The literature on plant growth-promoting bacteria pertaining to the present investigations is reviewed under the following major heads:

1. Plant growth-promoting bacteria;
2. Genetic diversity among plant growth-promoting bacteria;
3. Characterization of plant growth-promoting bacteria;
4. Plant growth-promoting attributes; and
5. Effect on plant growth.

2.1 Plant Growth-Promoting Bacteria

Plant growth-promoting bacteria are closely associated and benefit plants by several mechanisms of growth promotion (Bashan and Halquin, 1998). They are of two general types: those that form symbiotic relationships by the formation of specialized structures or nodules on roots, and those that are free-living in the soil often found in the close vicinity or within the roots of plants (Kloepper et al., 1988; van Peer and Schipper, 1989; Frommel et al., 1991). The nitrogen-fixing bacteria nodulating roots of leguminous plants are collectively known as rhizobia and the plant beneficial bacteria colonizing root surfaces and adhering soil interface are known as plant growth-promoting rhizobacteria (PGPR) (Kloepper and Schroth, 1981; Kloepper et al., 1989; Willems, 2006; Lugtenberg and Kamilova, 2009; Weir, 2011). The extent of colonization of host plant organs, tissues and rhizosphere reflects the ability of bacteria to selectively adapt to these specific ecological niches. Consequently, intimate associations between bacteria and plants can be formed, which benefit both plant and bacteria.

Inoculation of plants with beneficial bacteria can be traced back for centuries. Farmers knew from experience that by mixing soil taken from a previous legume crop with soil in which legumes were to be grown would often improve the yields. By the end of the 19th century, the practice of mixing "naturally inoculated" soil with seeds became a recommended method of legume inoculation in the USA. A decade later, the first patent "Nitragin" was registered for plant inoculation with Rhizobium sp. (Nobbe and Hiltner, 1896). Eventually, the practice of legume inoculation with rhizobia became common practice (Smith, 1992). The beneficial effects of rhizobia are well known in terms of biological nitrogen fixation in legumes. For almost 100 years, rhizobia inoculants have been produced around the world. In Brazil legumes, like soybean (Glycine max (Merr.) L.), are
only inoculated with rhizobia and are not fertilized with nitrogen (Bashan and Halguin, 1998). Apart from soybean inoculation which has made a major agricultural impact in the USA, Brazil, and Argentina, significant contributions to the production of other legumes using rhizobia has been made in Australia, North America, Eastern Europe, Egypt, Israel, South Africa, New Zealand, and Southeast Asia (Bashan, 1998). The success of leguminous crops depends critically on the availability of compatible rhizobia in the field. The introduction of soybean cultivation in the United States has been reported to depend on the deliberate inoculation with *Bradyrhizobium japonicum* (Lohrke *et al*., 1996). Compatible symbionts have been required during the introduction of European *Lotus corniculatus* a forage legume in New Zealand and Asian *Cicer arietinum* as a grain legume in Australia (Sullivan *et al*., 1995; Howieson *et al*., 2000).

Inoculation with non-symbiotic, associative rhizosphere bacteria like *Azotobacter* has been used on a large scale in Russia in the 1930s and 1940s (Bashan, 1998). Major breakthrough in plant inoculation technology occurred in late 1970s, with enhanced non-legume plant growth and direct effect on metabolism by inoculations with *Azospirillum* (Döbereiner and Day, 1976; Bashan and Holguin, 1997), and intensive investigation of biocontrol agents, mainly *Pseudomonas fluorescens* and *P. putida* groups (Kloepper and Schroth, 1981; Défago *et al*., 1992; Glick, 1995; Glick and Bashan, 1997). Subsequently, a large number of bacterial strains have been isolated and screened for plant growth-promoting activities and evaluated for plant growth promotion (Chanway *et al*., 1989; Bashan, 1998; Glick *et al*., 1999; Bent *et al*., 2001; Rodríguez *et al*., 2008; Gulati *et al*., 2009; Vyas *et al*., 2010). In recent years, strains belonging to genus *Acinetobacter*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Brachybacterium*, *Delftia*, *Enterobacter*, *Escherichia*, *Micrococcus*, *Paenibacillus*, *Pantoae*, *Providencia*, *Pseudomonas*, *Rahnella*, *Rhizobium*, *Serratia*, *Staphylococcus*, *Stenotrophomonas* and *Streptomyces* have been reported for performing plant growth-promoting activities in rhizosphere (Arcand and Schneider, 2006; Chen *et al*., 2006; El-Tarabily, 2008; Gulati *et al*., 2009; Lal and Tabacchioni, 2009; Rameshkumar and Nair, 2009; Abbas-Zadeh *et al*., 2010; Ali *et al*., 2010; Khare and Arora, 2010; Mamta *et al*., 2010, Siddikee *et al*., 2010; Vyas *et al*., 2010; Gontia *et al*., 2011; Rana *et al*., 2011).

The importance of PGPB offering an environmentally sustainable approach to increasing crop productivity and soil health has been increasingly recognized with the selection of beneficial microbes involved in biological nitrogen fixation, solubilization of insoluble phosphates, production of plant growth hormones, and disease suppression.
(Kloepper et al., 1989; Glick, 1995; Cakmakci et al., 2006; Babalola, 2010). Microbial inoculants based on PGPB have been described as promising components for integrated solutions to agro-environmental problems because of their capacity to promote plant growth, enhance nutrient availability and uptake, and support the health of plants (Barea et al., 1998; Dobbelaere et al., 2001; Hodge et al., 2001; Bonfante, 2003; Vessey, 2003; Kloepper et al., 2004; Han and Lee, 2005; Weller, 2007; Adesemoye et al., 2009; Anthony et al., 2009). Benefits to plants from plant-PGPB interactions have been shown to include increases in seed germination rate, leaf area, root and shoot growth and weight, delayed senescence, chlorophyll content, protein content, nutrient uptake, hydraulic activity, biocontrol, tolerance to abiotic stress, and yield (Mahaffee and Kloepper, 1997; Raaijmakers et al., 2002; Bashan et al., 2004; Mantelin and Touraine, 2004; Bakker et al., 2007; Adesemoye et al., 2009; Adesemoye and Kloepper, 2009; Cheng et al., 2009; Yang et al., 2009; Babalola, 2010).

