003). Filamentous actinobacteria are also considered as one of the important community in rhizosphere microbiota (Benizri et al. 2001) being able to influence the plant development as well to protect the plant roots against phytopathogens. Plant exudates such as amino acids and sugars provide a rich source of energy and nutrients for the bacteria in rhizosphere, resulting in more microbial populations in the region than outside the region (Haas and Defago 2005). Plant-root interactions in rhizosphere may include root–root, root-insect and root-microbe interactions, resulting in the production of more root exudates that ultimately favours maximum microbial populations (rhizosphere engineering) in this ecologically significant region. Changes in rhizobacterial community structure have been reported with the application of polymerase chain reaction (PCR) and denaturing gradient gel electrophoresis (DGGE) resulting in significant alterations in plant–microbes interactions (Herschkovitz et al. 2005). However, successful root colonization and persistence of PGPRs in plant rhizosphere are required in order to exert their beneficial effect on the plant (Elliot and Lynch 1984). The intimacy between the plants and the environment in rhizosphere is thus essential for better acquisition of water and nutrients by plants as well beneficial interactions of plants with soil-borne microorganisms (Ryan et al. 2009). According to Cardoso and Freitas (1992) the rhizosphere microbial communities are vigorously associated with the biogeochemical cycling of nutrients like C, P, N and S, removal of toxins and production of phytohormones or antibiotics etc. Rhizobacteria may depend on other microbes for nutrient sources as one microbe may convert plant exudates into a form that can be used by another microbe. Thus, rhizosphere has appeared as a versatile and dynamic ecological environment of intense plant-microbe interactions (Mayak et al. 2004) harnessing essential micro and macro-nutrients affecting plant growth, although, the process of root colonization is under the influence of various parameters such as bacterial traits, root exudates and several other biotic and abiotic factors (Benizri et al. 2001). In many rhizospheric relationships, the PGPRs are known to colonize the plant root (Andrews and Harris 2000) and stimulate plant growth. The colonization of plant rhizosphere by *Azospirillum* sp., *Bacillus subtilis* sp., and *Pseudomonas* sp., has been well studied (Steenhoudt and Vanderleyden 2000; Trivedi et al. 2005). Moreover, immobilized form of PGPR inoculants in comparison to free forms has greater ability of survival and plant root colonization. Recently, it has been reported that soil microorganisms, including free-living as well as associative and symbiotic rhizobacteria belonging to the genera like *Acinetobacter*, *Alcaligenes*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Proteus*, *Pseudomonas*, *Rhizobium*, *Serratia*, *Xanthomonas* in particular, are the integral parts of rhizosphere biota (Glick 1995; Kaymak 2011) exhibiting successful rhizosphere colonization. Lugtenberg et al. (2001) reported a large number of cell surface molecules as responsible for the effective rhizosphere colonization. Rhizospheric colonization is thus, considered as a crucial step in the application of microorganisms for beneficial purposes such as biofertilization, phytostimulation, biocontrol and phytoremediation, although the colonization of rhizosphere by PGPRs is not a uniform process. For example, *Kluyvera ascorbata* colonized the upper two-thirds of the surface of canola roots but no bacteria were detected around the root tips (Ma et al. 2001).

Mechanism of action

The search for PGPRs and their mode of action are increasing at a rapid rate in order to use the best PGPR

strain as commercial biofertilizer. Investigations into the mechanisms of plant growth promotion by PGPR strains indicated that the effective PGPRs increased plant growth basically by changing the whole microbial community structure in rhizosphere (Kloepper and Schroth 1981). According to Glick et al. (1999) the general mechanisms of plant growth promotion by PGPR includes associative nitrogen fixation, lowering of ethylene levels, production of siderophores and phytohormones, induction of pathogen resistance, solubilization of nutrients, promotion of mycorrhizal functioning, decreasing pollutant toxicity etc. Castro et al. (2009) suggested that PGPR strains can promote plant growth and development either directly and indirectly. Direct stimulation includes biological nitrogen fixation, producing phytohormones like auxins, cytokinins and gibberellins, solubilizing minerals like phosphorus and iron, production of siderophores and enzymes and induction of systemic resistance, while indirect stimulation is basically related to biocontrol, including antibiotic production, chelation of available Fe in the rhizosphere, synthesis of extracellular enzymes to hydrolyze the fungal cell wall and competition for niches within the rhizosphere (Zahir et al. 2004; van Loon 2007). PGPR strains, especially, *Pseudomonas fluorescens* and *Bacillus subtilis* are best recorded as the most promising candidates of indirect stimulation (Damayanti et al. 2007). Besides, nitrogen transformation, increasing bioavailability of phosphate, iron acquisition, exhibition of specific enzymatic activity and plant protection from harmful pathogens with the production of antibiotics can also successfully improve the quality of crops in agriculture (Spaepen et al. 2007). Thus, based on their mechanism of action, PGPRs can be categorized into three general forms such as biofertilizer, phytostimulator and biopesticide (Table 1). The phenomenon of quorum regulation can affect the expression of each of these traits as PGPRs are reported for their regular interactions with the resident microbial community in rhizosphere (Lugtenberg and Kamilova 2009). Recent investigations on PGPR revealed that it can promote plant growth mainly by following means; (1) producing ACC deaminase to reduce the level of ethylene in the roots of developing plants (Dey et al. 2004) (2) producing plant growth regulators like indole acetic acid (IAA) (Mishra et al. 2010), gibberellic acid (Narula et al. 2006), cytokinins (Castro et al. 2008) and ethylene (Saleem et al. 2007) (3) asymbiotic nitrogen fixation (Ardakani et al. 2010) (4) exhibition of antagonistic activity against phytopathogenic microorganisms by producing siderophores, β-1,3-glucanase, chitinases, antibiotics, fluorescent pigment and cyanide (Pathma et al. 2011) and (5) solubilization of mineral phosphates and other nutrients (Hayat et al. 2010). PGPR may use more than one of these mechanisms to enhance plant growth as experimental evidence suggests that the plant growth stimulation is the net result of multiple mechanisms that may be activated simultaneously (Martinez-Viveros et al. 2010). Recently, biochemical and molecular approaches are providing new insight into the genetic basis of these biosynthetic pathways, their regulation and importance in biological control (Joshi and Bhatt 2011). However, to be more effective in the rhizosphere, PGPR must maintain a critical population density for a longer period, although inoculation of plants with PGPR can temporarily enhance the population size.

Potential role of PGPR in agriculture

Production of plant growth regulators

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 PGPRs as well as some pathogenic, symbiotic and free living rhizobacterial species are

Table 1 Forms of PGPRs and their mechanism of action stimulating plant growth

PGPR forms	Definition	Mechanism of action	References
Biofertilizer	A substance that contains live microorganisms which, when applied on the seed, plant surface or soil, colonizes the rhizosphere and promote plant growth through increased supply of primary nutrients for the host plant	Biological nitrogen fixation	Vessey (2003)
		Utilization of insoluble phosphorus	Somers et al. (2004)
Phytostimulator	Microorganism, with the ability to produce phytohormones such as indole acetic acid, gibberellic acid, cytokinins and ethylene	Production of phytohormones	Lugtenberg et al. (2002), Somers et al. (2004)
Biopesticide	Microorganisms that promote plant growth by controlling phytopathogenic agents	Production of antibiotics, siderophores, HCN	Vessey (2003)
		Production of hydrolytic enzymes	Somers et al. (2004)
		Acquired and Induced systemic resistance	Chandler et al. (2008)

reported to produce IAA and gibberllic acid in the rhizospheric soil and thereby plays 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. The phytopathogenic bacteria rather use the indole acetamide pathway to synthesize IAA that has been implicated earlier in the tumor induction in plants. Swain et al. (2007) reported a positive effect of IAA producing strains of *Bacillus subtilis* on *Dioscorea rotundata* L. They applied a suspension of *B. subtilis* on the surface of the plant, which resulted in an increase in the root: stem ratio as well as number of sprouts as compared with the non-inoculated plants. Potentiality of *Azotobacter* spp., to produce high amount of IAA (7.3–32.8 mg/ml) in agriculture was reported by Ahmad et al. (2005). Similarly, significant shoot growths in maize and rice dwarf mutants were promoted by gibberellins-like substances excreted by *Azospirillum* spp. (Boiero et al. 2007). Table 2 represents some of the efficient PGPR strains as the producer of different plant growth regulators. IAA-mediated ethylene production could increase root biomass, root hair number and consequently the root surface area of PGPR inoculated tomato plants (Ribaudo et al. 2006). Involvement of PGPR-formulated cytokinins were also observed in root initiation, cell division, cell enlargement and increase in root surface area of crop plants through enhanced formation of lateral and adventitious roots (Werner et al. 2003). Recently, it has been established that the working pathways of these phytostimulators leading to overall development in crop plants are differently regulated by catabolite repression (Zaied et al. 2009) as physiological regulator of biofilm formation.

Phosphorous solubilization

Phosphorus is one of the most essential nutrient requirements in plants. Ironically, soils may have large reservoir of total phosphorous (P) but the amounts available to plants are usually a tiny proportion of this total. This low availability of phosphorous to plants is because of the vast majority of soil P is found in insoluble forms, while the plants can only absorb it in two soluble forms, the monobasic ($H_2PO_4^-$) and the diabasic (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 solubilise phosphate in soil. Release of plant root exudates such as organic ligands can also alter the concentration of P in soil solution (Hinsinger 2001). According to Nahas (1996) phosphate solubilization takes place through various microbial processes including organic acid production and proton extrusion. In certain cases, phosphate solubilization is induced by phosphate starvation (Gyaneshwar et al. 1999). A general sketch of phosphorous solubilization in soil is shown in Fig. 2. Bacterial genera like *Azospirillum*, *Azotobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas*, *Rhizobium* and *Serratia* are reported as the most significant phosphate solubilizing bacteria (Sturz and Nowak 2000; Sudhakar et al. 2000; Mehnaz and Lazarovits 2006). Rhizobacteria can solubilize inorganic P sources and enhance growth and yield of crop plants. Besides, examples of some widely reported P solubilising microbial species intimately associated with a large number of agricultural crops like potato, tomato, wheat, radish, pulses etc., are *Azotobacter chroococcum* (Kumar and Narula

Table 2 Efficient PGPR strains as phytohormone producer in numbers of plants

Hormone produced	PGPR	Host	References
IAA	*Aeromonas veronii*	Rice	Mehnaz et al. (2001)
	Agrobacterium sp.	Lettuce	Barazani and Friedman (1999)
	Alcaligenes piechaudii	Lettuce	Barazani and Friedman (1999)
	Azospirillum brasilense	Wheat	Kaushik et al. (2000)
	Bradyrhizobium sp.	Radish	Antoun et al. (1998)
	Comamonas acidovorans	Lettuce	Barazani and Friedman (1999)
	Enterobacter cloacae	Rice	Mehnaz et al. (2001)
	Rhizobium leguminosarum	Radish	Antoun et al. (1998)
Cytokinin	*Paenibacillus polymyxa*	Wheat	Timmusk et al. (1999)
	Pseudomonas fluorescens	Soybean	Garcia de Salamone et al. (2001)
	Rhizobium leguminosarum	Rape & lettuce	Noel et al. (1996)
Gibberellin	*Bacillus* sp.	Alder	Gutierrez-Manero et al. (2001)

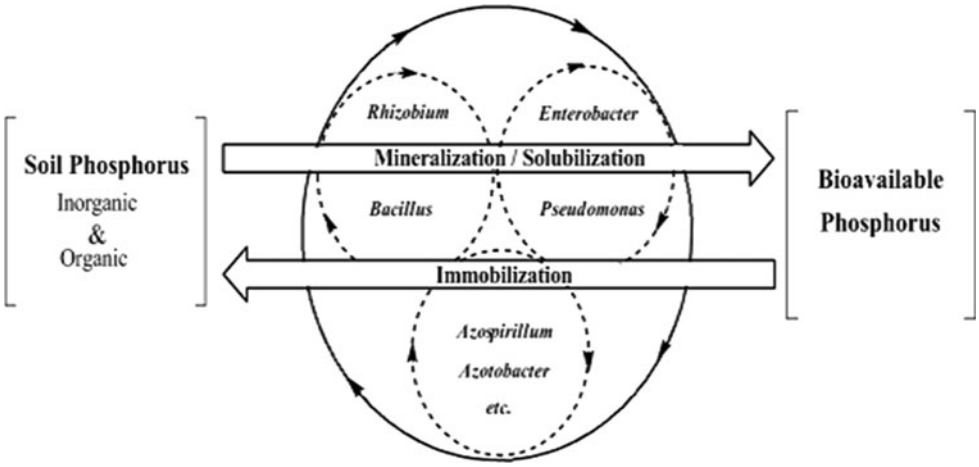

Fig. 2 Schematic representation of solubilisation of soil phosphorus by rhizobacteria (Khan et al. 2009)

1999), *Bacillus circulans* and *Cladosporium herbarum* (Singh and Kapoor 1999), *Bradyrhizobium japonicum* (Antoun et al. 1998), *Enterobacter agglomerans* (Kim et al. 1998), *Pseudomonas chlororaphis* and *P. putida* (Cattelan et al. 1999) and *Rhizobium leguminosarum* (Chabot et al. 1998). The ability of PGPRs to solubilize mineral phosphate, therefore, has been of immense interest to agricultural microbiologists since it can enhance the availability of phosphorus for effective plant growth. PGPRs have been recorded to solubilize precipitated phosphates to plants, representing a possible mechanism of plant growth promotion under field conditions (Verma et al. 2001). Synthesis of organic acids by rhizosphere microorganisms could be the possible reason for solubilization of inorganic P sources.

