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Review Article

Diversity of Plant Growth Promoting Rhizobacteria (PGPR)

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Abstract

Plant growth promoting rhizobacteria (PGPR), which promote plant growth, are closely associate with various plants around rhizosphre as well in the plant tissues as endophytes. The present review focus the establishment process of plant associated bacterial diversity and the bacterial genera associated with their plant species. *Pseudomonas sp., Serratia sp., Azotobacter sp., Klebsiella sp., Burkholderia sp., Alkaligenes sp. Enterobacter sp., Bacillus polymyxa, Gluconacetobacter sp. Azoarcus sp., Paenibacillus sp., Brevibacterium halotolerans and Pseudomonas putida* have been predominantly reported as PGPR.

Keywords: PGPR; Rhizobacteria; Diazotroph; Rhizosphere; Microbial diversity

Introduction

Rhizosphere is a narrow zone of soil surrounding the root is which is directly influenced by the root system. This zone is rich in nutrients in comparison to the bulk soil, due to the accumulation of a variety of organic compounds released from roots by exudation, secretion, and deposition (Ligaba *et al.*, 2004). It facilitates niche for rhizospheric diazotrophs belonging to different genera due to rich nutrient availability. 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). Endophytic bacteria 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.*, 1998), *Azorhizobium caulinodans* (Dreyfus *et al.*, 1988), To determine the diversity of non-culturable diazotrophs, phylogenetic studies of nitrogen-fixing bacteria associated with rice roots using PCR primer designed to amplify fragments from *nif* genes have been carried out (Ueda *et al.*, 1995a,b). The genetic diversity of putative diazotrophic bacteria is evaluated using amplified ribosomal DNA restriction analysis (ARDRA), rep-PCR genomic fingerprinting and small subunit (SSU) ribosomal DNA (rDNA) sequencing etc. (Grange and Hungria, 2004). The present review focus on the process of establishment of plant associate microbial diversity and various microbes which gives benefit to the plants due to their plant growth promoting characters.

Establishment of Plant-Associated Microbial Diversity

The plant-soil microbial flow that we have depicted are reliant on and create spatial structure in the microbial community. At the mainland scale, the accomplishment of intrusive species frequently relies on upon discharge from microbial foes (Callaway *et al.*, 2004; Reinhart *et al.*, 2003). Inside bacterial community, constructive plant-soil microbial criticism strengthens spatial detachment of bacterial community (Molofsky and Bever, 2002), and contrary input brings about plant substitution, which requires recolonization of locally novel roots. At the littlest scale inside the root arrangement of an individual plant, the interaction of plant guard, plant portion, and microbial rivalry decides the course of inputs. At each of these scales, a few aspects of microbial environment and development decide the capacity of earlier or new microbial variations to set up themselves. It is essential to describe the significance of dormancy and capacity impacts, dispersal, flat quality exchange, and mutation in this establishment procedure.

Dormancy

All soil microorganisms, extending from oomycetes, nematodes, AM parasites, to microscopic organisms, can enter a lethargic state under unpleasant or unsatisfactory conditions (Jones and Lennon, 2010; Sussman and Douthit, 1973). Dormancy permits organisms to continue amid unfavorable conditions, expanding nearby scalemicrobial differences. Reviews appraise that more than 80% of the bacterial cells in the soil are dormant (Lennon and Jones, 2011). Besides, the group of physiologically dynamic microscopic organisms inside the soil are unmistakable from those that are dormant (Lennon and Jones, 2011). Comparable refinements are likely in different gatherings, for example, AM fungi (Pringle and Bever, 2002). Therefore, evaluations of microbial synthesis utilizing standard DNA extractions from soil may not give measures that mirror the dynamic players in the plant-organism collaboration, conceivably clouding field endeavors to recognize the agents of microbial inputs.

For plant-related microorganisms, shifts into and out of dormancy might be dictated by the accessibility of appropriate plants. Dormancy can be activated by asset hardship, change in supplement organization of the soil (expanded carbon or phosphorus), or other natural conditions (e.g. pH, water content), all components that can be influenced by plants. Collaborations with different individuals from the microbial community likewise animate microbial dormancy, as competitors may drain assets or hinder development through antibiotic generation (D¨orr *et al.*, 2010; Lewis, 2007). The environment and advancement of microbial dormancy are likewise affected by predation in the dormant state (Jones and Lennon, 2010), which can be huge for gatherings with extensive, consumable dormant structures, for example, spores of AM fungi.