2.2 Genetic Diversity among Plant Growth-Promoting Bacteria
Several studies demonstrated the influence of plant species on the microbial population associated with their root systems (Weiland and Sundsbak, 2000; Marschner et al., 2001; Garbeva et al., 2004; Houlden et al., 2008; İnceoğlu et al., 2012). The rhizosphere behaves like other well-formed ecosystems and changes in some of its components can affect entire or part of its resident microbial diversity. The differing physical, chemical and biological properties of the root associated soil as compared with the root-free bulk soil have been found responsible for diverse microbial population and diverse microbial activities in the rhizosphere microenvironment (Kennedy, 1998). Diverse genetic structures of rhizosphere microbial communities have been related to the variations of rhizosphere environment (Grayston et al., 1998; Yang and Crowley, 2000; Wieland et al., 2001; Mougel et al., 2006; Dennis et al., 2010).

Several molecular methods have been used to examine genetic relationships of PGPB strains. These methodologies include allozyme profiling and restriction fragment length polymorphism (RFLP) analysis (Eardly et al., 1990; Demezas et al., 1991), pulsed-field gel electrophoresis-fingerprinting (Huber and Selenska-Pobell, 1994), DNA-DNA hybridization analysis (van Berkum et al., 1993), and PCR based DNA fingerprinting (Kuykendall et al., 1992). Some of the fingerprinting strategies with PCR include random amplified polymorphic DNA (RAPD) (Sikora et al., 1997; Vinuesa et al., 1998), enterobacter repetitive intergenic consensus (ERIC), repetitive extragenic palindromic elements (REP) and BOX elements (BOX) (De Bruijn, 1992; Selenska Pobell, 1994;
Saldaña et al., 2003; Naik et al., 2008). A somewhat simpler approach amplified ribosomal DNA restriction analysis (ARDRA) has been employed for identifying strains of PGPB (Laguerre et al., 1994; Vinuesa et al., 1998; Lawongsa et al., 2008; Sklarz et al., 2009; Zhang et al., 2011). 16S-23S intergenic spacer (IGS)-RFLP has also been employed by many workers for analyzing the diversity among PGPB (Vinuesa et al., 1998; Han et al., 2008; Li et al., 2011).

2.2.1 Root-Nodulating Bacteria

The rhizobia-legume symbiosis varies in specificity for both host range and the diversity of bacterial species nodulating a host plant. Plant seems to be an important determinant for rhizobial diversity. High diversity has been recorded for rhizobia at both species and strain levels for the plant family Fabaceae (Leguminosae). Different species and different strains within a species of rhizobia have been reported from the same soil (Bala et al., 2001), while similar isolates have also been found at distant places (Abaidoo et al., 2007; Alvarez-Martinez et al., 2009; Tian et al., 2010). The promiscuous nature of legumes have been revealed by their capacity to nodulate with different rhizobial species (Gao et al., 2001; Mhamdi et al., 2002; Han et al., 2008; Liu et al., 2005, 2007; Man et al., 2008). Bradyrhizobium canariense, B. elkanii, B. japonicum, B. liaoningense, B. yuanmingense, Mesorhizobium tianshanense, Rhizobium tropici and Sinorhizobium fredii have been reported to nodulate soybean in different geographic regions (Jordan, 1982; Chen et al., 1988; Kuykendall et al., 1992; Chen et al., 1995; Yao et al., 2002; Vinuesa et al., 2005; Hungria et al., 2006). The role of environmental factors have also been implied in the legume-rhizobia symbiosis based on rhizobial species and ecological regions (Fierer and Jackson, 2006; Gu et al., 2007; Tian et al., 2007; Yan et al., 2007). Biogeographic patterns of distribution among rhizobia have been addressed in several recent studies (Gu et al., 2007; Lin et al., 2007; Tian et al., 2007; Han et al., 2009; Li et al., 2011; Zhang et al., 2011). Genetic variants have been reported in rhizobia associated with Caragana spp. in Liaoning Province (Yan et al., 2007), faba bean (Vicia faba) in temperate and subtropical regions of China (Tian et al., 2007), and soybean in subtropical regions of China (Man et al., 2008) and India (Appunu et al., 2008).

2.2.2 Plant Growth-Promoting Rhizobacteria

Bacteria possessing plant growth-promoting ability belong to diverse groups (Peix et al., 2007; El-Tarabily, 2008; Viruel et al., 2011). The structure of rhizosphere microbial communities is influenced by the plant species due to difference in root exudations and rhizodepositions (Brimecombe et al., 2001; Dennis et al., 2010). Cultivation-based
techniques on the bacterial community structure of rhizosphere have indicated plant-
dependent diversity (Liljeroth et al., 1990; Lemanceau et al., 1995; Mahaffee and Kloeppe,
1997; Germida et al., 1998; Grayston et al., 1998). Plant species and root exudates, and soil
pH, soil type and soil parental material, and fertilizers also influence significantly the
structure and diversity of soil microbial community (Marschner et al., 2001; Fierer and
Jackson, 2006; Suzuki et al., 2009). Several studies have been performed on the genetic
diversity of *Pseudomonas* isolated from pearl millet, cotton and paddy rhizospheres
(Rangarajan et al., 2001), *Pseudomonas* spp. from rice rhizosphere (Rangarajan et al.,
2002), seasonal diversity changes in alder culturable rhizobacterial communities (Palomino
et al., 2005), phosphate-solubilizing fluorescent pseudomonads from rice rhizosphere (Naik
et al., 2008), plant growth-promoting bacilli from wheat rhizosphere (Beneduzi et al.,
2008), rice-associated bacteria antagonistic to certain phytopathogens (Yang et al., 2008),
sulphate-reducing bacteria from reed rhizosphere (Vladár et al., 2008), plant growth-
promoting rhizobacteria of *Bacillus* sp. (Bahri et al., 2009), moso bamboo-associated
bacteria (Han et al., 2009), PGPR from wheat rhizosphere under saline condition
(Uiapday et al., 2009), antagonistic fluorescent pseudomonads from rice rhizosphere
(Pathma et al., 2010), phosphate-solubilizing strains from rhizosphere of *Lotus tenuis*
(Castagno et al., 2011), antagonistic bacteria from tobacco rhizosphere (Jin et al., 2011),
endophytic siderophore-producing bacteria from rice (Loaces et al., 2011), chitinolytic-
bacteria from rhizospheres of agronomic plants (Someya et al., 2011), bacteria associated
with maize roots (Pereira et al., 2011), and bacteria associated with roots of tree peony
plants (Han et al., 2011).