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 promotes root growth. The term, biofertilizer should not be used interchangeably with green manure, manure, intercrop or organic-supplemented chemical fertilizer. Interestingly some PGPR species have appeared to promote plant growth by acting both as biofertilizer and biopesticide. For instances, strains of *Burkholderia cepacia* have been observed with biocontrol characteristics to *Fusarium* spp., while, can also stimulate growth of maize under iron-poor conditions via siderophore production (Bevivino et al. 1998). *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium* and *Sinorhizobium* are reported as the potent PGPR strains for their ability to act as biofertilizers (Vessey 2003). The relationship between the PGPR and their host can be categorized into two basic levels of complexity: (1) rhizospheric and (2) endophytic. In rhizospheric relationship, the PGPRs 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 physico-chemical properties of rhizospheric soil such as soil pH, water potential and partial pressure of O_2 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 resides 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). Best examples can be cited from legume-rhizobia symbioses in leguminous plants (Vessey 2003). Thus, the means by which the PGPRs enhance nutrient status of host plants and thereby act as biofertilizers can be categorized into five distinct areas such as biological N_2 fixation, increasing the availability of nutrients in rhizosphere, increase in root surface area, enhancing beneficial symbioses of the host and finally the combinations of all the above modes of action. However, the degree of intimacy between the PGPRs and host plant can vary depending on where and how the PGPR colonizes the plant.

Quorum sensing signal interference and inhibition of biofilm formation

Quorum sensing (QS) is a community genetic regulation mechanism that controls microbiological functions of medical, agricultural and industrial importance. Discovery of microbial QS signaling led to identification of numerous enzymatic and non-enzymatic signal interference mechanisms that could quench microbial QS signaling (Zhang and Dong 2004) and inhibition of biofilm formation (Ren et al. 2001). QS activation is mediated by a small autoinducer (AI) molecule, responsible for cell–cell communication and the

coordinated action in many bacteria, including PGPRs. Commonly reported autoinducer signals are N-acyl homoserine lactones (AHLs) (von Bodman et al. 2003), although half a dozen of other molecules, including diketopiperazines in several Gram-negative bacteria (Holden et al. 1999), furanosyl borate diester in *Vibrio harveyi* (Chen et al. 2002) and γ-butyrolactone in *Streptomyces* (Yamada and Nihira 1998) have also been implicated in density-dependent signaling. Investigations on QS signal interference mechanisms thus might significantly broaden the scope of research in modern biotechnology.

Production of ACC deaminase and regulation of ethylene level in plants

Although ethylene is essential for normal growth and development in plants, at high concentration it can be harmful as it induces defoliation and other cellular processes that may lead to reduced crop performance. Using their 1-amino cyclopropane-1-carboxylic acid (ACC) deaminase activity, PGPR can divert ACC from the ethylene biosynthesis pathway in the root system of *Arabidopsis thaliana* plant (Desbrosses et al. 2009). Thus, rhizobacteria assist in diminishing the accumulation of ethylene levels and re-establish a healthy root system needed to cope with environmental stress. The primary mechanism includes the destruction of ethylene via enzyme ACC deaminase. There are number of publications (Ghosh et al. 2003; Govindasamy et al. 2008; Duan et al. 2009) mentioning rhizosphere bacteria such as *Achromobacter*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Pseudomonas* and *Rhizobium* with ACC deaminase activity. Most of the studies have demonstrated the production of ACC deaminase gene in the plants treated with PGPR under environmental stress. Grichko and Glick (2001) inoculated tomato seeds with *Enterobacter cloacae* and *Pseudomonas putida* expressing ACC deaminase activity and registered an increase in plant resistance. Ghosh et al. (2003) recorded ACC deaminase activity in three *Bacillus* species namely, *Bacillus circulans* DUC1, *Bacillus firmus* DUC2 and *Bacillus globisporus* DUC3 that stimulated root elongation in *Brassica campestris*. Mayak et al. (2004) observed tomato plants inoculated with the bacterium *Achromobacter piechaudii* under water and saline stress conditions and reported a significant increase in fresh and dry weight of inoculated plants. Similar increase in root dry matter and aerial parts in canola (*Brassica napus*) seeds with the inoculation of ACC deaminase gene producing bacterium, *Pseudomonas asplenii* are reported by Reed and Glick (2005). Morphological changes in certain plant species after inoculation with PGPR containing ACC deaminase gene has been presented in Table 3.

Genetic modification of PGPR strains expressing ACC deaminase gene are helpful in biological control of various plant diseases. PGPR containing ACC deaminase can boost the plant growth particularly under stressed environmental conditions like salinity, drought, water logging, temperature, pathogenicity and contaminants in response to a multitude of abiotic and biotic stresses (Saleem et al. 2007). In canola, ACC deaminase containing bacteria conferred salt tolerance and promoted plant growth by lowering the synthesis of salt-induced ethylene (Cheng et al. 2007). Recently, a bacterial strain, *Pseudomonas fluorescens* TDK1 containing ACC deaminase is reported to enhance the saline resistance and overall yield in groundnut as compared to those inoculated with *Pseudomonas* strains lacking ACC deaminase activity (Govindasamy et al. 2008). Although efforts have thus, been made to introduce ACC deaminase genes into plants for optimum growth, the genetic modifications for all the plant species are not yet possible due to many handicaps like proprietary rights and international trade agreements on genetically modified (GM) crops and limitations of DNA recombinant technology.

Production 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 signalling 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 signalling plants to register plant defence more investigations into the volatile components in plant-rhizobacteria system should follow.

Rhizosphere engineering

Rhizosphere microbial populations are tremendously affected by the interactions between the plants and the soil

Table 3 Morphological changes in plants brought about by PGPR strains containing ACC deaminase gene

Plant species	PGPR strains	Morphological changes	References
Brassica campestris	*Methylobacterium fujisawaense*	Bacterium promoted root elongation in canola	Madhaiyan et al. (2006)
B. campestris	*Bacillus circulans DUC1*, *B. firmus DUC2*, *B. globisporus DUC3*	Bacterial inoculation enhanced root and shoot elongation	Ghosh et al. (2003)
B. napus	*Alcaligenes* sp. *Bacillus pumilus*, *Pseudomonas* sp. *Variovorax paradoxus*	Inoculated plant demonstrated more vigorous growth than the uninoculated (control)	Belimov et al. (2001)
B. napus	*Enterobacter cloacae*	Significant increases in root and shoot lengths were observed	Saleh and Glick (2001)
Dianthus caryophyllus L.	*Azospirillum brasilense* Cd1843	Inoculated cuttings produced longest roots	Li et al. (2005)
Glycine max	*Pseudomonas cepacia*	Rhizobacterium caused an early soybean growth	Cattelan et al. (1999)
Pisum sativum L.	*Rhizobium leguminosarum bv. viciae* 128C53 K	Bacterium enhanced nodulation in plants	Ma et al. (2003)
Vigna radiata L.	*Pseudomonas* sp. *Bradyrhizobium* sp.	Bacterium promoted nodulation in mung bean	Shaharoona et al. (2006)
V. radiata L.	*Pseudomonas putida*	The ethylene production was inhibited in inoculated cuttings	Mayak et al. (1999)
Zea mays L.	*Enterobacter sakazakii* 8MR5, *Pseudomonas* sp. 4MKS8, *Klebsiella oxytoca* 10MKR7	Inoculation increased agronomic parameters of maize	Babalola et al. (2003)
Zea mays L.	*Pseudomonas* sp.	Bacterium caused root elongation in maize	Shaharoona et al. (2006)

environment. Rhizosphere engineering involves the selection of beneficial microbial populations by plant rhizosphere. For instances, some crop species or cultivars select populations of antibiotic-producing strains that play a major role in soils, naturally suppressive to soil-borne fungal pathogens (Ryan et al. 2009). Persistent organic pollutants such as polychlorinated biphenyls (PCBs) are a global problem. Using root-associated microbes in rhizospheric engineering approach, the levels of PCBs can be successfully depleted as these microbes can use plant secondary metabolites such as phenylpropanoids (Narasimhan et al. (2003). Similar technology has been developed by Lugtenberg et al. (2001) during their investigation on the growth of microbes with the ability to metabolize exotic nutrients exuded by plants. One of the earliest success of this technology was based on the favourable partitioning of the exotic nutrient opines, produced by the transgenic plants (Oger et al. 1997) that led to the improved and competitive growth of the metabolizing strains in comparison with the microbes unable to metabolize opines. Rhizosphere engineering ultimately reduces our reliance on agrochemicals by replacing their functions with beneficial microbes, biodegradable biostimulants or transgenic plants (Ryan et al. 2009). It is now possible to create a nutritional bias that may be especially successful in identifying microbial populations due to the general nutrient-limiting conditions in rhizosphere. Molecular microbiological advances are tremendously been exploiting in order to achieve a complete knowledge of the complex chemical and biological interactions that generally occurs in the rhizosphere, ensuring that the strategies to engineer the rhizosphere are safe and eco-friendly to agricultural systems. For example, plants are genetically engineered to modify the rhizosphere pH to release the compounds that could improve nutrient availability, protect plants against biotic and abiotic stresses or encourage the proliferation of beneficial microorganisms. Growth stimulation can be mediated directly through enhanced nutrient acquisition or modulation of phytohormone synthesis. While, indirect stimulation involves the induction of plant antagonism (Ryan et al. 2009). Sundheim et al. (1988) observed that an engineered strain of *Pseudomonas* expressing chitinase gene from *Serratia marcescens* more effectively controlled *Fusarium oxysporum* f. sp. *redolens* and *Gaeumannomyces graminis* var. *tritici* in vitro. Recently, experiments targeting on the DAPG-producing PGPR strain, *Pseudomonas fluorescens* (*phlD*$^{+}$) have demonstrated that plant species can differentially enrich and support different microbial populations (De La Fuente et al. 2006) and genotypes (Landa et al. 2006) in the rhizosphere. Notz et al. (2001) significantly correlated DAPG accumulation by *Pseudomonas fluorescens* CHA0 with the expression of DAPG biosynthesis gene phlA and observed that the expression was significantly greater in the rhizosphere of monocots

than dicots. Although the exact mechanism is not totally understood, Di Gregorio et al. (2006) noticed a combined application of Triton X-100 and *Sinorhizobium* sp. Pb002 inoculums for the improvement of lead phytoextraction by *Brassica juncea* in EDTA amended soil.

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 defence 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 towards 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 *Eschscholtzia californica* Cham. are treated with a yeast elicitor (Roberts and Shuler 1997). Some of the well reported PGPRs as biotic elicitors have been exemplified in Table 4. Ajmalicine, serpentine, picrocrocin, 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.

Induction of systemic disease resistance

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 non-pathogenic, 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 potyvirus (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* 89B-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, *Flavomonas oryzihabitans* INR-5, *Serratia marcescens* 90–166 and *Bacillus pumilus* INR-7 has 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. 3). Based on their experiments they concluded that

Table 4 PGPR species as biotic elicitors to elicit plant response

PGPR species	Plant	Metabolite induced in plant	Sample references
Pseudomonas fluorescens	*Catharanthus roseus* (L.) G. Don	Ajmalicine	Jaleel et al. (2007)
P. fluorescens	*Catharanthus roseus* (L.) G. Don	Serpentine	Jaleel et al. (2009)
P. putida and *P. fluorescens*	*Hyoscyamus niger* L	Hyoscyamine and Scopolamine	Ghorbanpour et al. (2010)
Bacillus subtilis	*Crocus sativus* L	Picrocrocin, Crocetin and Safranal compounds	Sharaf-Eldin et al. (2008)
B. cereus	*Salvia miltiorrhiza* Bunge	Tanshinone	Zhao et al. (2010)

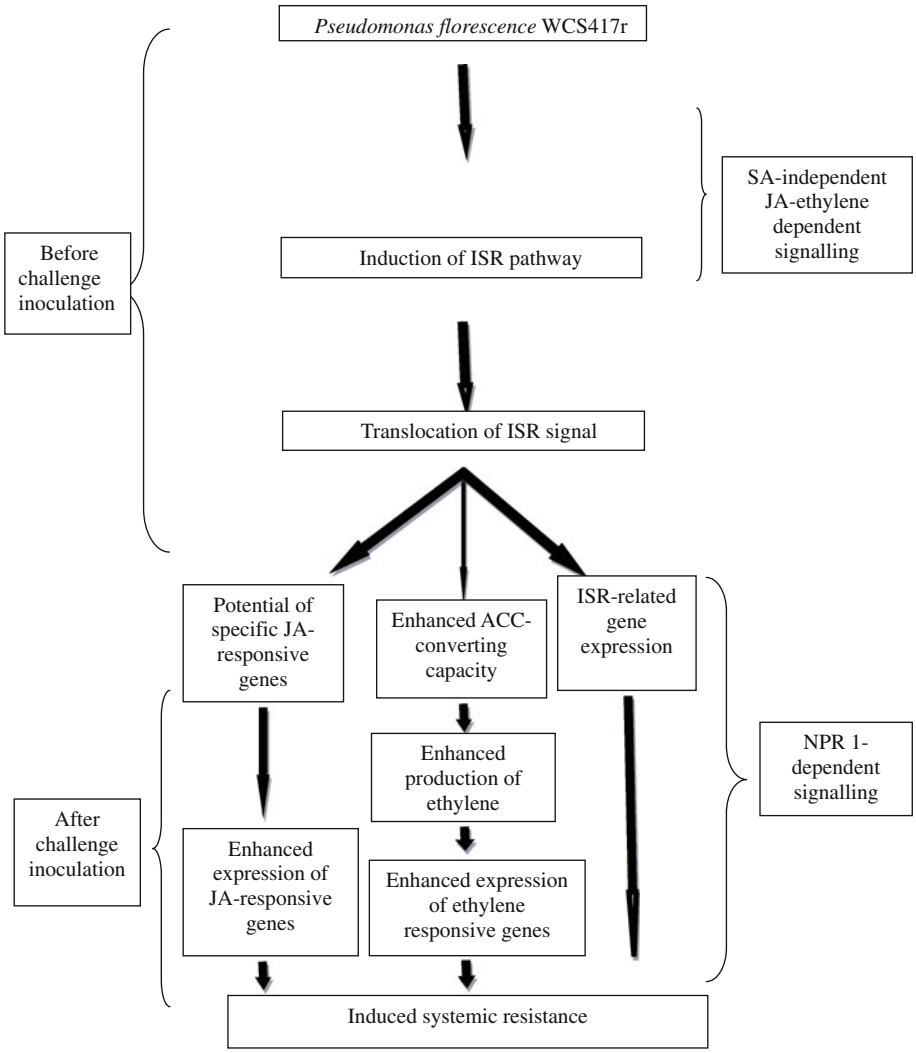

Fig. 3 Possible involvement of jasmonic acid and ethylene in *Pseudomonas fluorescens* WCS417r-mediated induced systemic resistance in Arabidopsis (Adapted from Pieterse et al. 2001)

Pseudomonas fluorescens strain WCS417r could elicit systemic disease resistance in plants through a variety of signal translocation pathways like SA-independent JA-ethylene dependent signalling, ISR-related gene expression, NPR 1-dependent signalling 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 green house and field trials on tomato, bell pepper, muskmelon, watermelon, sugarbeet, tobacco and cucumber. Through the activation of various defence-related enzymes like chitinases, β-1, 3-glucanase, peroxidise (PO), phenylalanine ammonia-lyase (PAL) and polyphenol oxidase (PPO), PGPR strains can induce this type of systemic resistance in plants (Bharathi 2004).