Dispersal.

On the off chance that plant-associated microorganisms are not present when the plant starts to develop, then dispersal can introduce new microorganisms. Wind, water, animals, and insects are significant dispersers of soil microorganisms (71). Over littler scales, soil microorganisms can encourage the spread of each other (Warmink *et al.*, 2011). Moreover, organisms have developed various methodologies to sense changes in the earth and move as needs be. In the rhizosphere, plant-exuded resources, for example, carbohydrates, amino acids, phenolics, and inorganic particles are open to the encompassing microflora, and microorganisms will chemotax toward these root-related exudates (Currier and Strobel, 1976). For instance rhizobia chemotax toward vegetable discharged flavonoids preceding the improvement of symbiotic nodules (Jones *et al.*, 2007).

Horizontal gene transfer

Horizontal gene transfer is uncontrolled in the microbial world, both inside and between species, happening at such high frequencies that the meaning of an animal varieties can be obscured (Ochman *et al.*, 2005). A solitary conjugation occasion between two types of microscopic organisms can change the total genetic material by more than 10% (Blanca-Ord ´o ˜ nez *et al.*, 2010; Chen *et al.*, 2002).Numerous bacterial virulence determinants are connected with mobile genetic materials (Hacker and Kaper, 2000; Schmidt and Hensel, 2004), as are genes for symbiotic interaction and the capacity to overcome or even use plant exudates and guards. Indeed, facultative symbionts have the best convergence of mobile components in their genome, recommending that level quality gene transfer can be especially vital to this group (Newton and Bordenstein, 2011). Conjugation, transduction, or change can change over free living microorganisms to plant pathogens or symbionts and produce novel mixes of specificity factors and harmfulness or mutualist functions (Cervantes *et al.*, 2011; Yang *et al.*, 1993). Genes for nitrogen fixation by the plant symbionts *Sinorhizobium meliloti* and *Rhizobium etli* are on mobile plasmids (Moriguchi *et al.*, 2001; Truchet *et al.*, 1984), similar to the genes encoding the effectors that decide host specificity of the pathogen *Pseudomonas syringae* (Guttman and Greenberg, 2001; Jackson *et al.*, 1999). Genetic transfers can be imperative in soil fungi also. There is solid proof that the pathogenicity genes of *Nectria haematococca*, the parasitic causative agent of pea foot rot infection, were on a level plane procured (Liu *et al.*, 2003). Conjugation of plant-related plasmids can be incited by vicinity to hosts, which improves the probability that recombinants coming about because of horizontal gene transfer will be critical at shorter time allotments (Fuqua and Winans, 1994).

Mutation

Mutation is another vital compel creating microbial variations that can interact diversely with plant host. Mutations influencing virulence-associated genes have noteworthy results for the advancement of destructiveness in a wide evolution of pathogens (McCann *et al.*, 2008; Sokurenko *et al.*, 1999). One clear focus of choice are mutants that can evade host protections (Pitman *et al.*, 2005; Zhou *et al.*, 2009), however other conceivable targets incorporate mutations that impact the wellness of the pathogen in the rhizosphere, for example, those presenting the capacity to catabolize plant-created resources (Lapointe *et al.*, 1992). Comparative impacts are likely in mutualistic plant-organism interaction. For instance, succession variety in the gesture quality of *R. etli* decides the host range of this mutualist (Schultze *et al.*, 1992). In spite of the fact that mutations happen at low rates, microbial populace sizes on plant roots are possibly vast. Thus, mutation consolidated with gene exchange may shape the evolution of host-pathogen interaction (Ma *et al.*, 2006).

Relative importance of modes of microbe (re)introduction

At the scale of a single root, plant defence reaction and particular assignment can change at fast timescales—in as short as hours (Jones and Dangl, 2006; Kiers *et al.*, 2003). At these little spatial and temporal scales, new variations are probably going to be reintroduced by local dispersal and reactivation of dormant cells. Over the lifetime of an individual plant, these nearby procedures are probably going to be supplemented by developmental formation of new variations (Pitman *et al.*, 2005). Inside agrobacteria, for instance, transformation may make freeloading variations that could stifle destructive sorts (Platt *et al.*, 2012). Over huge spatial and worldly scales, advancement of nearby inhabitant microbial populaces can defeat the novel defence of introduced plant species. This may have added to the expanded negative feedbacks amassed over several years taking after the attack of *Cerastium alpinum* in New Zealand (Diez *et al.*, 2010). Diagrammatic representation of plant–soil–microbial interactions in the rhizosphere is shown in Fig. 1.