### 2.3 Characterization of Plant Growth-Promoting Bacteria

An integrated approach based on the different type of information generated by phenotypic,
genotypic, and phylogenetic analyses of bacteria has been advocated for the delineation of
taxa (Colwell, 1970; Vandamme et al., 1996; Prakash et al., 2007; Guedes et al., 2008;
Tindall et al., 2010). Advancement in the field of sequencing of genes coding for rRNA has
revolutionized the understanding of bacterial phylogeny and taxonomy. The limitations of
classical methods have led to the development of “analytical microbiology” where
analytical instrumental methods have been applied for the identification of microorganisms
(Fox et al., 1990). Lipid profiling is the analysis of microbial fatty acid methyl esters
(FAME) and has been used as one of the most common approach for the classification of
bacteria (Kaneda, 1967; Miller, 1982; Brondz et al., 1991). For some genera whole-cell
fatty acid analysis allows differentiation and identification of individual species or even
subspecies but for some organisms different species have identical fatty acid profiles (Welch, 1991; Vreeland et al., 2006; Logan et al., 2009). Substrate utilization in GN microplates gives a standardized method for conducting 95 sole carbon source tests in a single microtitre plate (Biolog, Hayward, CA, USA). Utilization of a particular source has been detected by colour change in a tetrazolium indicator dye when the carbon source is oxidized during respiration (Bochner, 1989). The use of 16S rRNA gene sequences to study bacterial phylogeny and taxonomy has been by far the most common genetic marker used for a number of reasons. The type strains *Bacillus globisporus* and *B. psychrophilus* share >99.5% sequence similarity with regard to their 16S rRNA genes, and but at DNA level exhibit only 23 to 50% relatedness in reciprocal hybridization reactions (Fox et al., 1992). Such examples indicate that 16S rRNA gene sequence similarity even to a very high level does not always imply identity in microbial identification (Janda and Abbott, 2007).

**2.3.1 Root-Nodulating Bacteria**

The application of modern taxonomic methods of classification has led to the recognition of a rapidly increasing number of new species and genera of root-nodulating bacteria. Rhizobia have been studied extensively due to production of nitrogen-fixing root nodules in legumes. First bacterium isolated from root nodules named as *Bacillus radicicola* was renamed soon after this as *Rhizobium leguminosarum* and other species belonging to the same group were also identified (Beijernick, 1888; Frank, 1889). The taxonomy, and nomenclature of the root-nodulating bacteria, has been in constant review ever since. The taxonomic diversity of root-nodulating bacteria at beginning was based on their growth rates (Fred et al., 1932). At present, the rhizobial taxonomy is undergoing frequent changes because strains with unique properties are being unearthed. The validly published names consist of 92 species in 12 genera (Weir, 2011). Most of these genera belong to alpha subdivision of the proteobacteria which include *Rhizobium*, *Ensifer* (formerly *Sinorhizobium*), *Mesorhizobium*, *Bradyrhizobium*, *Azorhizobium*, *Methylobacterium*, *Devosia*, *Phyllobacterium*, and *Ochrobactrum* (Trujillo et al., 2005; Valverde et al., 2005; Weir, 2011), while *Burkholderia* and *Cupriavidus* belong to beta-proteobacteria (Chen et al., 2003; Rasolomampianina et al., 2005).

*Rhizobium leguminosarum* bv. *viciae* has been recorded as the specific symbiont of the legumes of the tribe Vicieae which is comprised of genera *Vicia*, *Pisum*, *Lens* and *lathyrus*. Recently, two new species, *Rhizobium pisi* (Ramirez-Bahena et al., 2008) and *R. fabae* (Tian et al., 2008), have been defined closely related to *R. leguminosarum*, and share similar biovar *viciae* symbiosis genes. Phylogenetic diversity based on *rrs, atpD, recA*
genes and 16S-23S inergenic sequence analyses of rhizobial strains isolated from *Vicia faba* and *Pisum sativum* in Peru has supported that 16S rRNA gene alone is not adequate for identification at species level within *Rhizobium* and suggested the existence of putative new species within the phylogenetic group of *R. leguminosarum* (Santillana et al., 2008). It has been desired to examine genes other than 16S rRNA in order to confirm the relationship among the rhizobia which are ambiguous in the 16S rRNA phylogeny (Gaunt et al., 2001). *atpD* and *recA* has been studied in order to assess the impact of gene transfer on the interpretation of single-gene phylogenies based on 16S rRNA (Gaunt et al., 2001; Santillana et al., 2008; Chang et al., 2011).

Rhizobial taxonomy based on 16S rRNA and house-keeping genes does not reflect the symbiotic features of rhizobia, particularly their host plant range. Both the type and the amount of Nod factors have been considered important in determining host specificity (Laguerre et al., 2001). The bacterial nodulation (nod) genes, induced by plant flavonoids, determine the synthesis of Nod factors, which are main nodulation signal molecules (Perret et al., 2000). Although it has been widely agreed that phylogenies based on stable chromosomal genes were necessary to establish biologically meaningful taxonomy. The characterization and phylogenetic classification based on symbiotic genes provided a complementary basic framework to understand the *Rhizobium*-legume symbiosis (Laguerre et al., 2001). As a nodulation gene marker, the *nodC* gene, encodes for N-acetylglucosaminyltransferase involved in the first step of Nod factor assembly, and is a determinant of host range (Laguerre et al., 2001; Gu et al., 2007; Chang et al., 2011; Rogel et al., 2011). *nifH* gene because of the availability of large number of sequences for comparison has been employed as a nitrogen fixation marker for phylogenetic analysis (Laguerre et al., 2001; Gu et al., 2007; Chang et al., 2011).