Nitrogen fixation

Nitrogen (N) is one of the principal plant nutrients, becoming a limiting factor in agricultural ecosystems due to heavy losses by rainfall or mineral leaching. Number of PGPR strains such as *Azoarcus* sp., *Beijerinckia* sp., *Klebsiella pneumoniae*, *Pantoea agglomerans* and *Rhizobium* sp. are reported to fix atmospheric N_2 in soil (Antoun et al. 1998; Riggs et al. 2001) and make it available to plants. Parmar and Dadarwal (1999) recorded fluorescent pseudomonads to promote nodulation in chickpea and latter demonstrated the role of this group of rhizosphere microbiota in N_2 fixation. Recently, Minorsky (2008) reported a PGPR strain, *Pseudomonas fluorescens* B16, exhibiting vigorous colonization in the roots of tomatoes, causing enhancement in plant height, flower number and total fruit weight. A similar investigation on rhizobia to replace the use of nitrogen fertilizer was made by Vessey (2003) and thereby demonstrated a clear picture of improvement in crop yield after the inoculation of

Table 5 PGPR species and their ability to fix atmospheric N_2 in certain plants

PGPR	Relationship to host	Host crops	Sample references
Azospirillum sp.	Rhizospheric	Maize	Garcia de Salamone et al. (1996)
		Rice	Malik et al. (1997)
		Wheat	Boddey et al. (1986)
Azoarcus sp.	Endophytic	Kallar grass	Hurek et al. (2002)
		Sorghum	Stein et al. (1997)
Azotobacter sp.	Rhizospheric	Maize	Pandey et al. (1998)
		Wheat	Mrkovacki and Milic (2001)
Bacillus polymyxa	Rhizospheric	Wheat	Omar et al. (1996)
Burkholderia sp.	Endophytic	Rice	Baldani et al. (2000)
Gluconacetobacter sp.	Endophytic	Sorghum	Isopi et al. (1995)
		Sugarcane	Boddey et al. (2001)
Herbaspirillum sp.	Endophytic	Rice	James et al. (2002)
		Sorghum	James et al. (1997)

rhizobacteria in agricultural soil. A list of PGPR species along with their ability to fix atmospheric N_2 in different plants has been illustrated in Table 5. PGPR can fix atmospheric N_2 either symbiotically or non-symbiotically. Symbiotic N_2 fixation to legume crops with the inoculation of effective PGPRs are well known (Dobereiner 1997; Barea et al. 2005; Esitken et al. 2006). Various rhizobacterial species like *Azotobacter* spp., *Bacillus* spp., *Beijerinckia* spp., etc., have the capacity to fix atmospheric N_2 symbiotically. However, the process of symbiotic N_2 fixation is limited only to legume crops and various trees and shrubs that form actinorrhizal roots with *Frankia*. On the other hand, non-symbiotic biological N_2 fixation is basically carried out by free living diazotrophics, belonging to the genera like *Azoarcus* (Reinhold-Hurek et al. 1993), *Azospirillum* (Bashan and de-Bashan 2010), *Burkholderia* (Estrada de los Santos et al. 2001), *Gluconacetobacter* (Fuentes-Ramirez et al. 2001) and *Pseudomonas* (Mirza et al. 2006). Besides, combined inoculations of rhizobacterial species to improve the quality of soil are also seemed to be a potent area of research in present day agriculture. For instances, combined inoculations of *Bradyrhizobium* sp., with *Pseudomonas striata* have established enhanced nodule occupancy in soya bean resulting in more biological N_2 fixation (Dubey 1996).

Growth enhancement

Application of PGPR strains in agriculture is a potential issue in increasing international demand for food and improving environmental quality. PGPRs have been continuously used to enhance the plant growth, seed emergence and overall yield of crops in different agroecosystems (Minorsky 2008). Inoculation of PGPR species could increase the growth attributes like leaf area, chlorophyll content and consequently, the total biomass of the musa plantlets under nitrogen-free hydroponics (Baset Mia et al. 2010) as compared to the uninoculated control. Dobbelaere et al. (2001) assessed the inoculation effect of *Azospirillum* sp., on the growth of some agriculturally important plants and observed a significant increase in the dry weight of both the root system and aerial parts of the PGPR inoculated plants, resulting in better development and flowering. Esitken et al. (2003) investigated the foliar applications of rhizobacterial microbes in mulberry and apricot and observed better development in total leaf area and chlorophyll production of the inoculated plants. Several PGPR strains such as *Achromobacter xylosoxidans*, *Bacillus subtilis*, *B. licheniformis*, *B. pumilus*, *Brevibacterium halotolerans* and *Pseudomonas putida* are identified as having crucial roles in cell elongation, increasing ACC deaminase activity and plant growth promotion (Sgroy et al. 2009). Total root length, surface area and volume in tomato and cucumber roots increased after inoculation with *Pseudomonas fluorescens* 92rk and P190r (Saravanakumar and Samiyappan 2007). PGPR induces changes in external layers of root cortex due to enhanced divisions of cells in root tips of maize and wheat seedlings (Baset Mia et al. 2010). 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). Khalid et al. (2004) observed the growth responses of wheat after the inoculation with rhizobacteria and suggested that the growth of wheat basically depends on a number of factors like plant genotype, nature of PGPR inoculants as well as environmental conditions. There are also reports concerning the root inoculation of apple trees with *Bacillus* M3 and *Microbacterium* FS01, resulting in significant tree growth and yield (Karlidag et al. 2007). One of the possible mechanisms of enhancing apple trees growth in the study might be due to enhanced production of plant growth regulators and mobilization of

available nutrients by PGPRs. Ahanthem and Jha (2007) observed the response of rice crops, inoculated with arbuscular mycorrhizal (AM) fungi and PGPR in soils differing in nitrogen concentrations. They recorded maximum shoot biomass, shoot phosphorus and nitrogen content in the rice plants inoculated with *Azotobacter chroococcum* in combination with *Glomus* sp., than when the plants were inoculated either of them above. Interactions between *Acaulospora* and *Azospirillum* and their synergistic effect on rice growth at different sources and regimes of soil phosphorus have also been made by Ahanthem and Jha (2008). The results thus, indicated the influence of microbial inoculants in reducing the inorganic fertilizer demand by 50%.

Rhizoremediation

The application of PGPRs in rhizoremediation technologies is now being considered as effective, since inoculation of PGPR strains could aid remarkable enhancement in plant growth and development on contaminated agroclimatic conditions. Rhizobacteria can directly assist rhizoremediation by producing IAA, biological nitrogen fixation, solubilizing P and secreting siderophores (Denton 2007). PGPR strains, pseudomonads and *Acinetobacter* enhance uptake of Fe, Zn, Mg, Ca, K and P by crop plants (Esitken et al. 2006). PGPR along with AM fungi are now being utilized in the nutrient poor agricultural soils to increase the solubility of heavy metals and thereby increasing the chances of success in rhizoremediation. Besides, investigations on the application of PGPR strains in decreasing the bioavailability of toxicity resulting in better growth and development in heavy metal contaminated soils through recycling of nutrients, maintaining soil structure, detoxifying chemicals and controlling pests are also well studied (Denton 2007). Studies on certain rhizobacteria in Ni uptake by *Alyssum murale* indicated that this group of bacteria can release the metal from its non-soluble phase by decreasing the pH of the environment (Zhuang et al. 2007).

Effects of PGPR on root growth

The treatment of seeds or cuttings in some plants with non-pathogenic bacteria, such as *Agrobacterium*, *Alcaligenes*, *Bacillus*, *Pseudomonas*, *Streptomyces*, etc., induces root formation (Esitken et al. 2003). This phenomenon might be attributed to the production of auxin, inhibition of ethylene synthesis or mineralization of nutrients by efficient PGPRs (Steenhoudt and Vanderleyden 2000). More likely, PGPRs have been reported for their immense potentiality to alter several hormonal pathways that could account for different morphological changes in plants like an increased elongation rate of lateral roots, resulting in more architecture in branched root system of growing plants (Kapulnik et al. 1985). However, considering about interactions between different hormone signalling pathways in plants, it is difficult to determine the exact pathway of elicitation of primary plant rootings by PGPRs. Growth promoting effects of PGPRs on rootings and root growth of *Actinidia deliciosa* stem cuttings was examined by Erturk et al. (2010). *Bacillus* RC23, *Bacillus* RC03, *B. megaterium* RC01, *B. subtilis* OSU142, *B. simplex* RC19, *Comamonas acidovorans* RC41 and *Paenibacillus polymyxa* RC05 were recorded as the successful PGPRs in the experiment. All the bacteria were tested for their IAA activity. Among the rhizobacterial treatments, the highest rooting ratios were obtained at 47.50% for semi-hardwood stem cuttings from *Bacillus* RC03 and *B. simplex* RC19 treatments and 42.50% for hardwood stem cuttings from *Bacillus* RC03. The results suggested the potentiality of PGPR strains to replace the use of synthetic auxins in organic nursery material production. Similarly, Desbrosses et al. (2009) investigated the PGPR-Arabidopsis interaction to establish the signalling pathways involved in controlling plant development and observed an ethylene-independent and auxin-independent mechanism, regulating the elongation of root hair in Arabiopsis. This is something of great interest since genetic screens for abnormal root hair phenotypes in Arabidopsis repeatedly led to the isolation of mutants altered in ethylene or auxin response. They finally concludes that a genetic screen based on inoculation triggered root hair elongation could be a successful tool to unravel mechanisms involved in the control of root hair elongation.

Maintenance of soil fertility and nutrient uptake

PGPR can change the plant physiology and certain nutritional and physical properties of rhizospheric soil and indirectly influence on the colonization patterns of soil microorganisms in that particular region. Inoculation of rhizobacteria increased uptake of nutrient elements like Ca, K, Fe, Cu, Mn and Zn by plants through stimulation of proton pump ATPase (Mantelin and Touraine 2004). Reports are available on the combinations of *Bacillus* and *Microbacterium* inoculants to improve the uptake of the mineral elements by crop plants (Karlidag et al. 2007). This increase in nutrient uptake by plants might be explained through organic acid production by the plants and PGPRs, decreasing the soil pH in rhizosphere. Ample evidences (Phillips 1980; Forde 2000; Glass et al. 2002) are there on the maintenance of soil fertility by the rhizobacterial isolates to increase the availability of nutrients for plants. Solubilization of unavailable forms of nutrients is one of the essential criteria in facilitating the transport of most of these nutrients (Glick 1995).

Resistance to water stress

Drought stress causes limitation to the plant growth and productivity of agricultural crops particularly in arid and semi-arid areas. Inoculation of plants with PGPR can enhance the drought tolerance (Figueiredo et al. 2008) that might be due to the production of IAA, cytokinins, antioxidants and ACC deaminase. Inoculation of seeds of *Phragmites australis* with *Pseudomonas asplenii* improved germination and protect the plants from growth inhibition (Bashan et al. 2008). PGPR are also reported as beneficial to the plants like tomatoes and peppers growing on water deficit soils for conferring resistance to water stress conditions (Aroca and Ruiz-Lozano 2009). More investigations into the mechanisms by which PGPR elicit tolerance to specific stress factors would improve our knowledge on the use of these rhizobacteria in agriculture to provide induced systemic tolerance to water stress.

Antagonistic activity of PGPR

Rhizobacteria can suppress the growth of various phytopathogens in variety of ways like competing for nutrients and space, limiting available Fe supply through producing siderophores, producing lytic enzymes and antibiosis (Jing et al. 2007). Among PGPRs, fluorescent pseudomonads are widely reported for their broad spectrum antagonistic activity against number of phytopathogens. Han et al. (2005) have reported *Delftia tsuruhatensis* strain, HR4, which suppressed the growth of various plant pathogens like *Pyricularia oryzae*, *Rhizoctonia solani* and *Xanthomonas oryzae*. Deliveries of microbial antagonists with urban and agricultural wastes are believed to be the most effective means in suppressing root pathogens of avocado and citrus (Sultana et al. 2006). Recently, different PGPR strains of *Rhizobium meliloti* have been reported to produce siderophores (Arora et al. 2001) in iron stress conditions and thereby added an advantage to exclude the pathogen, *Macrophomina phaseolina*, causing charcoal rot of groundnut. Application of *Pseudomonas aeroginosa* in combination with common medicinal plant *Launaea nudicaulis* also holds good promises for effective control of root infecting fungi of mungbean (Mansoor et al. 2007).