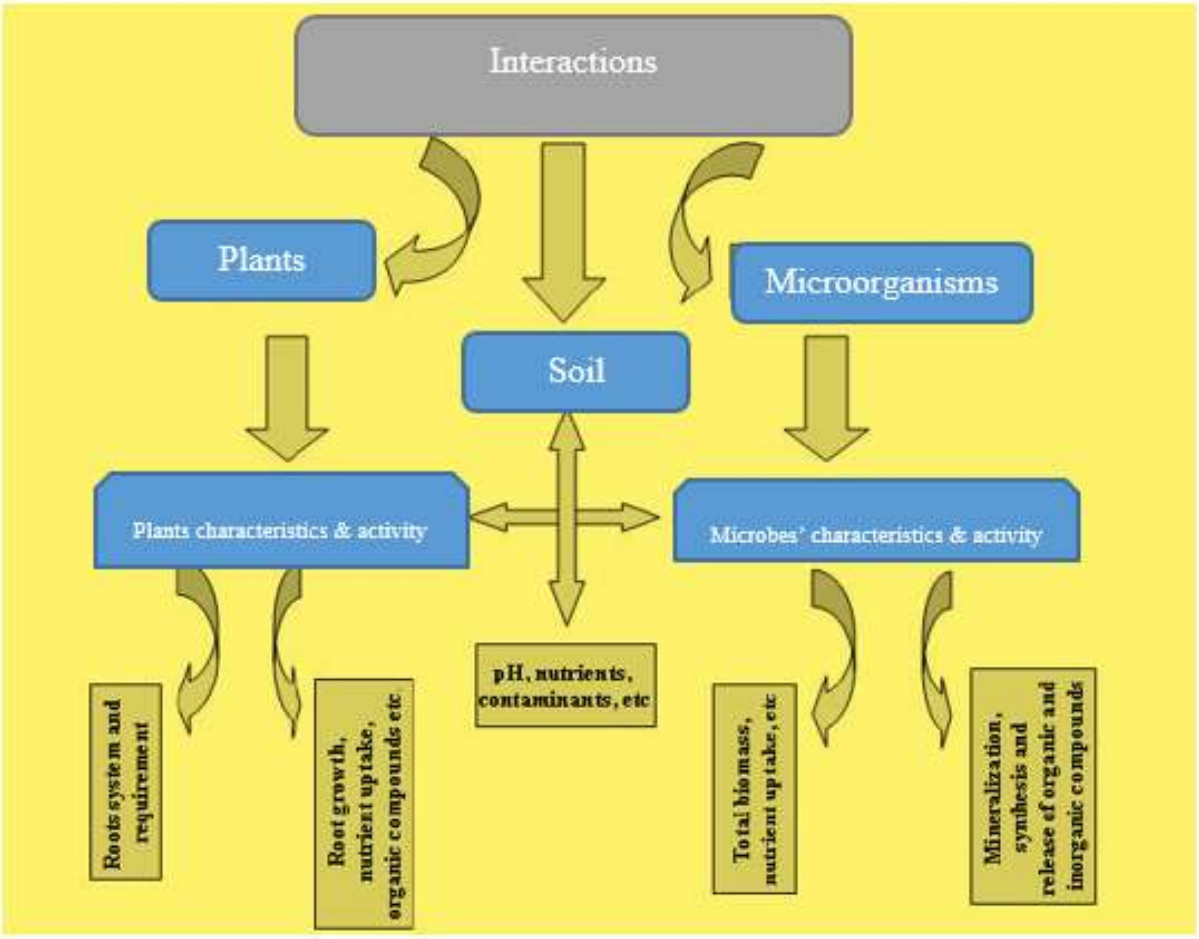

Fig. 1: Plant–soil–microbial interactions in the rhizosphere (Adapted from Jing *et al.*, 2007).