### 2.3.2 Plant Growth-Promoting Rhizobacteria

Various workers have characterized plant-associated bacteria using polyphasic approach: plant growth-promoting *Stenotrophomonas maltophilia*, *Bacillus fusiformis* and *Pseudomonas fluorescens* from rhizosphere of agricultural crops based on phenotypic features, carbon source utilization pattern and 16S rRNA gene sequencing (Park et al., 2005); phosphate-solubilizing *Enterobacter*, *Pantoea* and *Klebsiella* from rhizosphere of different crops based on FAME analysis and 16S rRNA gene sequencing (Chung et al., 2005); plant growth-promoting *Delftia tsuruhatensis* from rice rhizoplane based on cell and colony morphology, biochemical characters, FAME analysis, DNA-DNA hybridization and 16S rRNA gene sequencing (Han et al., 2005); plant growth-promoting and fungal
antagonist *Pseudomonas aeruginosa* from banana rhizosphere based on phenotypic, biochemical traits and 16S rRNA gene sequencing (Ayyadurai et al., 2006); *Pseudomonas* spp. from wheat rhizosphere based on phenotypic features, ARDRA and 16S rRNA gene sequencing (Fischer et al., 2007); endophytic *Gluconacetobacter diazotrophicus* strains from sugarcane varieties based on carbon source utilization pattern, ARDRA and RFLP of 16S-23S rDNA intergenic spacer region (Guedes et al., 2008); plant growth-promoting and cold-tolerant *Serratia marcescens* from the flowers of summer squash plants based on biochemical features, carbon source utilization pattern and 16S rRNA gene sequencing (Selvakumar et al., 2008); plant growth-promoting *Acinetobacter rhizosaerae* from seabuckthorn rhizosphere based on phenotypic features, carbon-source utilization pattern, FAME analysis and 16S rRNA gene sequencing (Gulati et al., 2009); cold-tolerant plant growth-promoting *Exiguobacterium acetylicum* from apple rhizosphere based on biochemical characterization, carbon source utilization pattern and 16S rRNA gene sequencing (Selvakumar et al., 2009a); cold-adapted plant growth-promoting *Rahnella* sp. from seabuckthorn rhizosphere based on phenotypic features, carbon-source utilization pattern, FAME analysis and 16S rRNA gene sequencing (Vyas et al., 2010); phosphate-solubilizing *Burkholderia gladioli* strain 10216, *B. gladioli* strain 10217, *Enterobacter aerogenes* strain 10208 and *Serratia marcescens* strain 10238 from *Stevia rebaudiana* rhizosphere based on carbon source utilization, FAME analysis and 16S rRNA gene sequencing (Gupta et al., 2011; Mamta et al., 2010), and potential plant growth-promoting *Bacillus* sp. (AW1), *Providencia* sp. (AW5) and *Brevundimonas diminuta* (AW7) isolated from wheat rhizosphere based on phenotypic and genotypic attributes (Rana et al., 2011). Recently, draft genomes of plant growth-promoting bacteria *Paenibacillus polymyxa* ATCC 842T and *Pantoea ananatis* B1-9 have been sequenced (Jeong et al., 2011; Kim et al., 2012).

### 2.4 Plant Growth-Promoting Attributes

Plant-PGPB interactions involve a combination of direct and indirect mechanisms (Kloepper et al., 1989; Glick, 1995; Rodríguez et al., 2008; Lugtenberg and Kamilova, 2009; Son et al., 2009; Babalola, 2010). The direct beneficial effects of PGPB strains include fixing atmospheric nitrogen (Bashan et al., 2004); enhancing phosphorus availability (Rodríguez and Fraga, 1999); sequestering iron for plants by production of siderophores (Raaijmakers et al., 1995; Bakker et al., 2007); producing plant hormones such as auxins, gibberellins and cytokinins (Glick, 1995; Gutierrez-Manero et al., 2001); and synthesizing the enzyme ACC deaminase, which lowers ethylene levels in plant rhizosphere, thereby reducing
environmental stress on plants (Glick et al., 2007). The indirect mechanisms of plant growth promotion by PGPB include antibiotic production, depletion of iron from the rhizosphere, synthesis of antifungal metabolites, production of fungal cell wall lysing enzymes, competition for space on roots and induced systemic resistance (Kloepper et al., 1988; Glick et al., 1999; Bakker et al., 2007; Sayyed and Chincholkar, 2009). Many PGPB possess multiple plant growth-promoting attributes which influence plant growth at different developmental stages (Naik et al., 2008; Poonguzhali et al., 2008; Gulati et al., 2009; Rokhbalkhsh-Zamin et al., 2011).

2.4.1 Nitrogen Fixation

The nitrogen cycle is an essential and complex biogeochemical cycle that has a great impact on soil fertility (Jetten, 2008). The cycle is dominated by four major microbial processes: N fixation, nitrification, denitrification, and N mineralization (Ogunseitan, 2005). A wide range of organisms have the ability to fix nitrogen including 87 species in 2 genera of archaea, 38 genera of bacteria, and 20 genera of cyanobacteria (Dixon and Wheeler, 1986; Sprent and Sprent, 1990; Zahran et al., 1995; Weir, 2011). The nitrogen-fixing bacteria include free-living aerobic Azotobacter, Beijernickia, Klebsiella and Paenibacillus, free-living anaerobic Clostridium and Desulfovibrio, symbiotic rhizobia and Frankia, and associative Azospirillum (Zehr et al., 2003; Kennedy et al., 2004; Betancourt et al., 2008; Jin et al., 2011; Weir, 2011). Microbial inoculants have demonstrated significant roles in N cycling and utilization of N fertilizer by plants (Ames et al., 1983; Briones et al., 2003; Adesemoye and Kloepper, 2009). The biological nitrogen-fixation has a great practical importance because the use of nitrogenous fertilizers has resulted in unacceptable levels of water pollution (Dixon and Wheeler, 1986; Sprent and Sprent, 1990; Lui et al., 2011).

Rhizobia-legume symbiosis has been reported to provide well over half of the biological source of fixed nitrogen and is the primary source of fixed nitrogen in land based systems (Tate, 1995; Fox et al., 2007). In legumes, bacteria reside in small growths on the roots called nodules and fix nitrogen which is absorbed by the plant. Notable values of fixed nitrogen have been estimated for various legume crops and pasture species (Peoples et al., 1995; Tate, 1995). Nitrogen fixation has been affected by many different physiological and environmental factors in soil, such as temperature, water holding capacity, water stress, salinity, pH and nutrients level (Keerio et al., 2001; Dogan et al., 2011). Synthetic agricultural inputs applied to soil, such as herbicides, chemical N fertilizers, or pesticides have been reported to affect rhizobial populations and legume nodulation (Bunemann et al., 2006; Fox et al., 2007). Nodulation and nitrogenase activity have been employed as major
traits for the evaluation of rhizobia-legume symbiosis and selecting potential strains of rhizobia (Annapurna et al., 2007; Ben Romdhane et al., 2007; Fox et al., 2007; Younis, 2007; Neeraj et al., 2008; Singh et al., 2010).

2.4.2 Phosphate Solubilization

Phosphorus is another plant growth-limiting nutrient as it affects plant structure at cellular level stimulates growth and hastens maturity. Plants with P deficiency exhibit stunted growth, wilting of leaves, delayed maturity and reduced yield (Mallarino et al., 2002; Loria and Sawyer, 2005). One reason to P not readily available to plants because of the high reactivity of P in the soil with some metal complexes such as iron (Fe), Al, and Ca (Igual et al., 2001; Richardson, 2001; Gyaneshwar et al., 2002; Fernández et al., 2007; Richardson et al., 2009).