PGPR as biocontrol agent

Competition for nutrients, niche exclusion, induced systemic resistance and production of anti-fungal metabolites (AFMs) is the probable means responsible for biocontrol activity of PGPRs (Bloemberg and Lugtenberg 2001). Most of the PGPRs are recorded to produce AFMs, of which phenazines, pyrrolnitrin, 2, 4-diacetylphloroglucinol (DAPG), pyoluteorin, viscosinamide and tensin are the frequently detected classes. Among PGPRs, *Pseudomonas* is the best-characterized biocontrol agent at molecular level. *P. fluorescens* strain, WCS374 has been recorded to suppress Fusarium wilt in radish leading to an average increase of 40% in yield (Bakker et al. 2007). The individual genes such as phzO and phzH responsible for the presence of functional group on phenazine compound have been detected (Chin-A-Woeng et al. 2001). More recently, informations have been generated on the biosynthesis of pyoluteorin in *Pseudomonas fluorescens* Pf-5 and 2, 4-diacetylphloroglucinol in *P. fluorescens* Q2-87 (Kidarsa et al. 2011). Biocontrol activity of *Streptomyces* spp. are reported by Kumar et al. (2009) indicating the tremendous potentiality of PGPRs as an alternative in controlling plant diseases in agriculture than that of conventional fungicides. A list of PGPR strains used as biocontrol agents against a large number of phytopathogens and insects affecting crop plants are shown in Table 6. *Azospirillum*, *Azotobacter*, *Bacillus*, *Enterobacter*, *Paenibacillus*, *Pseudomonas* and *Streptomyces* are recorded as the potent genera of rhizobacteria acting against the pathogens like *tomato mottle virus*, *tobacco necrosis virus*, *Rhizoctonia bataticola*, *Myzus persicae*, *Acyrthosiphon kondoi*, *Fusarium avenaceum* etc. Besides, experiments on the dual effect of PGPR and AM fungi on *Fusarium oxysporum f.* sp., *melongenae* causing brinjal wilt has been made by Kalita et al. (2009). PGPR strains such as *Azotobacter* sp., *Azospirillum* sp., and *Pseudomonas fluorescens* and AM fungi like *Glomus fasciculatum*, *G. mossae* and *Gigaspora margarita* are recorded as the most promising microbes to suppress the wilt disease of brinjal, in vitro. The microbial inoculants when used as composite inoculum exhibited maximum efficiency in the suppression of diseases with the characteristic increase in chlorophyll content, total number of leaves, shoot height and thereby facilitating overall crop yield than when inoculated singly. However, application of these PGPR strains did not affect populations of beneficial indigenous rhizosphere bacteria including the fluorescent pseudomonads and the siderophore-producing bacterial strains.

Selection and characterization of PGPR strains

PGPR strains have diverse applications in agriculture, horticulture and forestry. The process of applying rhizobacteria in soil and plant parts to eradicate bacterial and fungal pathogens was pioneered in Soviet Union by 1958 (Suslow et al. 1979) even though the selection of efficacious PGPR strains at that period was highly complicated. Specific PGPR strains are initially selected from several hundreds of root-colonizing bacteria isolated from excised

Table 6 PGPR used as bio control agents against different diseases, pathogens and insects affecting different crops

PGPRs	Crops	Disease/pathogen/insect	Sample references
Bacillus amyloliquefaciens	Tomato	*Tomato mottle virus*	Murphy et al. (2000)
Pseudomonas fluorescens	Tobacco	*Tobacco necrosis virus*	Park and Kloepper (2000)
Bacillus pumilus SE 34	Tobacco	Blue mold	Zhang et al. (2003)
Pseudomonas sp.	Groundnut	*Rhizoctonia bataticola*	Gupta et al. (2002)
Streptomyces marcescens 90–116	Tobacco	Blue mold	Zhang et al. (2003)
Bacillus sp.	Cucumber	Cotton aphids	Stout et al. (2002)
Bacillus licheniformis	Pepper	*Myzus persicae*	Lucas et al. (2004)
Bacillus cereus MJ-1	Red pepper	*Myzus persicae*	Joo et al. (2005)
Pseudomonas sp.	White clover *Medicago*	*Acyrthosiphon kondoi*	Kempster et al. (2002)
Paenibacillus polymyxa E681	Sesame	Fungal disease	Ryu et al. (2006)
Enterobacter sp.	Chickpea	*Fusarium avenaceum*	Hynes et al. (2008)
Azospirillum brasilense	*Prunus cerasifera* L.	Rhizosphere fungi	Russo et al. (2008)
Pseudomonas aeruginosa	Mung bean	Root rot	Siddiqui et al. (2001)
Bacillus subtilis G803	Pepper	*Myzus persicae*	Kokalis-Burelle et al. (2002)
Bacillus amyloliquefaciens	Bell pepper	*Myzus persicae* Sluzer	Herman et al. (2008)

roots of field grown plants. Potential PGPRs are then selected for their ability to inhibit the growth of various phytopathogens or miscellaneous rhizosphere bacteria and fungi in vitro. Pure cultures of antagonistic rhizobacterial strains are screened in greenhouse trials. Seed or seed pieces of test plants are then treated with bacterial suspension (10^8 cfu/ml) and planted in replicated pot tests. During the experiment, those PGPRs that consistently caused statistically significant increases in root or shoot development or both are selected for further testing in agricultural field. Recently, selections of efficacious PGPR strains have been made by mass screening technique (Compant et al. 2005). Here, primary screenings of new isolates are done based on physiological, nutritional and biochemical characteristics as in Bergey's Manual of Determinative Bacteriology (Holt et al. 1994). While DNA and RNA homology tests are also considered as most reliable tools for the characterization of potent PGPR strains (Bashan et al. 1993). Now-a-days, application of protein profile analysis technique (Maiti et al. 2009) proved to be useful for patenting procedures. Restriction fragment length polymorphism (RFLP) analysis (Osborn et al. 2000) by using probe-target sequence and restriction endonuclease digestion pattern are useful for specific strain identification. However, gas chromatographic analysis of cellular fatty acid is very useful and proved to be accurate enough for identifying efficacious bacterial strains (Sasser 1990).

Commercialization of PGPR

The success and commercialization of PGPR strains depend on the linkages between the scientific organizations and industries. According to Nandakumar et al. (2001) 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. Thus, isolation of an effective strain is a prime criterion for better agricultural development, which is usually done from pathogen suppressive soils either by dilution plate technique or by baiting the soil with fungal structures like sclerotia (Nakkeeran et al. 2005). The selection of best antagonistic strain is carried out by screening for antimicrobial action against different soil borne pathogens apart from the target pathogen. The plant, pathogen and antagonists are then co-exposed to controlled environmental conditions. Promising antagonists are further tested for their efficacy in field trials along with standard recommended fungicides (Pengnoo et al. 2000). Mass production is achieved through liquid (Manjula and Podile 2001), semisolid and solid fermentation techniques (Lewis 1991). Moreover, commercial success of PGPR strains requires economical and viable market demand, consistent and broad spectrum action, safety and stability, longer shelf life, low capital costs and easy availability of career materials. Thus, the first

requirement for entrepreneurship requires a patent application of the identified strain. Quality control in this step is crucial to retain the confidence of farmers on the efficacy of the antagonistic strain. Research inventions from China, Russia and several other western countries have now proved the potential use of PGPRs towards plant disease management. The first commercial product of *Bacillus subtilis* was developed during 1985 in US. 60–75% of cotton, peanut, soya bean, corn, vegetables and small grain crops raised in US are now treated with commercial product of *B. subtilis*, which become effective against soil borne pathogens such as *Fusarium* and *Rhizoctonia* (Nakkeeran et al. 2005). In China, PGPRs have been successfully applied over two decades about an area of 20 million hectares of different crop plants for commercial development. Owing to the potentiality of *Bacillus* spp., more than 20 different commercial products of *Bacillus* origin are sold in China to mitigate soil borne diseases (Backman et al. 1997). Besides, *Bacillus* spp., certain other PGPR strains belonging to the genera such as *Agrobacterium*, *Azospirillum*, *Bulkholderia*, *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., *Mucor pyroformis*, *Geotrichum candidum*, *Erwinia amylovora*, russet-inducing bacteria, *Fusarium* sp., *Rhizoctonia* sp., *Pythium* sp., *Fusarium* sp., *Phytophthora* sp., and *P. tolassii* (Nakkeeran et al. 2005). Some of the important PGPR strains along with their commercial products as formulated by Chet and Chernin (2002) and Glick et al. (1999) are represented in Table 7. Since PGPRs have its own potentiality in controlling plant diseases and pest management, these commercial products such as Diegall, Galltrol-A, Zea-Nit, Epic, Quantum 4000, Victus, Mycostop etc., have, therefore, been registered for the practical use of farming community. Besides, the potentiality of PGPR inoculants in beneficial improvement of agricultural plants in developing countries can never be ignored. In India, more than 40 stakeholders from different provinces have registered themselves for the mass production of PGPRs with Central Insecticide Board (CSI), Faridabad, Haryana through collaboration with Tamil Nadu Agricultural University, Coimbatore, India.

Future prospects and challenges

PGPR inoculants can fulfil diverse beneficial interactions in plants leading to promising solutions for sustainable and environment-friendly agriculture. The applications of rhizosphere soil of agricultural crops with desirable bacterial populations have established considerable promises in both the laboratory and greenhouse experiment. Further, improved understanding on the way by which PGPRs promote plant growth can lead to expanded exploitation of these 'biofertilizers' to reduce the potential negative environmental effects associated with the food and fiber production. An effort of applying genetically engineered PGPRs to remediate complex contaminated soil (Denton 2007) and thereby increasing the productivity of crop plants in agriculture is another attractive idea of research in recent decade. The rhizobacterial community can be specifically engineered to target various pollutants at co-contaminated sites to provide customized rhizoremediation system (Wu et al. 2006). Recent progress of molecular biology and biotechnology in the understanding of rhizobacterial interactions with the nodules of crop plants will encourage a suitable area of research in PGPR mechanisms relating to rhizosphere colonization. Reports are now available from genetically engineered *Arabidopsis thaliana* plants to remove lead and cadmium contaminates after inoculating with rhizobacterial population. However,

Table 7 Commercial products developed using different PGPR strains

PGPR	Products	Intended crop
Agrobacterium radiobacter	Diegall, Galltrol-A, Nogall, Norbac 84 C	Fruit, nut, ornamental nursery stock and trees
Azospirillum brasilense	Azo-Green	Turf and forage crops
Bacillus subtilis	Epic, HiStick N/T, Kodiak, Rhizo-Plus, Serenade, Subtilex	Barley, beans, cotton, legumes peanut, pea, rice and soybean
B. amyloliquefaciens GB99	Quantum 4000	Broccoli, cabbage, cantaloupe, cauliflower, celery, cucumber, lettuce, ornamentals, peppers, tomato and watermelon
Burlkholderia cepacia	Blue Circle, Deny, Intercept	Alfalfa, barley, beans, clover, cotton, maize, peas, sorghum, vegetables and wheat
Pseudomonas fluorescens	BlightBan A506, Conquer, Victus	Almond, apple, cherry, mushroom, peach, pear, potato, strawberry and tomato
P. syringae	Bio-save10	Citrus and pome fruit
Streptomyces griseovirdis K61	Mycostop	Field, ornamental and vegetable crops

combined applications of transgenic plants with PGPRs have proved another promising future (Ali and Hj 2010) in advancing rhizoremediation technologies. Efforts have, therefore, been concentrated on the production of transgenic plants which can increase remediation efficiency by expressing a particular PGPR protein (Zhuang et al. 2007). Farwell et al. (2007) compared the growth of a transgenic canola, *Brassica napus* inoculated with PGPR strain, *Pseudomonas putida* UW4, to normal canola and found a significant growth in the former. Besides, the symbiotic relationship of *Pseudomonas putida* and sunflower seeds with synthetic phytochelatins has been investigated by Wu et al. (2006). They observed that the engineered strain could protect the sunflower plants against the toxic effects of cadmium at 300 μM concentration. Thus, biotechnology can be applied to improve the efficacy of PGPR strains through transgenics for agricultural improvement. However, 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 and 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. Thus, future success of industries producing microbial inoculants, especially PGPRs, will depend on innovative business management, product marketing, extension education and extensive research. Further optimization is required for better fermentation and formulation processes of effective PGPR strains to introduce in agriculture.

Conclusion

The present review indicates the development and formulations of PGPRs in biological promotion of different characteristics of plant growth. Most of the PGPR isolates significantly increased plant height, root length and dry matter production in various agricultural crops like potato, tomato, maize, wheat, etc. The development of stable formulations of antagonistic PGPRs in sustainable agricultural systems thus, established as another promising approach replacing the use of chemical fertilizers. Besides, PGPRs are protecting natural environments as well as biological resources by playing a significant role in integrated pest management system (IPM). In addition to this, certain PGPR strains have also the ability to activate octadecanoid, shikimate and terpenoid pathways (Gouws 2009) which in turn assists in the alterations of VOCs production in host plants. In accordance with their mode of action, PGPRs can be classified as biofertilizers, phytostimulators and biopesticides with certain bacteria having overlapping applications. However, screening strategies for selecting the best rhizobacterial strain for rhizosphere competence and studies on the ecology of introduced PGPR with the resident PGPR and other microbial species in the plant rhizosphere will require more comprehensive knowledge, although the involvement of ACC deaminase gene, siderophore, phosphate, phytohormones like IAA, cytokinin, gibberellins etc., noduation, disease suppression and their coordinated expression seemed to be responsible in enhancing the plant growth, yield and nutrient uptake of various crop plants in different agro ecosystems. Thus, it is becoming increasingly apparent that most of the PGPR strains can promote plant growth by several mechanisms, though most studies currently focus on individual mechanisms and have not yet been able to sort out the relative contributions of different processes that are also responsible for successful plant growth promotion. However, carefully controlled field trials of crop plants inoculated along with rhizobacteria are necessary for maximum commercial exploitation of PGPR strains.