Plant Associated Bacterial Diversity

Comparative phylogenetic analysis of the DNA sequences of cloned *16S rRNA* genes has shown that members of four major phylogenetic groups are ubiquitous to almost all soil types: class α-proteobacteria and phyla Actinobacteria, Acidobacteria and Verrucomicrobia. These four groups are represented in >75% of *16S rRNA* gene clone library studies of soil bacterial communities (Hugenholtz *et al.*, 1998). Other classes of the phylum Proteobacteria and phyla Firmicutes and Planctomycetes are detected in 25–75% of studies (Hugenholtz *et al.*, 1998).

Phyla Proteobacteria, Cytophagales, Actinobacteria and Firmicutes are well represented by cultivated organisms and these four phyla account for 90% of all cultivated bacteria characterized by *16S rRNA* sequences from cultivated organisms in ARB database (Hugenholtz *et al.*, 1998). Some phyla which are revealed by clonal analysis, such as Acidobacteria and Verrucomicrobia, are poorly represented by sequences from cultivated organisms. For example, Acidobacteria appear to be numerically dominant and active members of most soils form up to 52% of *16S rRNA* gene sequences in clone libraries (Felske *et al.*, 2000). However, only few isolates have been obtained from soil (Sait *et al.*, 2002). The Proteobacteria not only contain a large number of cultivated species but also are well represented by cloned *16S rRNA* gene sequences (Dunbar *et al.*, 1999; Saul *et al.*, 2005).

With the advances in PCR-based techniques, numerous rDNA- based strategies have been developed in recent years, which provide efficient tool for studying microbial community and their relationship. Currently most investigators analyse rDNA with methods such as denaturing gradient gel electrophoresis (DGGE) (Reiter *et al.* 2003), temperature gradient gel electrophoresis (Heuer *et al.* 1997), terminal random fragment length polymorphism analysis (Liu *et al.*, 1997), ribosomal intergenic spacer analysis (Borneman and Triplett, 1997) and oligonucleotide fingerprinting of rRNA genes (Valinsky *et al.*, 2002). The development of *nifD* and *nifH* specific primers has also proved very useful in screening diazotrophic strains (Stoltzfus *et al.*, 1997; (Yanni *et al.*, 1997).

Identification at strain level can be done by PCR fingerprinting. These methods are applied with cultured and non-culturable bacterial cells (avoiding DNA extraction) and combines convenient analysis with universal

applicability and the potential information (Ueda *et al.*, 1995b). Several workers are currently using oligonucleotide primers derived from eukaryotic consensus LINE sequence applied for PCR fingerprinting (Ueda *et al.*, 1995a). The electrophoretically separated band patterns were highly reproducible and strain specific PCR assay provides easy detection of bacteria without prior cultivation. Direct sequencing of PCR products may even allow identification of the uncultivated or cultivated strain by phylogenetic analysis of partial SSU (small sub-unit) rDNA sequences in environment (Ueda *et al.*, 1995a; Eckert *et al.*, 2001). Identification of rhizospheric bacteria can also be obtained by development of specific probes. Two 16S rDNA-targeting oligonucleotide probes were developed, which differentiate the new species from the other *Azospirillum* species by whole-cell fluorescence hybridization probes (Eckert *et al.*, 2001). Analysis of the 16S-23S ribosomal DNA (rDNA) intergenic spacer (IGS) sequences allows intraspecies differentiation (Tan *et al.*, 2001).

The diversity within certain species of nitrogen-fixing soil bacteria including *Azospirillum* (Sevilla and Kennedy, 1999), *Herbaspirillum* (Baldani *et al.* 1992) and *Azoarcus* sp. (Hurek and Reinhold-Hurek, 2003) has been already studied by using genomic finger printing like rep-PCR with primers directed to arbitrary or repetitive sequences. With multilocus enzymes electrophoresis (MLEE), RFLP and plasmid pattern, the variability of Brazilian and Mexican isolates of *Acetobacter diazotrophicus* was investigated and a limited genetic diversity was found (Sevilla and Kennedy, 1999). The levels of genetic diversity in many species of bacteria may be related to their habitat.