PGPB play significant roles in the solubilization of inorganic phosphate and mineralization of organic phosphates (Fig. 2.1). Several strains have been reported from different environments with the capacity to solubilize mineral phosphate (Illmer and Schinner, 1992; Whitelaw et al., 1999; Nautiyal et al., 2000; Gyaneshwar et al., 2002; Gulati et al., 2008; Patel et al., 2008; Harvey et al., 2009; Park et al., 2009; Richardson et al., 2009; Son et al., 2009; Zaidi et al., 2009; Khan et al., 2010). Achromobacter, Aerobacter, Agrobacterium, Bacillus, Burkholderia, Erwinia, Flavobacterium, Gluconoacetobacter, Micrococcus, Pseudomonas, Ralstonia, Rhanello, Rhizobium, Serratia and others have been reported for the conversion of insoluble inorganic phosphates into soluble forms (Rodríguez and Fraga, 1999; Richardson, 2001; Chung et al., 2005; Pandey et al., 2006; Pérez et al., 2007; Gulati et al., 2008; Park et al., 2008; Poonguzhal et al., 2008; Richardson et al., 2009; Linu et al., 2009; Vyas et al., 2010; Zabihi et al., 2011).

Production of organic acids has been reported as the principal mechanism for microbial solubilization of inorganic phosphates (Dave and Patel, 1999; Whitelaw et al., 1999; Chen et al., 2006; Patel et al., 2008; Park et al., 2009; Richardson et al., 2009; Vyas and Gulati, 2009; Richardson and Simpson, 2011). Gluconic acid is the major organic acid produced by phosphate-solubilizing bacteria (Rodríguez et al., 2004; Patel et al., 2008; Park et al., 2009; Vyas and Gulati, 2009). Direct periplasmic oxidation of glucose to gluconic acid is the metabolic basis of inorganic phosphate solubilization by many Gram-negative bacteria as a competitive strategy to transform the readily available carbon sources into less readily utilizable products by other microorganisms (Whiting et al., 1976; Goldstein, 1995; Goldstein and Krishnaraj, 2007). Other organic acids such as 2-ketogluconic, acetic, citric,
glycolic, isovaleric, isobutyric, lactic, malonic, oxalic, propionic, and succinic acids have also been detected during phosphate solubilization by microorganisms (Rodríguez and Fraga, 1999; Chen et al., 2006; Vyas and Gulati, 2009; Gulati et al., 2010). The organic acids reduce pH and act as chelating agents, forming complexes with Ca, Fe, or Al, and thereby releasing P. Other mechanisms of solubilization are comprised of other chelating substances and inorganic acids such as sulphideric, nitric, and carbonic acids. Secretion of enzymes like acid and alkaline phosphatase, phytase, and phosphohydrolase has also been recorded as a common mode of conversion of insoluble forms of P (Kohler et al., 2007; Richardson and Simpson, 2011).

Fig. 2.1 Schematic representation of the importance of soil microorganisms to phosphorus (P) availability in soil (after Richardson and Simpson, 2011).

The solubilization of inorganic phosphates has been reported for several species of root-nodulating bacteria of different legumes (Chabot et al., 1996; Peix et al., 2001; Hara and de Oliveira, 2004; Alikhani et al., 2006; Rivas et al., 2007; Xie, 2008; Marra et al., 2011). The process of formation of the nitrogen-fixing nodule has been reported to be limited by the availability of P (MacDermott, 1999). High positive response has been recorded to P supplementation in legumes like alfalfa, clover, common bean, cow pea and pigeon pea (Cassman et al., 1981; Itoh, 1987; Al-Niemi et al., 1997; Deng et al., 1998). The nitrogen-fixing potential of aquatic legume Sesbania rostrata has also been limited by P availability (Ladha et al., 1992; Ventura and Ladha, 1997). The root-nodulating bacteria with phosphate-solubilizing ability have been proved to be good plant growth-promoting bacteria for non-legumes (Antoun et al., 1998; Chabot et al., 1996; Yanni et al., 2001).

The phosphate-solubilizing bacteria isolated from the rhizosphere of various plants have been known to be metabolically more active than those isolated from sources other than rhizosphere (Baya et al., 1981; Gyaneshwar et al., 2002). Increased plant growth,
biomass and yield of different crops and plants have been recorded with the inoculation of phosphate-solubilizing rhizobacteria (Hariprasad and Niranjana, 2009; Khan et al., 2009; Vyas and Gulati, 2009).

2.4.3 IAA Production

Auxins constitute an important class of phytohormones which influence many cellular functions regulating plant growth and development. Auxins play an important role in the orientation of root and shoot growth in response to light and gravity, differentiation of vascular tissues, apical dominance, initiation of lateral and adventitious roots, cell division and elongation of stems and roots (Arshad and Frankenberger, 1991; Patten and Glick, 1996; Spaepen et al., 2007; Spaepen and Vanderleyden, 2010). Auxins particularly IAA has also been reported to be involved in host-parasite interactions (Gutierrez et al., 2009; Spaepen and Vanderleyden, 2010). Various authors have reported the biocontrol action of IAA either due to the inhibition of spore germination and mycelium growth of pathogenic fungi or due to its involvement together with glutathione S-transferase in defense-related plant reactions (Brown and Hamilton, 1993; Jha et al., 2009). The auxin concentration is critical to the physiological response by the plant. The production of IAA in the presence of tryptophan has been reported for several bacteria, including *Acinetobacter*, *Acetobacter*, *Alcaligenes*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Bradyrhizobium*, *Pantoea*, *Pseudomonas*, *Rhizobium* and *Xanthomonas* (Patten and Glick, 1996; Bent et al., 2001; Kang et al., 2006; Idris et al., 2007; Spaepen et al., 2007; Tsavkelova et al., 2007; Park et al., 2009; Jha et al., 2009; Abbas-Zadeh et al., 2010).

Starting with tryptophan as main precursor, at least five different pathways have been described in microorganisms for the synthesis of IAA (Fig. 2.2) (Patten and Glick, 1996; Woodward and Bartel, 2005; Spaepen et al., 2007; Spaepen and Vanderleyden, 2010). The pathways described are mostly named according to a key intermediate of the pathway. In several microorganisms, redundancy of IAA biosynthetic pathways has been observed with the presence of multiple pathways active in single microorganism.

The indole-3-acetamide (IAM) pathway has been reported from several pathogens such as *Agrobacterium tumefaciens*, *Pseudomonas savastanoi*, *Pseudomonas syringae*, *Pantoea agglomerans*, and also in symbiotic nitrogen-fixing bacteria belonging to *Rhizobium* and *Bradyrhizobium* species (Sekine et al., 1989; Clark et al., 1993; Morris, 1995; Theunis et al., 2004). The indole-3-pyruvate (IPA) pathway has also been reported in many bacteria including, phytopathogens (*Erwinia herbicola* and *Pantoea agglomerans*), and plant beneficial bacteria (*Azospirillum*, *Bacillus*, *Bradyrhizobium*, *Enterobacter*...
cloacae, Paenibacillus, Pseudomonas, and Rhizobium) (Costacurta et al., 1994; Brandl and Lindow, 1996; Patten and Glick, 2002; Schutz et al., 2005; Spaepen et al., 2007; Malhotra and Sirvastava, 2008). The tryptamine (TAM) pathway has been reported for Bacillus cereus and Azospirillum sp. (Perley and Stowe, 1966; Hartmann et al., 1983; Spaepen et al., 2007). In several Agrobacterium and rhizobial species nitrile hydratase and amidase activity have been measured in the conversion of indole-3-acetonitrile (IAN) to IAA via IAM (Vega-Hernandez et al., 2002; Spaepen and Vanderleyden, 2010). Tryptophan side-chain oxidase (TSO) pathway has been reported only in Pseudomonas fluorescens CHA0 (Oberhansli et al., 1991; Spaepen et al., 2007).