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References

Ahanthem S, Jha DK (2007) Response of rice crop inoculated with arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria to different soil nitrogen concentrations. Mycorrhiza News 18(4):15–20

Ahanthem S, Jha DK (2008) Interactions between *Acaulospora* and *Azospirillum* and their synergistic effect on rice growth at different sources and regimes of soil phosphorus. Mycorrhiza News 20(2):6–12

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

Ali K, Hj SZ (2010) Phytoremediation of heavy metals with several efficiency enhancer methods. Afr J Biotechnol 9(25):3689–3698

Alstroem S (1991) Induction of disease resistance in common bean susceptible to halo blight bacterial pathogen after seed bacterization with rhizosphere pseudomonads. J Gen Appl Microbiol 37(6):495–501

Amarger N, Macheret V, Laguerre G (1997) *Rhizobium gallicum* sp. nov. and *Rhizobium giardinii* sp. nov., from *Phaseolus vulgaris* nodules. Int J Syst Bacteriol 47(4):996–1006

Andrews JH, Harris RF (2000) The ecology and biogeography of microorganisms on plant surfaces. Annu Rev Phytopathol 38:145–180. doi:10.1146/annurev.phyto.38.1.145

Antoun H, Beauchamp CJ, Goussard N, Chabot R, Lalande R (1998) Potential of *Rhizobium* and *Bradyrhizobium* species as plant

growth promoting rhizobacteria on non-legumes: Effect on radishes (*Raphanus sativus* L.). Plant Soil 204:57–67. doi: 10.1023/A:1004326910584

Ardakani SS, Heydari A, Tayebi L, Mohammedi M (2010) Promotion of cotton seedlings growth characteristics by development and use of new bioformulations. Int J Bot 6(2):95–100

Aroca R, Ruiz-Lozano JM (2009) Induction of plant tolerance to semi-arid environments by beneficial soil microorganisms-a review. In: Lichtouse E (ed) Climate change, intercropping, pest control and beneficial microorganisms, sustainable agriculture reviews. Springer, The Netherlands 2:121–135

Arora NK, Kang SC, Maheshwari DK (2001) Isolation of siderophore-producing strains of *Rhizobium meliloti* and their biocontrol potential against *Macrophomina phaseolina* that causes charcoal rot of groundnut. Curr Sci 81(6):673–677

Babalola OO, Osir EO, Sanni AI, Odhaimbo GD, Bulimo WD (2003) Amplification of 1-aminocyclopropane-1-carboxylic (ACC) deaminase from plant growth promoting rhizobacteria in *Striga*-infested soils. Afr J Biotechnol 2(6):157–160

Backman PA, Wilson M, Murphy JF (1997) Bacteria for biological control of plant diseases. In: Rechcigl NA, Rechcigl JE (eds) Environmentally safe approaches to crop disease control. Lewis Publishers, Boca Raton, FL, pp 95–109

Bakker PAHM, Pieterse CMJ, van Loon LC (2007) Induced systemic resistance by fluorescent *Pseudomonas* spp. Phytopathology 97(2):239–243

Baldani VLD, Baldani JI, Dobereiner J (2000) Inoculation of rice plants with the endophytic diazatrophs *Herbaspirillum seropedicae* and *Burkholderia* spp. Biol Fertil Soils 30:485–491

Barazani O, Friedman J (1999) Is IAA the major root growth factor secreted from plant-growth-mediating bacteria? J Chem Ecol 25(10):2397–2406. doi:10.1023/A:1020890311499

Barea JM, Pozo MJ, Azcon R, Aguilar CA (2005) Microbial co-operation in the rhizosphere. J Exp Bot 56(417):1761–1778

Baset Mia MA, Shamsuddin ZH, Wahab Z, Marziah M (2010) Effect of plant growth promoting rhizobacterial (PGPR) inoculation on growth and nitrogen incorporation of tissue-cultured musa plantlets under nitrogen-free hydroponics condition. Aust J Crop Sci 4(2):85–90

Bashan Y, de-Bashan LE (2010) Chapter two—How the plant growth-promoting bacterium *Azospirillum* promotes plant growth–a critical assessment. Adv Agron 108:77–136

Bashan Y, Holguin G, Lifshitz R (1993) Isolation and characterization of plant growth-promoting rhizobacteria. In: Glick BR, Thompson JE (eds) Methods in plant molecular biology and biotechnology. CRC Press, BocaRaton, FL, pp 331–345

Bashan Y, Puente ME, de-Bashan LE, Hernandez JP (2008) Environmental uses of plant growth-promoting bacteria. In: Barka EA, Clement C (eds) Plant-microbe interactions. Trivandrum, Kerala, India, pp 69–93

Beattie GA (2006) Plant-associated bacteria: survey, molecular phylogeny, genomics and recent advances. In: Gnanamanickam SS (ed) Plant-associated bacteria. Springer, The Netherlands, pp 1–56. doi: 10.1007/978-1-4020-4538-7_1

Belimov AA et al (2001) Characterization of plant growth promoting rhizobacteria isolated from polluted soils and containing 1-aminocyclopropane-1-carboxylate deaminase. Can J Microbiol 47:642–652

Benizri E, Baudoin E, Guckert A (2001) Root colonization by inoculated plant growth-promoting rhizobacteria. Biocontrol Sci Technol 11(5):557–574

Bevivino A et al (1998) Characterization of a free-living maize rhizosphere population of *Burkholderia cepacia*: effect of seed treatment on disease suppression and growth promotion of maize. FEMS Microbiol Ecol 27(3):225–237. doi:10.1111/j.15746941.1998.tb00539.x

Bharathi S (2004) Development of botanical formulations for the management of major fungal diseases of tomato and onion. PhD Thesis, Tamil Nadu Agricultural University, Coimbatore, India, p 152

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

Boddey RM, Baldani VLD, Baldani JI, Dobereiner J (1986) Effect of inoculation of *Azospirillum* spp. on nitrogen accumulation by field-grown wheat. Plant Soil 95(1):109–121. doi: 10.1007/BF02378857

Boddey RM, Polidoro JC, Resende AS, Alves BJR, Urquiaga S (2001) Use of the ^{15}N natural abundance technique for the quantification of the contribution of N_2 fixation to sugar cane and other grasses. Aust J Plant Physiol 28:889–895

Boiero L, Perrig D, Masciarelli O, Penna C, Cassan F, Luna V (2007) Phytohormone production by three strains of *Bradyrhizobium japonicum* and possible physiological and technological implications. Appl Microbiol Biotechnol 74:874–880. doi:10.1007/s00253-006-0731-9

Bringhurst RM, Cardon ZG, Gage DJ (2001) Galactosides in the rhizosphere: utilization by *Sinorhizobium meliloti* and development of a biosensor. Proc Natl Acad Sci USA 98:4540–4545

Cakmakci R, Donmez F, Aydin A, Sahin F (2006) Growth promotion of plants by plant growth-promoting rhizobacteria under greenhouse and two different field soil conditions. Soil Biol Biochem 38(6):1482–1487

Cao L, Qiu Z, Dai X, Tan H, Lin Y, Zhou S (2004) Isolation of endophytic actinomycetes from roots and leaves of banana (*Musa acuminata*) plants and their activities against *Fusarium oxysporum* f. sp. *cubense*. World J Microbiol Biotechnol 20:501–504

Cardoso EJBN, Freitas SS (1992) A rizosfera. In: Cardoso EJBN, Tsai SM, Neves PCP (eds) Microbiologia do solo. Sociedade Brasileira de Ciencia do Solo, Campinas, pp 41–57

Carson KC, Meyer JM, Dilworth MJ (2000) Hydroxamate siderophores of root nodule bacteria. Soil Biol Biochem 32:11–21

Castro RO, Cantero EV, Bucio JL (2008) Plant growth promotion by *Bacillus megaterium* involves cytokinin signalling. Plant Signal Behav 3(4):263–265

Castro RO, Cornejo HAC, Rodriguez LM, Bucio JL (2009) The role of microbial signals in plant growth and development. Plant Signal Behav 4(8):701–712

Cattelan AJ, Hartel PG, Fuhrmann JJ (1999) Screening for plant growth-promoting rhizobacteria to promote early soybean growth. Soil Sci Soc Am J 63:1670–1680

Chabot R, Beauchamp CJ, Kloepper JW, Antoun H (1998) Effect of phosphorus on root colonization and growth promotion of maize by bioluminescent mutants of phosphate-solubilizing *Rhizobium leguminosarum* biovar *phaseoli*. Soil Biol Biochem 30:1615–1618

Chandler D, Davidson G, Grant WP, Greaves J, Tatchell GM (2008) Microbial biopesticides for integrated crop management: an assessment of environmental and regulatory sustainability. Trends Food Sci Tech 19:275–283

Chen WX, Yan GH, Li JL (1988) Numerical taxonomic study of fast growing soybean rhizobia and a proposal that *Rhizobium fredii* be assigned to *Sinorhizobium* gen. nov. Int J Syst Bacteriol 38(4):392–397. doi: 10.1099/00207713-38-4-392

Chen X, Schauder S, Potier N et al (2002) Structural identification of a bacterial quorum-sensing signal containing boron. Nature 415:545–549

Cheng Z, Park E, Glick BR (2007) 1-Aminocyclopropane-1-carboxylate deaminase from *Pseudomonas putida* UW4 facilitates the growth of canola in the presence of salt. Can J Microbiol 53(7):912–918

Chet I, Chernin L (2002) Biocontrol, microbial agents in soil. In: Bitton G (ed) Encyclopedia of environmental microbiology. Willey, New York, USA, pp 450–465

Chew K (2002) Georgics. Hackett Publishing Company, Indianapolis, USA, p 152

Chin-A-Woeng TF, Thomas-Oates JE, Lugtenberg BJ, Bloemberg GV (2001) Introduction of the phzH gene of *Pseudomonas chlororaphis* PCL1391 extends the range of biocontrol ability of phenazine-1-carboxylic acid producing *Pseudomonas* spp. strains. Mol Plant Microbe Interact 14(8):1006–1015

Choudhary DK, Johri BN (2009) Interactions of *Bacillus* spp. and plants—with special reference to induced systemic resistance (ISR). Microbiol Res 164:493–513

Compant S, Duffy B, Jerzy N, 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(9):4951–4959

Cook RJ (2002) Advances in plant health management in the twentieth century. Annu Rev Phytopathol 38:95–116

Damayanti TA, Pardede H, Mubarik NR (2007) Utilization of root-colonizing bacteria to protect hot-pepper against *Tobacco Mosaic Tobamovirus*. Hayati J Biosci 14(3):105–109

De La Fuente L, Landa BB, Weller DM (2006) Host crop affects rhizosphere colonization and competitiveness of 2, 4-diacetylphloroglucinol-producing *Pseudomonas fluorescens*. Phytopathology 96:751–762. doi:10.1094/PHYTO-96-0751

de Lajudie P, Laurent-Fulele E, Willems A et al (1998a) *Allorhizobium undicola* gen. nov., sp. nov., nitrogen-fixing bacteria that efficiently nodulate *Neptunia natans* in Senegal. Int J Syst Bacteriol 48:1277–1290

de Lajudie P, Willems A, Nick G, Moreira F et al (1998b) Characterization of tropical tree rhizobia and description of *Mesorhizobium plurifarium* sp. nov. Int J Syst Bacteriol 48:369–382. doi:10.1099/00207713-48-2-369

de Vasconcellos RLF, Cardoso EJBN (2009) Rhizospheric streptomycetes as potential biocontrol agents of *Fusarium* and *Armillaria* pine rot and as PGPR for *Pinus taeda*. Biocontrol 54:807–816. doi:10.1007/s10526-009-9226-9

de Vasconcellos RLF, da Silva MCP, Ribeiro CM, Cardoso EJBN (2010) Isolation and screening for plant growth-promoting (PGP) actinobacteria from *Araucaria angustifolia* rhizosphere soil. Sci Agric 67:743–746

Denton B (2007) Advances in phytoremediation of heavy metals using plant growth promoting bacteria and fungi. MMG 445 Basic Biotechnol 3:1–5

Desbrosses G, Contesto C, Varoquaux F, Galland M, Touraine B (2009) PGPR-Arabidopsis interactions is a useful system to study signalling pathways involved in plant developmental control. Plant Signal Behav 4:321–323

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

Di Gregorio S, Barbafieri M, Lampis S, Sanangelantoni AM, Tassi E, Vallini G (2006) Combined application of Triton X-100 and *Sinorhizobium* sp. Pb002 inoculum for the improvement of lead phytoextraction by *Brassica juncea* in EDTA amended soil. Chemosphere 63:293–299

Dobbelaere S, Croonenborghs A, Thys A, Ptacek D et al (2001) Responses of agronomically important crops to inoculation with *Azospirillum*. Aust J Plant Physiol 28:871–879

Dobereiner J (1997) Biological nitrogen fixation in the tropics: social and economic contributions. Soil Biol Biochem 29(5):771–774

Dong Z, McCully ME, Canny MJ (1997) Does *Acetobacter diazotrophicus* live and move in the xylem of sugarcane stems? Anatomical and physiological data. Ann Bot 80:147–158

Dreyfus B, Garcia JL, Gillis M (1988) Characterization of *Azorhizobium caulinodans* gen. nov., sp. nov., a stem-nodulating nitrogen-fixing bacterium isolated from *Sesbania rostrata*. Int J Syst Bacteriol 38:89–98

Duan J, Muller KM, Charles TC, Vesely S, Glick BR (2009) 1-Aminocyclopropane-1-carboxylate (ACC) deaminase genes in rhizobia from Southern Saskatchewan. Microb Ecol 57:423–436. doi:10.1007/s00248-008-9407-6

Dubey SK (1996) Combined effect of *Bradyrhizobium japonicum* and phosphate-solubilizing *Pseudomonas striata* on nodulation, yield attributes and yield of rainfed soybean (*Glycine max*) under different sources of phosphorus in Vertisols. Ind J Microbiol 33:61–65

Elbadry M, Taha RM, Eldougdoug KA, Gamal-Eldin H (2006) Induction of systemic resistance in faba bean (*Vicia faba* L.) to bean yellow mosaic potyvirus (BYMV) via seed bacterization with plant growth promoting rhizobacteria. J Plant Dis Protect 113(6):247–251

Elliot LF, Lynch JM (1984) Pseudomonads as a factor in the growth of winter wheat (*Triticum aestivum* L.) Soil Biol Biochem 16:69–71. doi:10.1016/0038-0717(84)90128-7

Elliot LF, Lynch JM (1995) The international workshop on establishment of microbial inocula in soils: cooperative research project on biological resource management of the organization for economic cooperation and development (OECD). Am J Alt Agric 10:50–73