nifH gene, encoding iron protein of nitrogenase enzyme is one of the most functionally important and evolutionarily conserved gene. Since several diazotrophic bacteria are known to be associated with rice roots, *nifH* sequence analysis directly from rice root DNA or from bacteria growing in rhizosphere of rice can be highly useful for the phylogenetic study of diazotrophic bacteria. Analysis of *nifH* gene amplified directly from rice root has been utilized to study the genetic diversity of N_2-fixing bacteria by the molecular evolutionary analysis of *nifH* sequences (Ueda *et al.*, 1995a). The outline of the *nifH* tree has also been reported to be largely consistent with the *16S rRNA* phylogeny (Ueda *et al.*, 1995a). On the other hand, by *nifH*DK approaches, evidence was obtained for the first time that natural host range of Azoarcus sp. might extend to plants other than Kallar grass. From rice roots grown in Japan, Nif protein sequence was obtained by Ueda *et al.*, (1995b) which could not be assigned to any known bacterial species or genus but for Azoarcus, *nifH* gene sequences. This indicates that Azoarcus sp. might naturally be colonizer of field grown rice, raising the question, if they fix N_2 in rice rhizosphere.

The lack of information about the diversity of bacteria specifically isolated from the rhizosphere of various plants needs to be filled up for our understanding of an important niche in the microbial ecology of grasses such as rice (Ladha and Reddy, 2000). Brief account of some of the typical rhizospheric and putative rhizospheric diazotrophs that have been found to be naturally present in the rhizosphere of the graminaceous plants like rice, sugarcane, wheat, kallar grass etc. is given below.

Herbaspirillum was first reported by (Baldani *et al.* 1992) as a N_2-fixing bacterium associated with the roots of rice, maize and sorghum. *Herbaspirillum seropedicae* and *Herbaspirillum rubrisubalbicans* (formerly known as *Pseudomonas rubrisabalbicans*) are the confirmed diazotrophic bacteria. Another diazotrophic species *Herbaspirillum frisingens* has been isolated from C-4 fibre plants (Kirchhof *et al.*, 2001).

Until now, this bacterium has been reported in 13 members of the graminaceae including sorghum, maize, sugarcane, rice and others, particularly within roots (Olivares *et al.*, 1996). The bacterium may colonize loosely (rhizoplane) or more intimately (endophyte) with the root and found more frequently in rhizosphere. It has been suggested that the *Herbaspirillum* sp. are translocated to the aerial parts of host plants through the transpiration stream (Pimentel *et al.*, 1991).

Herbaspirillum is a gram negative, curved rod with polar flagellation and grows best on dicarboxylic acids, gluconate, glucose and mannitol, fixing N_2 at a pH range of 5.3 to 8 (Baldani *et al.*, 1992; Ureta *et al.*,1995). *Herbaspirillum* sp. grow and fix N_2 under relatively high PO_2 (3%) compared with *Azospirillum* sp. (2%). *H. seropedicae* expresses nitrate reductase and is able to grow, but not fix N_2, in the presence of fixed N (Reinhold-Hurek and Hurek, 1998). Several species of *Herbaspirillum* may show some phytopathogenic potential on sugarcane and sorghum (James *et al.*, 1997; Olivares *et al.*, 1997).

The genus *Sphingomonas* comprises over 55 species, with the *Sphingomonas paucimobilis* identified as the type species (Yabuuchi *et al.*, 1990). Recently, only one species, named *Sphingomonas azotifigens* has been isolated from rice rhizosphere and have been reported to fix nitrogen (Xie and Yokota, 2006). *Sphingomonas* is a gram negative, aerobic, straight rod, 0.5–1.0 X 1.0–3.0 *m*m in size and motile by means of peritrichous flagella. Nitrogen- fixing colonies are circular, smooth, convex, opaque and yellow–orange on agar medium. The visible absorption spectrum of the acetone extract of the yellow pigment has two peaks at 452 and 480 nm. Cells contain poly-β-hydroxybutyrate granules. Optimum temperature for growth is 25–37ºC; growth is inhibited at 42ºC and in 2.5% NaCl. Starch, aesculin and Tween 80 are hydrolysed but not chitin.

Catalase, oxidase, β -galactosidase, phosphatase and DNase are present but not indole or arginine dihydrolase.