**Fig. 2.2** Tryptophan-dependent pathways of bacterial indole-3-acetic acid synthesis (after Patten and Glick, 1996).

IAA is involved in founder cell specification, nodule initiation and differentiation, vascular bundle formation, and nodule numbers in process of nodule formation by root-nodulating bacteria in legume plants. In general, root nodules contain more IAA than non-nodulated roots (Badenoch-Jones et al., 1983; Ghosh and Basu, 2006). Higher amounts of IAA have been reported in the nodules induced with a Bradyrhizobium japonicum mutant overproducing IAA (Hunter, 1989). Conversely, lower concentration of IAA has been observed in the nodules induced with low IAA-producing Rhizobium mutants than the nodules initiated by the wild-type (Theunis, 2005). The introduction and expression of the IAM biosynthetic pathway in Rhizobium leguminosarum bv. viciae resulted in Vicia hirsuta root nodules containing up to 60-fold more IAA than nodules invoked by the wild-type
strain and the nitrogen fixation capacity in the former nodule number also increased (Camerini et al., 2008).

Changes in the root architecture mainly as an increase in root hairs and lateral roots have been observed on the inoculation of plants with IAA producing PGPR strains (Spaepen and Vanderleyden, 2010). These morphological changes of the root have been attributed to bacterial IAA production studied with mutants altered in IAA production (Barbieri and Galli, 1993; Malik and Sindhu, 2008). However, most IAA knock-out mutants still exhibit some plant growth promotion indicating IAA biosynthesis alone is not responsible for the overall effect (Xie et al., 1996; Dobbelaere et al., 1999; Dobbelaere et al., 2003).

### 2.4.4 ACC-deaminase Activity

The gaseous plant hormone ethylene is involved in a wide range of biological processes in plants. Low concentrations of ethylene enhance root extension while higher concentrations cause inhibition of root elongation (Arshad and Frankenberger, 1991; Ma et al., 1998; Glick et al., 2007). Several PGPB such as Alcaligenes xylosoxidans, Alcaligenes sp., Agrobacterium genomovars, Azospirillum lipoferum, Alcaligenes sp., Bacillus pumilus, Bacillus spp., Burkholderia sp., Enterobacter cloacae, Pseudomonas brassicacearum, P. chloroaphis, P. putida, P. fluorescens, P. marginalis, P. oryziphabitans, Ralstonia solanacearum, Rhizobium spp., Sinorhizobium meliloti and Variovorax paradoxus produce the enzyme ACC deaminase which cleaves the plant ethylene precursor ACC to α-ketobutyrate and ammonia, thereby lowering the level of ethylene in the rhizosphere (Jacobson et al., 1994; Shah et al., 1998; Belimov et al., 2001; Ma et al., 2003; Sergeeva et al., 2006; Cheng et al., 2007; Glick et al., 2007; Farajzadeh et al., 2010). IAA produced by PGPB can stimulate plant cell proliferation, plant cell elongation or induce the transcription of ACC synthase, catalyzing the formation of ACC (Bayliss et al., 1997; Kim et al., 2001). The cleavage of ACC by ACC deaminase leads to more ACC exudation from inside the plant to maintain the equilibrium, thus reducing ACC and ethylene levels evolved by the plant (Fig. 2.3). ACC deaminase producing bacteria have also been found to provide resistance to plants against pathogens, tolerance against salinity, drought, flooding, and metal and organic contamination (Sergeeva et al., 2006; Glick et al., 2007; Bano and Fatima, 2009; Cheng et al., 2009; Yang et al., 2009; Ahmad et al., 2011).

Ethylene is involved in the responses of plants to microbial pathogens and microbial symbionts. ACC-deaminase producing rhizobia may use this mechanism to lower the level of ethylene produced in the root during the early stages of nodulation. Rhizobial strains with ACC deaminase activity have been reported as more efficient for nodulation (Hirsch and
Fang, 1994; Guinel and Geil, 2002; Ma et al., 2003; Ma et al., 2004; Duan et al., 2009). Inactivation of acdS gene in Mesorhizobium loti resulted in reduced number of nodules on Lotus japonicus as compare to the number of nodules formed by the wild-type strain (Uchiumi et al., 2004). The introduction of multiple copies of the acdS gene has increased ACC-deaminase activities of Rhizobium sp. strain TAL1145 and also enhanced its symbiotic efficiency on Leucaena leucocephala (Tittabutr et al., 2008).

2.4.5 Siderophore Production

Iron is an essential plant micronutrient as it serves as a cofactor of many enzymes with redox activity. A large portion of the soil iron is in highly insoluble form of ferric hydroxide which acts as a limiting factor for plant growth even in iron rich soils. Several microorganisms such as Alcaligenes, Azotobacter, Azospirillum, Bacillus, Enterobacter, Pseudomonas and Rhizobium produce low-molecular weight iron-binding molecules usually less than 1 kDa called siderophores under low-iron conditions (Yang et al., 1991; Raaijmakers et al., 1995; da Silva and de Almeida, 2006; Storey et al., 2006; Sayyed and Chincholkar, 2006, 2009; Jin et al., 2010). Siderophores bind Fe$^{3+}$ with high affinity and help in iron uptake (Glick et al., 1999). Studies on inoculation with siderophore-producing bacteria have provided evidence for the absorption of bacterial iron-siderophore complexes by plants, especially in calcareous soils (Masalha et al., 2000). Siderophore-producing rhizobacteria suppress fungal pathogens by making iron unavailable for fungal growth (Mahmoud and Abd-Alla, 2001; Sharma and Johri, 2003; Sayyed et al., 2007; Sayyed and Chincholkar, 2009). These bacteria also enhance availability of P to the plants through the solubilization of iron-bound phosphorus in soil (Gaur, 1990; Duponois et al., 2006; Jing et
Siderophore-mediated competition for iron is also a major factor in determining the interaction among bacterial strains during rhizosphere competence by PGPR (Loper and Henkels, 1999; Jing et al., 2007).