El-Tarabily KA, Sivasithamparam K (2006) Non-streptomycete actinomycetes as biocontrol agent of soil-borne fungal plant pathogens and as plant growth promoters. Soil Biol Biochem 38:1505–1520

Erturk Y, Ercisli S, Haznedar A, Cakmakci R (2010) Effects of plant growth promoting rhizobacteria (PGPR) on rooting and root growth of kiwifruit (*Actinidia deliciosa*) stem cuttings. Biol Res 43:91–98

Esitken A, Karlidag H, Ercisli S, Turan M, Sahin F (2003) The effect of spraying a growth promoting bacterium on the yield, growth and nutrient element composition of leaves of apricot (*Prunus armeniaca* L. cv. Hacihaliloglu). Aust J Agric Res 54(4): 377–380

Esitken A, Pirlak L, Turan M, Sahin F (2006) Effects of floral and foliar application of plant growth promoting rhizobacteria (PGPR) on yield, growth and nutrition of sweet cherry. Sci Hort 110:324–327

Estrada de los Santos P, Bustillos-Cristales MR, Caballero-Mellado J (2001) *Burkholderia*, a genus rich in plant-associated nitrogen fixers with wide environmental and geographic distribution. Appl Environ Microb 67:2790–2798

Farmer EE (2001) Surface-to-air signals. Nature 411:854–856

Farwell AJ et al (2007) Tolerance of transgenic canola plants (*Brassica napus*) amended with plant growth-promoting bacteria to flooding stress at a metal-contaminated field site. Environ Pollut 147:540–545

Figueiredo MVB, Burity HA, Martinez CR, Chanway CP (2008) Alleviation of drought stress in the common bean (*Phaseolus vulgaris* L.) by co-inoculation with *Paenibacillus polymyxa* and *Rhizobium tropici*. Appl Soil Ecol 40:182–188

Forde BG (2000) Nitrate transporters in plants: structure, function and regulation. Biochim Biophys Acta 1465:219–235

Forlani GM, Mantelli M, Nielsen E (1999) Biochemical evidence for multiple acetoin-forming enzymes in cultured plant cells. Phytochemistry 50:255–262

Franco-Correa M, Quintana A, Duque C et al (2010) Evaluation of actinomycete strains for key traits related with plant growth promotion and mycorrhiza helping activities. Appl Soil Ecol 45:209–217

Fuentes-Ramirez LE, Bustillos-Cristales R, Tapia-Hernandez A et al (2001) Novel nitrogen-fixing acetic acid bacteria, *Gluconacetobacter johannae* sp. nov. and *Gluconacetobacter azotocaptans* sp.

nov., associated with coffee plants. Int J Syst Evol Micr 51:1305–1314
Garcia de Salamone IE, Dobereiner J, Urquiaga S, Boddey RM (1996) Biological nitrogen fixation in *Azospirillum* strain-maize genotype associations as evaluated by the ^{15}N isotope dilution technique. Biol Fertil Soils 23:249–256. doi:10.1007/BF00335952
Garcia de Salamone IE, Hynes RK, Nelson LM (2001) Cytokinin production by plant growth promoting rhizobacteria and selected mutants. Can J Microbiol 47:404–411
Ghorbanpour MNM, Hosseini S, Rezazadeh M, Omidi KK, Etminan A (2010) Hyoscyamine and scopolamine production of black henbane (*Hyoscyamus niger*) infected with *Pseudomonas putida* and *P. fluorescens* strains under water deficit stress. Planta Med 76(12):167
Ghosh S, Penterman JN, Little RD, Chavez R, Glick BR (2003) Three newly isolated plant growth-promoting bacilli facilitate the seedling growth of canola, *Brassica campestris*. Plant Physiol Biochem 41:277–281. doi:10.1016/S0981-9428(03)00019-6
Glass ADM (1989) Plant nutrition: an introduction to current concepts. Jones and Bartlett Publishers, Boston, p 234
Glass ADM, Britto DT, Kaiser BN et al (2002) The regulation of nitrate and ammonium transport systems in plants. J Exp Bot 53:855–864
Glick BR (1995) The enhancement of plant growth by free living bacteria. Can J Microbiol 41:109–117
Glick BR, Patten CL, Holguin G, Penrose DM (1999) Biochemical and genetic mechanisms used by plant growth-promoting bacteria. Imperial College Press, London
Gomes RC, Semedo LTAS, Soares RMA, Alviano CS, Linhares LF, Coelho RRR (2000) Chitinolytic activity of actinomycetes from a cerrado soil and their potential in biocontrol. Lett Appl Microbiol 30:146–150
Gouws LM (2009) The molecular analysis of the effects of lumichrome as a plant growth promoting substance. Dissertation, University of Stellenbosch, South Africa
Govindasamy V, Senthilkumar M, Gaikwad K, Annapurna K (2008) Isolation and characterization of ACC deaminase gene from two plant growth-promoting rhizobacteria. Curr Microbiol 57(4): 312–317
Gray EJ, Smith DL (2005) Intracellular and extracellular PGPR: commonalities and distinctions in the plant-bacterium signalling processes. Soil Biol Biochem 37:395–412
Grichko VP, Glick BR (2001) Amelioration of flooding stress by ACC deaminase-containing plant growth-promoting bacteria. Plant Physiol Bioch 39:11–17
Griffiths BS, Ritz K, Ebblewhite N, Dobson G (1999) Soil microbial community structure: Effects of substrate loading rates. Soil Biol Biochem 31:145–153. doi:10.1016/S0038-0717(98)00117-5
Guerinot ML, Chelm BK (1984) Isolation and expression of the *Bradyrhizobium japonicum* adenylate cyclase gene (*cya*) in *Escherichia coli*. J Bacteriol 159:1068–1071
Gupta CP, Dubey RC, Maheshwari DK (2002) Plant growth enhancement and suppression of *Macrophomina phaseolina* causing charcoal rot of peanut by fluorescent *Pseudomonas*. Biol Fertl Soils 35:399–405. doi:10.1007/s00374-002-0486-0
Gutierrez-Manero FJ, Ramos-Solano B, Probanza A, Mehouachi J, Tadeo FR, Talon M (2001) The plant-growth promoting rhizobacteria *Bacillus pumilus* and *Bacillus licheniformis* produce high amounts of physiologically active gibberellins. Physiol Plantarum 111:206–211
Gyaneshwar P et al (1999) Involvement of a phosphate starvation inducible glucose dehydrogenase in soil phosphate solubilization by *Enterobacter asburiae*. FEMS Microbiol Lett 171:223–229
Haas D, Defago G (2005) Biological control of soil-borne pathogens by fluorescent pseudomonads. Nat Rev Microbiol 3:307–319
Halder AK, Mishra AK, Chakarbartty PK (1991) Solubilization of inorganic phosphates by *Bradyrhizobium*. Ind J Exp Biol 29:28–31
Hameeda B, Harini G, Rupela OP, Wani SP, Reddy G (2008) Growth promotion of maize by phosphate-solubilizing bacteria isolated from composts and macrofauna. Microbiol Res 163:234–242
Han J, Sun L, Dong X, Cai Z, Sun X, Yang H, Wang Y, Song W (2005) Characterization of a novel plant growth-promoting bacteria strain *Delftia tsuruhatensis* HR4 both as a diazotroph and a potential biocontrol agent against various plant pathogens. Syst Appl Microbiol 28(1):66–76
Hayat R, Ali S, Amara U, Khalid R, Ahmed I (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. Ann Microbiol 60(4):579–598. doi:10.1007/s13213-010-0117-1
Hellriegel H, Wilfarth H (1888) Untersuchungen uber die Stickstoffnahrung der Gramineen und Leguminosen. Beilageheft zu der Zeitschrift des Vereins fur Rubenzucker-Industrie Deutschen Reichs, p 234
Herman MAB, Nault BA, Smart CD (2008) Effects of plant growth-promoting rhizobacteria on bell pepper production and green peach aphid infestations in New York. Crop Prot 27:996–1002. doi:10.1016/j.cropro.2007.12.004
Herschkovitz Y, Lerner A, Davidov Y, Rothballer M, Hartmann A, Okon Y, Jurkevitch E (2005) Inoculation with the plant-growth-promoting rhizobacterium *Azospirillum brasilense* causes little disturbance in the rhizosphere and rhizoplane of maize (*Zea mays*). Microb Ecol 50(2):277–288
Hiltner L (1904) Uber neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbakteriologie und unter besonderer Berucksichtigung der Grundungung und Brache. Arbeiten der Deutschen Landwirtschaftlichen Gesellschaft 98:59–78
Hinsinger P (2001) Bioavailability of soil inorganic P in the rhizosphere as affected by root induced chemical changes: a review. Plant Soil 237:173–195
Holden MTG et al (1999) Quorum-sensing cross-talk: isolation and chemical characterization of cyclic dipeptides from *Pseudomonas aeruginosa* and other gram-negative bacteria. Mol Microbiol 33:1254–1266
Holguin G, Glick BR (2001) Expression of the ACC Deaminase Gene from *Enterobacter cloacae* UW4 in *Azospirillum brasilense*. Microb Ecol 41(3):281–288
Holt JG, Krieg NR, Sneath PHA, Staley JT, Williams ST (1994) Bergey's manual of determinative bacteriology, 9th edn. Williams and Wikins co, Baltimore, USA, p 566
Hurek T, Handley LL, Reinhold-Hurek B, Piche Y (2002) *Azoarcus* grass endophytes contribute fixed nitrogen to the plant in an unculturable state. Mol Plant Microbe Interact 15:233–242
Hynes RK, Leung GC, Hirkala DL, Nelson LM (2008) Isolation, selection, and characterization of beneficial rhizobacteria from pea, lentil and chickpea grown in western Canada. Can J Microbiol 54:248–258
Isopi R, Fabbri P, Del-Gallo M, Puppi G (1995) Dual inoculation of *Sorghum bicolor* (L.) Moench ssp. *bicolor* with vesicular arbuscular mycorrhizas and *Acetobacter diazotrophicus*. Symbiosis 18:43–55
Jaleel CA et al (2007) *Pseudomonas fluorescens* enhances biomass yield and ajmalicine production in *Catharanthus roseus* under water deficit stress. Colloids Surf B Biointerfaces 60:7–11
Jaleel CA, Gopi R, Gomathinayagam M, Panneerselvam R (2009) Traditional and non-traditional plant growth regulators alter phytochemical constituents in *Catharanthus roseus*. Process Biochem 44:205–209. doi:10.1016/j.procbio.2008.10.012
James EK, Olivares FL, Baldani JI, Dobereiner J (1997) *Herbaspirillum*, an endophytic diazotroph colonizing vascular tissue in leaves of *Sorghum bicolor* L. Moench. J Exp Bot 48:785–797

James EK, Olivares FL, de Oliveira ALM, dos Reis FB, da Silva LG, Reis VM (2001) Further observations on the interaction between sugar cane and *Gluconacetobacter diazotrophicus* under laboratory and greenhouse conditions. J Exp Bot 52:747–760

James EK, Gyaneshwar P, Mathan N et al. (2002) Infection and colonization of rice seedlings by the plant growth-promoting bacterium *Herbaspirillum seropedicae* Z67 Mol Plant Microbe Interact 15:894–906

Jing YD, He ZL, Yang XE (2007) Role of soil rhizobacteria in phytoremediation of heavy metal contaminated soils. J Zhejiang Univ Sci 8(3):192–207

Joo GJ, Kin YM, Kim JT, Rhee IK, Kim JH, Lee IJ (2005) Gibberellins-producing rhizobacteria increase endogenous gibberellins content and promote growth of red peppers. J Microbiol 43(6):510–515

Joshi P, Bhatt AB (2011) Diversity and function of plant growth promoting rhizobacteria associated with wheat rhizosphere in North Himalayan region. Int J Environ Sci 1(6):1135–1143

Kalita RB, Bhattacharyya PN, Jha DK (2009) Effects of plant growth promoting rhizobacteria and arbuscular mycorrhizal fungi on *Fusarium oxysporum* causing brinjal wilt. JAPS 4:29–35

Kapulnik Y, Okon Y, Henis Y (1985) Changes in root morphology of wheat caused by *Azospirillum* inoculation. Can J Microbiol 31:881–887. doi:10.1139/m85-165

Karlidag H, Esitken A, Turan M, Sahin F (2007) Effects of root inoculation of plant growth promoting rhizobacteria (PGPR) on yield, growth and nutrient element contents of leaves of apple. Sci Hort 114(1):16–20

Kaushik R, Saxena AK, Tilak KVBR (2000) Selection of Tn5:lacZ mutants isogenic to wild type *Azospirillum brasilense* strains capable of growing at sub-optimal temperature. World J Microbiol Biotechnol 16:567–570. doi:10.1023/A:1008901331991

Kaymak HC (2011) Potential of PGPR in Agricultural Innovations. In: Maheshwari DK (ed) Plant growth and health promoting bacteria. Microbiol monographs. Springer, Berlin 18:45–79

Kempster VN, Scott ES, Davies KA (2002) Evidence for systemic, cross-resistance in white clover (*Trifolium repens*) and annual medic (*Medicago truncatula* var *truncatula*) induced by biological and chemical agents. Biocontrol Sci Technol 12(5):615–623. doi:10.1080/0958315021000016270

Khalid A, Arshad M, Zahir ZA (2004) Screening plant growth-promoting rhizobacteria for improving growth and yield of wheat. J Appl Microbiol 96(3):473–480

Khan AA, Jilani G, Akhtar MS, Naqvi SMS, Rasheed M (2009) Phosphorus solubilizing bacteria: occurrence, mechanisms and their role in crop production. J Agric Biol Sci 1:48–58

Kidarsa TA, Goebel NC, Zabriskie TM, Loper JE (2011) Phloroglucinol mediates cross-talk between the pyoluteorin and 2, 4 diacetylphloroglucinol biosynthetic pathways in *Pseudomonas fluorescens* Pf-5. Mol Microbiol 81(2):395–414. doi:10.1111/j.1365-2958.2011.07697.x