Azospirillum sp. is known to be the most efficient diazotrophic bacteria isolated from rhizosphere of various plants, such as *A. zeae* sp. Nov strain N6 and N7 have been isolated from rhizosphere of maize (Mehnaz *et al.*, 2007), rice (Xie and Yokota, 2006, sorghum, and wheat (Baldani *et al.*, 1993). *Azospirillum* sp. is motile and grows best in a semi-solid medium with formation of a pellicle, as their nitrogenase expression/activity is sensitive to PO_2 above 2%. The preferred C sources for all *Azospirillum* sp. are organic acids, such as malate and succinate. It is generally regarded as a rhizospheric bacterium and has often been reported to give best results upon inoculation to crop plants. Certain strains penetrate the roots suggesting that some strains of *Azospirillum* may also colonize within wheat tissues (Naiman *et al.*, 2009). Till date a number of rhizospheric diazotrophic *Azospirillum* species including *Azospirillum lipoferum, A. amazonense, A. halopreferens A. irakense* and *A. doebereinerae* sp. nov have been reported (Khammas *et al.*, 1989; Eckert *et al.*, 2001).

Pseudomonas sp., Serratia sp., Azotobacter sp., Klebsiella sp., Burkholderia sp., Alkaligenes sp. Enterobacter sp., Bacillus polymyxa, Gluconacetobacter sp. Azoarcus sp., Paenibacillus sp., Bacillus subtilis, B. licheniformis, B. pumilus, Brevibacte-rium halotolerans and *Pseudomonas putida* are plant associated bacteria reported by various research workers from different plants (Table 1).

Table 1: Plant associated PGPR reported from various plants

PGPR	**Host crops**	**References**
Burkholderia sp.	Rice	Baldani *et al.* (2000)
Azospirillum sp.	Wheat	Boddey *et al.* (1986)
Gluconacetobacter sp.	Sugarcane	Boddey *et al.* (2001)
Azospirillum sp.	Maize	Garcia de Salamone *et al.* (1996)
Pseudomonas putida and *P. fluorescens*	*Hyoscyamus niger* L	Ghorbanpour *et al.* (2010)
Pseudomonas sp.	Groundnut	Gupta *et al.* (2002)
Bacillus amyloliquefaciens	Bell pepper	Herman *et al.* (2008)
Azoarcus sp.	Kallar grass	Hurek *et al.* (2002)
Enterobacter sp.	Chickpea	Hynes *et al.* (2008)
Gluconacetobacter sp.	Sorghum	Isopi *et al.* (1995)
Pseudomonas fluorescens	*Catharanthus roseus* (L.) G. Don	Jaleel *et al.* (2007)
Pseudomonas fluorescens	*Catharanthus roseus* (L.) G. Don	Jaleel *et al.* (2009)
Herbaspirillum sp.	Sorghum	James *et al.* (1997)
Herbaspirillum sp.	Rice	James *et al.* (2002)
Bacillus cereus MJ-1	Red pepper	Joo *et al.* (2005)
Pseudomonas sp.	White clover Medicago	Kempster *et al.* (2002)
Bacillus subtilis G803	Pepper	Kokalis-Burelle *et al.* (2002)
Bacillus licheniformis	Pepper	Lucas *et al.* (2004)
Azospirillum sp.	Rice	Malik *et al.* (1997)
Azotobacter sp.	Wheat	Mrkovacki and Milic (2001)
Bacillus amyloliquefaciens	Tomato	Murphy *et al.* (2000)
Bacillus polymyxa	Wheat	Omar *et al.* (1996)
Azotobacter sp.	Maize	Pandey *et al.* (1998)
Pseudomonas fluorescens	Tobacco	Park and Kloepper (2000)
Azospirillum brasilense	*Prunus cerasifera* L.	Russo *et al.* (2008)
Paenibacillus polymyxa E681	Sesame	Ryu *et al.* (2006)
Bacillus subtilis	*Crocus sativus* L	Sharaf-Eldin *et al.* (2008)
Pseudomonas aeruginosa	Mung bean	Siddiqui *et al.* (2001)
Azoarcus sp	Sorghum	Stein *et al.* (1997)
Bacillus sp.	Cucumber	Stout *et al.* (2002)
Bacillus pumilus SE 34	Tobacco	Zhang *et al.* (2003)
Streptomyces marcescens 90–116	Tobacco	Zhang *et al.* (2003)
Bacillus cereus	*Salvia miltiorrhiza* Bunge	Zhao *et al.* (2010)

*PGPR reported either endophytes or isolated from rhizosphere of given plants.

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