Siderophores are classified based on the functional groups into hydroxamate, catecholate or carboxylate types (Glick et al., 1999; Baakza et al., 2004). Catecholate and hydroxamate-type siderophores have been widely reported in bacteria, including Aeromonas hydrophila, Azotobacter sp., Methylobacterium spp., Pseudomonas fluorescens, P. aeruginosa, P. pseudomallei, P. putida, P. stutzeri, Pseudomonas sp., and Rhizobium leguminosarum (Yang et al., 1991; Glick et al., 1999; Mahmoud and Abd-Alla, 2001; Sayyed et al., 2005; Thirumurugan et al., 2006; Storey et al., 2006; Lacava et al., 2008). Carboxylate-type siderophores have been reported in a few bacteria like Pseudomonas mediterranea, Pseudomonas sp. and Rhizobium meliloti (Baakza et al., 2004; Tian et al., 2008, 2009). Catecholate-type siderophores have been reported for stronger binding to iron than hydroxamate-type siderophores (Matzanke, 1991; Sayyed and Chincholkar, 2006).

Legume-rhizobia interaction is iron dependent as iron is required for nodule formation as well as synthesis of nitrogenase complex and leghaemoglobin, required for nitrogen fixation (Raychaudhuri et al., 2005). Rhizobia produce variety of siderophores some of these are unique in their functional group like phenolate, rhizobactin and vicibactin (Smith et al., 1985; Patel et al., 1988; Dilworth et al., 1998). Rhizobium sp. isolated from stem nodules of Sesbania procumbens has been reported for the production of catechol-type of siderophores (Sridevi et al., 2008). Stimulated iron uptake and shoot transport have been observed in clover plant on the application of purified rhizobial siderophore isolated from Rhizobium leguminosarum bv trifolii (Derylo and Skoruska, 1992). Strong antagonism has been observed against Macrophomina phaseolina by siderophore producing strains RMP3 and RMP5 of Rhizobium meliloti (Arora et al., 2001).

2.4.6 Antagonism against Phytopathogens

Biological control of plant pathogens using antagonistic rhizobacteria is an effective and eco-friendly alternative to the use of synthetic chemicals (Emmert and Handelsman, 1999; Jayaraj and Radhakrishnan, 2008; Postma et al., 2009; Fischer et al., 2010). PGPR produce several metabolites including siderophores, antibiotics such as 2, 4-diacetylphloroglucinol, hydrogen cyanide (HCN), phenazine, pyoluteorin, pyrrolnitrin, and cell-wall degrading enzymes such as chitinases, cellulases and proteases that reduce the growth or activity of phytopathogens (Kremer and Souissi, 2001; Raaijmakers et al., 2002; Kloeper et al., 2004;
Compant et al., 2005; Domenech et al., 2006; Fischer et al., 2010; Zhang et al., 2010). Biological control may also result from direct interactions between PGPR and the host plants, whereby the host disease defense response is stimulated leading to induced systemic resistance (ISR) (Ryu et al., 2004; Choudhary et al., 2007; De Vleesschauwer et al., 2009).

Several bacteria have been reported to inhibit soil-borne plant pathogens: *Paenibacillus lentimorbus* against *Fusarium oxysporum* f. sp. *ciceri* through the production of chitinase and β-1,3-glucanase (DasGupta et al., 2006), *Pseudomonas* spp. against *Verticillium dahliae* through pseudobactin and salicylic acid production (Mercado-Blanco et al., 2004), *Pseudomonas putida* against *Alternaria alternata* and *Fusarium solani* through chitinase, β-1,3-glucanase, salicylic acid, siderophore and HCN production (Pandey et al., 2006), *Bacillus* spp. against *Sclerotinia* and *Fusarium* through the production of cellulases and proteases (Príncipe et al., 2007), *Bacillus subtilis* against *Fusarium oxysporum* and *Phytophthora capsici* through bacilysin and iturin production (Chung et al., 2008), *Enterobacter cloacae* and *Serratia ficaria* against *Phytophthora cactorum* in a dual-culture plate assay (Okamoto et al., 2000), *Serratia marcescens* against *Alternaria alternate*, *Aspergillus niger*, *Fusarium oxysporum*, *Helminthosporium* sp. and *Curvularia* sp. through chitinase production (Parani and Saha, 2009), *Pseudomonas fluorescens* against *Piricularia oryzae* and *Rhizoctonia solani* through 2, 4-diacylphloroglucinol production (Reddy and Reddy, 2009), and *Pseudomonas* spp. against *Rhizoctonia solani*, *Sclerotinia minor* and *S. sclerotiorum* through extracellular enzymes, hydrogen cyanide and siderophores (Fischer et al., 2010).

### 2.5 Effect of Plant Growth-Promoting Bacteria on Plant Growth

Inoculations with a target microorganism at a much higher concentration than that found in the soil is necessary to take advantage of PGPB for plant growth and yield enhancement. The benefits of PGPB application depend upon plant species/variety, growth conditions, and PGPB strains (Nowak et al., 1998; Mehnaz and Lazarovits, 2006). Increased yields have been reported with the application of PGPB selected for various plant growth-promoting activities.

#### 2.5.1 Root-Nodulating Bacteria

Increased plant growth has been reported on inoculation with root-nodulating and nitrogen-fixing bacteria: *Bradyrhizobium* sp. in mung bean and peanut (Wani et al., 2007b; Badawi et al., 2011); *Rhizobium leguminosarum* sv. *trifolii* in common bean and white clover (Svenning et al., 2001; Abril et al., 2007); *Rhizobium leguminosarum* sv. *viciae* in pea, lentil and faba bean (Cordovilla et al., 1994; Stancheva et al., 2006; Jida and Asefa, 2011);
Rhizobium spp. in chickpea and lentil (Ahemad and Khan, 2010; Verma et al., 2010); and Sinorhizobium meliloti in alfalfa (Castillo et al., 1999). Significant increase has also been recorded in total N in plants and soils with rhizobial inoculation (Badawi et al., 2011). Increase in yield has also been recorded with rhizobial inoculations in leguminous crops such as chickpea, lentil, horsegram and pea (Tellawi et al., 1986; Martinez-Romero and Rosenblueth, 1990; Micanovic et al., 1996; Feng et al., 1997; Svenning et al., 2001; Ahmed et al., 2007; Ali et al., 2008; Verma et al., 2010; Kala et al., 2011). Inoculations with rhizobia have also been reported to increase plant growth and yield in non-leguminous crops like maize, radish, rice, and wheat (Chabot et al., 1996; Antoun et al., 1998; Biswas et al., 2000; Yanni et al., 2001; Andrews et al., 2003).