Kilian M, Steiner U, Krebs B, Junge H, Schmiedeknecht G, Hain R (2000) FZB24 *Bacillus subtilis*-mode of action of a microbial agent enhancing plant vitality. Pflanzenschutz Nachr Bayer 1:72–93

Kim KY, Jordan D, McDonald GA (1998) Effect of phosphate-solubilizing bacteria and vesicular-arbuscular mycorrhizae on tomato growth and soil microbial activity. Biol Fertil Soils 26:79–87. doi:10.1007/s003740050347

Kloepper JW, Schroth MN (1978) Plant growth-promoting rhizobacteria on radishes. In: Proceedings of the 4th international conference on plant pathogenic bacteria. Gilbert-Clarey, Tours, pp 879–882

Kloepper JW, Schroth MN (1981) Relationship of in vitro antibiosis of plant growth promoting rhizobacteria to plant growth and the displacement of root microflora. Phytopathology 71:1020–1024

Kloepper JW, Tuzun S, Liu L, Wei G (1993) Plant growth-promoting rhizobacteria as inducers of systemic disease resistance. In: Lumsden RD, Waughn JL (eds) Pest management: biologically based technologies. American Chemical Society Books, Washington, DC, pp 156–165

Kloepper JW, Ryu CM, Zhang S (2004) Induced systemic resistance and promotion of plant growth by *Bacillus* spp. Phytopathology 94(11):1259–1266

Kloepper JW, Gutierrez-Estrada A, Mclnroy JA (2007) Photoperiod regulates elicitation of growth promotion but not induced resistance by plant growth-promoting rhizobacteria. Can J Microbiol 53(2):159–167

Kokalis-Burelle N, Vavrina CS, Rosskopf EN, Shelby RA (2002) Field evaluation of plant growth-promoting rhizobacteria amended transplant mixes and soil solarization for tomato and pepper production in Florida. Plant Soil 238:257–266

Kumar V, Narula N (1999) Solubilization of inorganic phosphates and growth emergence of wheat as affected by *Azotobacter chroococcum* mutants. Biol Fertil Soils 28:301–305. doi:10.1007/s003740050497

Kumar A, Salini P, Shrivastava JN (2009) Production of peptide antifungal antibiotic and biocontrol activity of *Bacillus subtilis*. Ind J Exp Biol 47:57–62

Landa BB, Mavrodi OV, Schroeder KL, Allende-Molar R, Weller DM (2006) Enrichment and genotypic diversity of *phlD*-containing fluorescent *Pseudomonas* spp., in two soils after a century of wheat and flax monoculture. FEMS Microbiol Ecol 55:351–368

Lewis JA (1991) Formulation and delivery system of biocontrol agents with emphasis on fungi *Beltsville symposia* in agricultural research. In: Keister DL, Cregan PB (eds) The rhizosphere and plant growth 14:279–287

Li Q, Saleh-Lakha S, Glick BR (2005) The effect of native and ACC deaminase-containing *Azospirillum brasilense* Cd1843 on the rooting of carnation cuttings. Can J Microbiol 51:511–514

Lindstrom K (1989) *Rhizobium galegae*, a new species of legume root nodule bacteria. Int J Syst Bacteriol 39:365–367

Liu L, Kloepper JW, Tuzun S (1995) Induction of systemic resistance in cucumber against *Fusarium* wilt by plant growth promoting rhizobacteria. Phytopathology 85:695–698

Lucas GJA, Probanza A, Ramos B, Palomino MR, Gutierrez Manero FJ (2004) Effect of inoculation of *Bacillus licheniformis* on tomato and pepper. Agronomie 24:169–176

Lugtenberg B, Kamilova F (2009) Plant growth-promoting rhizobacteria. Annu Rev Microbiol 63:541–556

Lugtenberg BJ, Dekkers L, Bloemberg GV (2001) Molecular determinants of rhizosphere colonization by *Pseudomonas*. Annu Rev Phytopathol 39:461–490

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

Ma W, Zalec K, Glick BR (2001) Biological activity and colonization pattern of the bioluminescence-labeled plant growth-promoting bacterium *Kluyvera ascorbata* SUD165/26. FEMS Microbiol Ecol 35:137–144

Ma W, Guinel FC, Glick BR (2003) *Rhizobium leguminosarum* Bovver viciae 1-aminocyclopropane-1-carboxylate deaminase promotes nodulation of pea plants. Appl Environ Microbiol 69:4396–4402

Madhaiyan M, Poonguzhali S, Ryu J, Sa T (2006) Regulation of ethylene levels in canola (*Brassica campestris*) by 1-aminocyclopropane-1-carboxylate deaminase-containing *Methylobacterium fujisawaense*. Planta 224:268–278

Maiti B, Shekar M, Khusiramani R, Karunasagar I, Karunasagar I (2009) Evaluation of RAPD-PCR and protein profile analysis to differentiate *Vibrio harveyi* strains prevalent along the southwest coast of India. J Genet 88(3):273–279

Malhotra M, Srivastava S (2009) Stress-responsive indole-3-acetic acid biosynthesis by *Azospirillum brasilense* SM and its ability to modulate plant growth. Eur J Soil Biol 45:73–80

Malik KA, Bilal R, Mehnaz S, Rasul G, Mirza MS, Ali S (1997) Association of nitrogen-fixing, plant promoting rhizobacteria (PGPR) with kallar grass and rice. Plant Soil 194:37–44

Manjula K, Podile AR (2001) Chitin-supplemented formulations improve biocontrol and plant growth promoting efficiency of *Bacillus subtilis* AF1. Can J Microbiol 47(7):618–625. doi:1139/w01-057

Mansoor F, Sultana V, Haque SE (2007) Enhancement of biocontrol potential of *Pseudomonas aeroginosa* and *Paecilomyces lilacinus* against root rot of mungbean by a medicinal plant *Launaea nudicaulis* L. Pak J Bot 39(6):2113–2119

Mantelin S, Touraine B (2004) Plant growth-promoting bacteria and nitrate availability: impacts on root development and nitrate uptake. J Exp Bot 55:27–34. doi:10.1093/jxb/erh010

Martinez-Viveros O, Jorquera MA, Crowley DE, Gajardo G, Mora ML (2010) Mechanisms and practical considerations involved in plant growth promotion by rhizobacteria. J Soil Sci Plant Nutr 10:293–319

Mayak S, Tirosh T, Glick BR (1999) Effect of wild-type and mutant plant growth-promoting rhizobacteria on the rooting of mung been cuttings. J Plant Growth Regul 18:49–53

Mayak S, Tirosh T, Glick BR (2004) Plant growth-promoting bacteria confer resistance in tomato plants to salt stress. Plant Physiol Biochem 42(6):565–572. doi:10.1016/j.plaphy.2004.05.009

McCully ME (2001) Niches for bacterial endophytes in crop plants: a plant biologist's view. Aust J Plant Physiol 28:983–990

Mehnaz S, Lazarovits G (2006) Inoculation effects of *Pseudomonas putida*, *Gluconacetobacter azotocaptans*, and *Azospirillum lipoferum* on corn plant growth under greenhouse conditions. Microb Ecol 51(3):326–335

Mehnaz S, Mirza MS, Haurat J, Bally R, Normand P, Bano A, Malik KA (2001) Isolation and 16S rRNA sequence analysis of the beneficial bacteria from the rhizosphere of rice. Can J Microbiol 472:110–117

Merzaeva OV, Shirokikh IG (2006) Colonization of plant rhizosphere by actinomycetes of different genera. Microbiology 75:226–230. doi:10.1134/S0026261706020184

Minorsky PV (2008) On the inside. Plant Physiol 146:323–324

Mirza MS, Mehnaz S, Normand P et al (2006) Molecular characterization and PCR detection of a nitrogen fixing *Pseudomonas* strain promoting rice growth. Biol Fertil Soils 43:163–170. doi:10.1007/s00374-006-0074-9

Mishra M, Kumar U, Mishra PK, Prakash V (2010) Efficiency of plant growth promoting rhizobacteria for the enhancement of *Cicer arietinum* L. growth and germination under salinity. Adv Biol Res 4(2):92–96

Montesinos E (2003) Plant-associated microorganisms: a view from the scope of microbiology. Int Microbiol 6:221–223. doi:10.1007/s10123-003-0141-0

Mrkovacki N, Milic V (2001) Use of *Azotobacter chroococcum* as potentially useful in agricultural application. Ann Microbiol 51:145–158

Murphy JF, Zehnder GW, Schuster DJ, Sikora EJ, Polston JE, Kloepper JW (2000) Plant growth-promoting rhizobacterial mediated protection in tomato against *tomato mottle virus*. Plant Dis 84:779–784

Nahas E (1996) Factors determining rock phosphate solubilization by microorganisms isolated from soil. World J Microbiol Biotechnol 12:567–572. doi:10.1007/BF00327716

Nakkeeran S, Fernando WGD, Siddiqui ZA (2005) Plant growth promoting rhizobacteria formulations and its scope in commercialization for the management of pests and diseases. In: Siddiqui ZA (ed) PGPR: biocontrol and biofertilization. Springer, Dordrecht, pp 257–296

Nandakumar R, Babu S, Viswanathan R, Sheela J, Raguchander T, Samiyappan R (2001) A new bio-formulation containing plant growth promoting rhizobacterial mixture for the management of sheath blight and enhanced grain yield in rice. Biocontrol 46(4):493–510. doi:10.1023/A:1014131131808

Narasimhan K, Basheer C, Bajic VB, Swarup S (2003) Enhancement of plant-microbe interactions using a rhizosphere metabolomics-driven approach and its application in the removal of polychlorinated biphenyls. Plant Physiol 132:146–153

Narula N, Deubel A, Gans W, Behl RK, Merbach W (2006) Paranodules and colonization of wheat roots by phytohormone producing bacteria in soil. Plant soil Environ 52(3):119–129

Nick G, de Lajudie P, Eardly BD et al (1999) *Sinorhizobium arboris* sp. nov. and *Sinorhizobium kostiense* sp. nov., isolated from leguminous trees in Sudan and Kenya. Int J Syst Bacteriol 49:1359–1368

Noel TC, Sheng C, Yost CK, Pharis RP, Hynes MF (1996) *Rhizobium leguminosarum* as a plant growth-promoting rhizobacterium: direct growth promotion of canola and lettuce. Can J Microbiol 42:279–283

Notz R, Maurhofer M, Schnider-Keel U, Duffy B, Haas D, Defago G (2001) Biotic factors affecting expression of the 2, 4-diacetylphloroglucinol biosynthesis gene *phlA* in *Pseudomonas fluorescens* biocontrol strain CHA0 in the rhizosphere. Phytopathology 91:873–881. doi:10.1094/PHYTO.2001.91.9.873

Nour SM, Fernandez MP, Normand P, Cleyet-Marel JC (1994) *Rhizobium ciceri* sp. nov., consisting of strains that nodulate chickpeas (*Cicer arietinum* L.). Int J Syst Bacteriol 44:511–522

Nowak J (1998) Benefits of in vitro "biotization" of plant tissue cultures with microbial inoculants. In Vitro Cell Dev Biol Plant 34:122–130

Oger P, Petit A, Dessaux Y (1997) Genetically engineered plants producing opines alter their biological environment. Nat Biotechnol 15:369–372

Omar MNA, Mahrous NM, Hamouda AM (1996) Evaluating the efficiency of inoculating some diazatrophs on yield and protein content of 3 wheat cultivars under graded levels of nitrogen fertilization. Ann Agric Sci 41:579–590

Osborn AM, Moore ER, Timmis KN (2000) An evaluation of terminal-restriction fragment length polymorphism (T-RFLP) analysis for the study of microbial community structure and dynamics. Environ Microbiol 2(1):39–50

Pandey A, Sharma E, Palni LMS (1998) Influence of bacterial inoculation on maize in upland farming systems of the Sikkim Himalaya. Soil Biol Biochem 30:379–384. doi:10.1016/S0038-0717(97)00121-1

Park KS, Kloepper JW (2000) Activation of PR-1a promoter by rhizobacteria that induce systemic resistance in tobacco against *Pseudomonas syringae* pv. *tabaci*. Biol Control 18:2–9. doi:10.1006/bcon.2000.0815

Parmar N, Dadarwal KR (1999) Stimulation of nitrogen fixation and induction of flavonoid like compounds by rhizobacteria. J Appl Microbiol 86:36–44

Pathma J, Kennedy RK, Sakthivel N (2011) Mechanisms of fluorescent pseudomonads that mediate biological control of phytopathogens and plant growth promotion of crop plants. In: Maheshwari DK (ed) Bacteria in agrobiology: plant growth responses. Springer, Berlin, pp 77–105. doi:10.1007/978-3-642-20332-9-4

Pengnoo A, Kusongwiriyawong C, Nilratana L, Kanjanamaneesathian M (2000) Greenhouse and field trials of the bacterial antagonists in pellet formulations to suppress sheath blight of rice caused by *Rhizoctonia solani*. Biocontrol 45(2):245–256. doi:10.1023/A:1009948404423

Phillips DA (1980) Efficiency of symbiotic nitrogen fixation in legumes. Annu Rev Plant Physiol 31:29–49