2.5.2 Plant Growth-Promoting Rhizobacteria

Acinetobacter rhizosphaerae, Bacillus megaterium, B. subtilis, Bradyrhizobium sp., Burkholderia sp., Enterobacter sp., Pantoea sp., Pseudomonas fragi, P. putida, P. striata, Pseudomonas spp., Serratia marcescens and Serratia sp. solubilizing phosphate have been reported to increase growth and yield in several crops including chinese cabbage, maize, pea, peanut, spinach, soybean, stevia and wheat (Urashima and Hori, 2003; Fernández et al., 2007; Hameeda et al., 2008; Poonguzhali et al., 2008; Selvakumar et al., 2009b; Taurian et al., 2009; Guiñazú et al., 2010; Gulati et al., 2010; Mamta et al., 2010). The potential use of phosphate-solubilizing bacteria along with rock phosphates has been studied for increasing P availability to plants (Vyas and Gulati, 2009; Gulati et al., 2010; Mamta et al., 2010; Sharma et al., 2010).

Many plant growth-promoting bacteria including Azotobacter, Azospirillum, Bacillus, Burkholderia, Flavobacterium, Pseudomonas and Pantoea producing IAA have shown enhanced growth and yield in many crops (Arshad and Frankenberger, 1991; Benizri et al., 1998; Kuklinsky-Sobral et al., 2004; Idris et al., 2007; Tsavkelova et al., 2007; Ahmed and Hasnain, 2010; Ali et al., 2010). Similarly, ACC-deaminase producing bacteria including Bacillus, Burkholderia, Enterobacter cloacae, Methylobacterium oryzae, Pseudomonas fluorescens, P. putida, Pseudomonas spp. and Variovorax paradoxus have been reported to enhance plant growth (Kausar and Shahzad, 2006; Madhaiyan et al., 2006; Glick et al., 2007; Belimov et al., 2008; Shaharoona et al., 2008; Rodríguez et al., 2008; Zahir et al., 2009; Zabihi et al., 2011). Likewise, a wide variety of siderophore-producing bacteria including Alcaligenes faecalis, Bacillus, Burkholderia, Proteus sp., Pseudomonas aeruginosa, P. chlororaphis, P. fluorescens, Pseudomonas spp., Serratia have been shown to enhance plant growth either directly by increasing the availability of iron or indirectly by
inhibiting the growth of phytopathogens due to the non-availability of iron (Barthakur, 2000; Mahmoud and Abd-Alla, 2001; Gupta et al., 2002; Sharma and Johri, 2003; Katiyar and Goel, 2004; Sayyed et al., 2007; Reddy and Reddy, 2009; Sayyed and Chincholkar, 2009). Several bacteria including Bacillus amylo liquefaciens, B. pasteurii, B. pumilus, B. subtilis, Burkholderia cepacia, Paenibacillus polymyxa, P. lentimorbus, Pseudomonas fluorescens, P. putida, Pseudomonas spp. and Serratia marcescens have also been reported to enhance plant growth indirectly through the suppression of phytopathogens (Raj et al., 2003; Pandey et al., 2006; DasGupta et al., 2006; Chung et al., 2008; Reddy and Reddy, 2009; Siddiqui and Akhtar, 2009; Son et al., 2009; Zhang et al., 2010).

Rhizobacteria with multiple plant growth-promoting activities have been reported to enhance growth in many plants: P. putida through phosphate solubilization and fungal antagonism in maize (Pandey et al., 2006); P. putida through IAA production, phosphate solubilization and antifungal activity in corn (Mehnaz and Lazarovits, 2006); P. fluorescens through the production of siderophores, salicylic acid and HCN in olives (Mercado-Blanco et al., 2004); Pseudomonas sp. through the production of IAA, HCN and siderophores in peanut (Gupta et al., 2002); Pseudomonas sp. through phosphate solubilization, nitrogen fixation, and the production of antifungal antibiotics, IAA, siderophores and HCN in maize (Pal et al., 2001); Pseudomonas sp. through phosphate solubilization, ACC-deaminase activity and the production of IAA, siderophore, and HCN in pearl millet (Hameeda et al., 2006; Vassilev et al., 2006); Micrococcus sp. through phosphate solubilization, IAA production, ACC-deaminase activity and siderophore production in cow pea (Dastager et al., 2010); Rahnella sp. through phosphate solubilization, IAA production, ACC-deaminase activity, ammonia generation, and siderophore production in pea (Vyas et al., 2010); and Acinetobacter spp. through phosphate solubilization, siderophores, and production of antifungal antibiotics in pearl millet (Rokhbakhsh-Zamin et al., 2011). Application of PGPR strains has been also reported to enhance nutrient use efficiency in wheat (Adesemoye and Kloepper, 2009).

2.5.3 Co-inoculation of Root-Nodulating Bacteria and Rhizobacteria

A synergistic influence of root-nodulating bacteria and PGPR has been reported for several crops- Pseudomonas, Mesorhizobium ciceri and Azotobacter chroococcum in chickpea (Wani et al., 2007a); fluorescent Pseudomonas strains and Rhizobium leguminosarum bv. viciae strains in pea (Kumar et al., 2001); Pseudomonas strains and Rhizobium leguminosarum bv. phaseoli strains in common beans (Martins et al., 2004); Pseudomonas fluorescens and P. putida with Rhizobium sp. in pigeonpea (Tilak et al., 2006);
Pseudomonas fluorescens with Azospirillum lipoferum in rice (Raja et al., 2006); Pseudomonas diminuta and Rhizobium leguminosarum bv. viciae in lentil (Kumar and Chandra, 2008); Pseudomonas, Azospirillum, Azotobacter and Rhizobium in chickpea (Rokhzadi et al., 2008); Pseudomonas and Rhizobium in maize (Bano and Fatima, 2009); Bacillus spp., Pseudomonas spp. and Sinorhizobium meliloti in alfalfa (Guiñazú et al., 2010); Pseudomonas spp. and Rhizobium in fodder galega (Egamberdieva et al., 2010) and Bradyrhizobium plus Serratia marcescens in peanut (Badawi et al., 2011). Soybean co-inoculated with Bradyrhizobium sp. and Bacillus megaterium have shown enhanced nodulation (Liu and Zinclair, 1990). Dual inoculations of pigeonpea plants with either Pseudomonas putida, P. fluorescens or Bacillus cereus and Rhizobium strain have been recorded to enhance plant growth, nodulation, and nitrogenase activity significantly over Rhizobium-inoculated and uninoculated control (Tilak et al., 2006). Co-inoculation with PGPR containing ACC deaminase and Rhizobium spp. improved growth and nodulation in mung bean under salt-affected conditions (Ahmad et al., 2011).