Pieterse CMJ, Johan A, Pelt V, Saskia CM, Wees V et al (2001) Rhizobacteria-mediated induced systemic resistance: triggering,

signaling and expression. Eur J Plant Pathol 107(1):51–61. doi:10.1023/A:1008747926678
Ramamoorthy V, Viswanathan R, Raguchander T, Prakasam V, Samiyappan R (2001) Induction of systemic resistance by plant growth promoting rhizobacteria in crop plants against pests and diseases. Crop Prot 20:1–11
Reed ML, Glick BR (2005) Growth of canola (*Brassica napus*) in the presence of plant growth-promoting bacteria and either copper or polycyclic aromatic hydrocarbons. Can J Microbiol 51:1061–1069
Reinhold-Hurek B, Hurek T, Gillis M et al (1993) *Azoarcus* gen. nov., nitrogen-fixing Proteobacteria associated with roots of Kallar grass (*Leptochloa fusca* (L.) Kunth), and description of two species, *Azoarcus indigens* sp. nov. and *Azoarcus communis* sp. nov. Int J Syst Bacteriol 43:574–584
Ren D, Sims JJ, Wood TK (2001) Inhibition of biofilm formation and swarming of *Escherichia coli* by (5Z)-4-bromo-5-(bromomethylene)-3-butyl-2(5H)-furanone. Environ Microbiol 3(11):731–736
Ribaudo C, Krumpholz E, Cassan F, Bottini R, Cantore M, Cura A (2006) *Azospirillum* sp. promotes root hair development in tomato plants through a mechanism that involves ethylene. J Plant Growth Regul 24:175–185. doi:10.1007/s00344-005-0128-5
Richardson AE, Barea JM, McNeill AM, Prigent-Combaret C (2009) Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. Plant Soil 321:305–339. doi:10.1007/s11104-009-9895-2
Riggs PJ, Chelius MK, Iniguez AL, Kaeppler SM, Triplett EW (2001) Enhanced maize productivity by inoculation with diazotrophic bacteria. Aust J Plant Physiol 28:829–836. doi:10.1071/PP01045
Roberts SC, Shuler ML (1997) Large scale plant cell culture. Curr Opin Biotechnol 8:154–159
Rome S, Fernandez MP, Brunel B, Normand P, Cleyet-Marel JC (1996) *Sinorhizobium medicae* sp. nov., isolated from annual *Medicago* spp. Int J Syst Bacteriol 46:972–980
Russo A, Vettori L, Felici C, Fiaschi G, Morini S, Toffanin A (2008) Enhanced micropropagation response and biocontrol effect of *Azospirillum brasilense* Sp245 on *Prunus cerasifera* L. clone Mr.S 2/5 plants. J Biotechnol 134:312–319
Ryan PR, Dessaux Y, Thomashow LS, Weller DM (2009) Rhizosphere engineering and management for sustainable agriculture. Plant Soil 321:363–383. doi:10.1007/s11104-009-0001-6
Ryu CM, Farag MA et al (2003) Bacterial volatiles promote growth in *Arabidopsis*. Proc Natl Acad Sci USA 100:4927–4932. doi:10.1073/pnas.0730845100
Ryu CM, Farag MA, Hu CH, Reddy MS, Wei HX, Kloepper JW et al (2004) Bacterial volatiles induce systemic resistance in Arabidopsis. Plant Physiol 134:1017–1026
Ryu CM, Kim J, Choi O, Kim SH, Park CS (2006) Improvement of biological control capacity of *Paenibacillus polymyxa* E681 by seed pelleting on sesame. Biol Control 39:282–289
Sabaratnam S, Traquair JA (2002) Formulation of a *Streptomyces* biocontrol agent for the suppression of *Rhizoctonia* damping-off in tomato transplants. Biol Control 23:245–253
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(10):635–648
Saleh SS, Glick BR (2001) Involvement of *gacS* and *rpoS* in enhancement of the plant growth-promoting capabilities of *Enterobacter cloacae* CAL2 and *Pseudomonas putida* UW4. Can J Microbiol 47:698–705. doi:10.1139/w01-072
Saravanakumar D, Samiyappan R (2007) ACC deaminase from *Pseudomonas fluorescens* mediated saline resistance in groundnut (*Arachis hypogea*) plants. J Appl Microbiol 102(5):1283–1292
Sasser M (1990) Identification of bacteria through fatty acid analysis. In: Klement Z, Rudolph K, Sands D (eds) Methods in phytobacteriology. Akademiai Kiato, Budapest, pp 199–204
Schippers B et al (1988) Biological control of pathogens with rhizobacteria. Philos Trans R Soc B-Biol Sci 318:283–293. doi:10.1098/rstb.1988.0010
Scholla MH, Elkan GH (1984) *Rhizobium fredii* sp. nov., a fast-growing species that effectively nodulates soybeans. Int J Syst Bacteriol 34:484–486
Segovia L, Young JPW, Matinez-Romero E (1993) Reclassification of American *Rhizobium leguminosarum* Biovar Phaseoli type I strains as *Rhizobium etli* sp. nov. Int J Syst Bacteriol 43:374–377
Sekar S, Kandavel D (2010) Interaction of plant growth promoting rhizobacteria (PGPR) and endophytes with medicinal plants–new avenues for phytochemicals. J Phytol 2:91–100
Sgroy V, Cassan F, Masciarelli O et al (2009) Isolation and characterization of endophytic plant growth-promoting (PGPB) or stress homeostasis-regulating (PSHB) bacteria associated to the halophyte *Prosopis strombulifera*. Appl Microbiol Biotechnol 85:371–381. doi:10.1007/s00253-009-2116-3
Shaharoona B, Arshad M, Zahir ZA, Khalid A (2006) Performance of *Pseudomonas* spp. containing ACC-deaminase for improving growth and yield of maize (*Zea mays* L.) in the presence of nitrogenous fertilizer. Soil Biol Biochem 38:2971–2975
Sharaf-Eldin M, Elkholy S, Fernandez JA et al (2008) *Bacillus subtilis* FZB24 affects flower quantity and quality of Saffron (*Crocus sativus*). Planta Med 74:1316–1320
Siddiqui IA, Ehteshamul-Haque S, Shaukat SS (2001) Use of rhizobacteria in the control of root rot-root knot disease complex of mungbean. J Phytopathol 149:337–346
Singh S, Kapoor KK (1999) Inoculation with phosphate-solubilizing microorganisms and a vesicular-arbuscular mycorrhizal fungus improves dry matter yield and nutrient uptake by wheat grown in a sandy soil. Biol Fertil Soils 28:139–144. doi:10.1007/s003740050475
Somers E, Vanderleyden J, Srinivasan M (2004) Rhizosphere bacterial signalling: a love parade beneath our feet. Crit Rev Microbiol 30:205–240
Sousa CS, Soares ACF, Garrido MS (2008) Characterization of streptomycetes with potential to promote plant growth and biocontrol. Sci Agric 65:50–55. http://dx.doi.org/10.1590/S0103-90162008000100007
Spaepen S, Vanderleyden J, Remans R (2007) Indole-3-acetic acid in microbial and microorganism-plant signaling. In: Unden F (ed) FEMS microbiol rev. Blackwell Publishing Ltd., New York pp 1–24. doi:10.1111/j.1574-6976.2007.00072.x
Steenhoudt O, Vanderleyden J (2000) *Azospirillum*, a free-living nitrogen-fixing bacterium closely associated with grasses: genetic, biochemical and ecological aspects. FEMS Microbiol Rev 24:487–506
Stein T, Hayen-Schneg N, Fendrik I (1997) Contribution of BNF by *Azoarcus* sp. BH72 in *Sorghum vulgare*. Soil Biol Biochem 29:969–971
Stout MJ, Zehnder GW, Baur ME (2002) Potential for the use of elicitors of plant defence in arthropode management programs. Arch Insect Biochem Physiol 51:222–235. doi:10.1002/arch.10066
Sturz AV, Nowak J (2000) Endophytic communities of rhizobacteria and the strategies required to create yield enhancing associations with crops. J Appl Soil Ecol 15:183–190
Stutz EW, Defago G, Kern H (1986) Naturally occurring fluorescent pseudomonads involved in suppression of black root rot of tobacco. Phytopathology 76:181–185. doi:10.1094/Phyto-76-181
Sudhakar P, Chattopadhyay GN, Gangwar SK, Ghosh JK (2000) Effect of foliar application of *Azotobacter*, *Azospirillum* and *Beijerinckia* on leaf yield and quality of mulberry (*Morus alba*). J Agric Sci 134:227–234
Sultana V, Ara J, Parveen G, Haque SE, Ahmad VU (2006) Role of Crustacean chitin, fungicides and fungal antagonists on the

efficacy of *Pseudomonas aeruginosa* in protecting Chilli from root rot. Pak J Bot 38(4):1323–1331

Sundheim L, Poplawsky AR, Ellingboe AH (1988) Molecular cloning of two chitinase genes from *Serratia marcescens* and their expression in *Pseudomonas* species. Physiol Mol Plant Pathol 33:483–491

Suslow TV, Kloepper JW, Schroth MN, Burr TJ (1979) Beneficial bacteria enhance plant growth. Calif Agric 33:15–17

Swain MR, Naskar SK, Ray RC (2007) Indole-3-acetic acid production and effect on sprouting of yam (*Dioscorea rotundata* L.) minisetts by *Bacillus subtilis* isolated from culturable cowdung microflora. Pol J Microbiol 56:103–110

Taechowisan T, Peberdy JF, Lumyong S (2003) Isolation of endophytic actinomycetes from selected plants and their antifungal activity. World J Microbiol Biotechnol 19:381–385. doi:10.1023/A:1023901107182

Terkina IA, Parfenova VV, Ahn TS (2006) Antagonistic activity of actinomycetes of Lake Baikal. Appl Biochem Microbiol 42:173–176

Timmusk S, Nicander B, Granhall U, Tillberg E (1999) Cytokinin production by *Paenibacillus polymyxa*. Soil Biol Biochem 31:1847–1852

Tisdale SL, Nelson WL (1975) Soil fertility and fertilizers, 3rd edn. Macmillan Publishing, New York, p 694

Trivedi P, Pandey A, Palni LMS (2005) Carrier-based preparations of plant growth-promoting bacterial inoculants suitable for use in cooler regions. World J Microbiol Biotechnol 21:941–945. doi:10.1007/s11274-004-6820-y

van Loon LC (2007) Plant responses to plant growth-promoting rhizobacteria. Eur J Plant Pathol 119:243–254. doi:10.1007/s10658-007-9165-1

Velazquez E, Igual JM, Willems A et al (2001) *Mesorhizobium chacoense* sp. nov., a novel species that nodulates *Prosopis alba* in the Chaco Arido region (Argentina). Int J Syst Evol Microbiol 51:1011–1021

Verma SC, Ladha JK, Tripathi AK (2001) Evaluation of plant growth promoting and colonization ability of endophytic diazotrophs from deep water rice. J Biotechnol 91:127–141

Verma JP et al (2010) Impact of plant growth promoting rhizobacteria on crop production. Int J Agric Res 5:954–983

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

von Bodman SB, Bauer WD, Coplin DL (2003) Quorum-sensing in plant-pathogenic bacteria. Annu Rev Phytopathol 41:455–482

Wang ET, Martinez-Romero E (2000) *Sesbania herbacea-Rhizobium huautlense* nodulation in flooded soils and comparative characterization of *S. herbacea*-nodulating rhizobia in different environments. Microb Ecol 40:25–32

Wei L, Kloepper JW, Tuzun S (1996) Induced systemic resistance to cucumber diseases and increased plant growth by plant growth-promoting rhizobacteria under field conditions. Phytopathology 86:221–224

Weller DM (1988) Biological control of soil borne plant pathogens in the rhizosphere with bacteria. Annu Rev Phytopathol 26:379–407. doi:10.1146/annurev.py.26.090188.002115

Weller DM, Raaijmakers JM, Gardener BB, Thomashow LS (2002) Microbial populations responsible for specific soil suppressiveness to plant pathogens. Annu Rev Phytopathol 40:309–348

Werner T, Motyka V, Laucou V, Smets R, Onckelen HV, Schmulling T (2003) Cytokinin-deficient transgenic Arabidopsis plants show multiple developmental alterations indicating opposite functions of cytokinins in the regulation of shoot and root meristem activity. Plant Cell 15:2532–2550

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

Whitelaw MA (2000) Growth promotion of plants inoculated with phosphate-solubilizing fungi. Adv Agron 69:99–151. doi:10.1016/S0065-2113(08)60948-7

Wu CH, Wood TK, Mulchandani A, Chen W (2006) Engineering plant-microbe symbiosis for rhizoremediation of heavy metals. Appl Environ Microbiol 72(2):1129–1134. doi:10.1128/AEM.72.2.1129-1134

Yamada Y, Nihira T (1998) Microbial hormones and microbial chemical ecology. In: Barton DHR, Nakanishi K (ed) Comprehensive natural products chemistry. Elsevier Sciences, Amsterdam 8:377–413

Zahir ZA, Muhammad A, Frankenberger WT (2004) Plant growth promoting rhizobacteria: applications and perspectives in agriculture. Adv Agron 81:97–168. doi:10.1016/S0065-2113(03)81003-9

Zaied KA, El-Diasty ZM, El-Rhman MMA, El-Sanossy ASO (2009) Effect of horizontal DNA transfer between *Azotobacter* strains on protein patterns of Azotobacter transconjugants and biochemical traits in bioinoculated Okra (*Abelmoschus Esculentus*, L.). Aust J Basic Appl Sci 3(2):748–760

Zehnder GW, Murphy JF, Sikora EJ, Kloepper JW (2001) Application of rhizobacteria for induced resistance. Eur J Plant Pathol 107:39–50

Zhang LH, Dong YH (2004) Quorum sensing and signal interference: diverse implications. Mol Microbiol 53:1563–1571

Zhang F, Dasthi N, Hynes RK, Smith DL (1996) Plant growth promoting rhizobacteria and Soybean [*Glycine max* (L.) Merr.] nodulation and nitrogen fixation at suboptimal root zone temperatures. Ann Bot 77:453–459

Zhang H et al (2003) *Gemmatimonas aurantiaca* gen. nov., sp. nov., a Gram-negative, aerobic, polyphosphate accumulating microorganism, the first cultured representative of the new bacterial phylum Gemmatimonadetes phyl. nov. Int J Syst Evol Microbiol 53:1155–1163. doi:10.1099/ijs.0.02520-0

Zhao J, Zhou L, Wub J (2010) Promotion of *Salvia miltiorrhiza* hairy root growth and tanshinone production by polysaccharide–protein fractions of plant growth-promoting rhizobacterium *Bacillus cereus*. Process Biochem 45:1517–1522. doi:10.1016/j.procbio.2010.05.034

Zhuang X, Chen J, Shim H, Bai Z (2007) New advances in plant growth-promoting rhizobacteria for bioremediation. Environ Int 33(3):406–413