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REVIEW

Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective

Munees Ahemad [a,b,*], Mulugeta Kibret [b]

[a] *Department of Agricultural Microbiology, Faculty of Agricultural Sciences, Aligarh Muslim University, Aligarh 202 002, UP, India*
[b] *Department of Biology, College of Science, Bahir Dar University, Bahir Dar, Ethiopia*

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ACC deaminase;
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Phosphate solubilization;
Rhizosphere

Abstract Plant growth promoting rhizobacteria are the soil bacteria inhabiting around/on the root surface and are directly or indirectly involved in promoting plant growth and development via production and secretion of various regulatory chemicals in the vicinity of rhizosphere. Generally, plant growth promoting rhizobacteria facilitate the plant growth directly by either assisting in resource acquisition (nitrogen, phosphorus and essential minerals) or modulating plant hormone levels, or indirectly by decreasing the inhibitory effects of various pathogens on plant growth and development in the forms of biocontrol agents. Various studies have documented the increased health and productivity of different plant species by the application of plant growth promoting rhizobacteria under both normal and stressed conditions. The plant-beneficial rhizobacteria may decrease the global dependence on hazardous agricultural chemicals which destabilize the agro-ecosystems. This review accentuates the perception of the rhizosphere and plant growth promoting rhizobacteria under the current perspectives. Further, explicit outlooks on the different mechanisms of rhizobacteria mediated plant growth promotion have been described in detail with the recent development and research. Finally, the latest paradigms of applicability of these beneficial rhizobacteria in different agro-ecosystems have been presented comprehensively under both normal and stress conditions to highlight the recent trends with the aim to develop future insights.

1. Introduction

Different bacterial genera are vital components of soils. They are involved in various biotic activities of the soil ecosystem to make it dynamic for nutrient turn over and sustainable for crop production (Ahemad et al., 2009; Chandler et al., 2008). They stimulate plant growth through mobilizing nutrients in soils, producing numerous plant growth regulators, protecting plants from phytopathogens by controlling or inhibiting them, improving soil structure and bioremediating the polluted soils by sequestering toxic heavy metal species

* Corresponding author at: Department of Agricultural Microbiology, Faculty of Agricultural Sciences, Aligarh Muslim University, Aligarh 202 002, UP, India. Tel.: +91 9305021113.
E-mail address: muneesmicro@rediffmail.com (M. Ahemad).
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Table 1 Various compounds in root exudates of different plant species.

Amino acids	α-Alanine, β-alanine, asparagines, aspartate, cystein, cystine, glutamate, glycine, isoleucine, leucine, lysine, methionine, serine, threonine, proline, valine, tryptophan, ornithine, histidine, arginine, homoserine, phenylalanine, γ-Aminobutyric acid,α-Aminoadipic acid
Organic acids	Citric acid, oxalic acid, malic acid, fumaric acid, succinic acid, acetic acid, butyric acid, valeric acid, glycolic acid, piscidic acid, formic acid, aconitic acid, lactic acid, pyruvic acid, glutaric acid, malonic acid, tetronic acid, aldonic acid, erythronic acid
Sugars	Glucose, fructose, galactose, ribose, xylose, rhamnose, arabinose, desoxyribose, oligosaccharides, raffinose, maltose
Vitamins	Biotin, thiamin, pantothenate, riboflavin, niacin
Purines/nucleosides	Adenine, guanine, cytidine, uridine
Enzymes	Acid/alkaline-phosphatase, invertase, amylase, protease
Inorganic ions and gaseous molecules	HCO_3^-, OH^-, H^+ $CO_2{\cdot}H_2$

Adapted from Dakora and Phillips (2002).

and degrading xenobiotic compounds (like pesticides) (Ahemad, 2012; Ahemad and Malik (2011); Hayat et al., 2010; Rajkumar et al., 2010; Braud et al., 2009). Indeed, the bacteria lodging around/in the plant roots (rhizobacteria) are more versatile in transforming, mobilizing, solubilizing the nutrients compared to those from bulk soils (Hayat et al., 2010). Therefore, the rhizobacteria are the dominant deriving forces in recycling the soil nutrients and consequently, they are crucial for soil fertility (Glick, 2012). Currently, the biological approaches for improving crop production are gaining strong status among agronomists and environmentalists following integrated plant nutrient management system. In this context, there is an ongoing rigorous research worldwide with greater impetus to explore a wide range of rhizobacteria possessing novel traits like heavy metal detoxifying potentials (Ma et al., 2011a; Wani and Khan, 2010), pesticide degradation/tolerance (Ahemad and Khan, 2012a,b), salinity tolerance (Tank and Saraf, 2010; Mayak et al., 2004), biological control of phytopathogens and insects (Hynes et al., 2008; Russo et al., 2008; Joo et al., 2005; Murphy et al., 2000) along with the normal plant growth promoting properties such as, phytohormone (Ahemad and Khan, 2012c Tank and Saraf, 2010), siderophore (Jahanian et al., 2012; Tian et al., 2009), 1-aminocyclopropane-1-carboxylate, hydrogen cyanate (HCN), and ammonia production, nitrogenase activity (Glick, 2012; Khan, 2005) phosphate solubilization (Ahemad and Khan, 2012c) etc. Hence, diverse symbiotic (*Rhizobium*, *Bradyrhizobium*, *Mesorhizobium*) and non-symbiotic (*Pseudomonas*, *Bacillus*, *Klebsiella*, *Azotobacter*, *Azospirillum*, *Azomonas*), rhizobacteria are now being used worldwide as bio-inoculants to promote plant growth and development under various stresses like heavy metals (Ma et al., 2011a,b; Wani and Khan, 2010), herbicides (Ahemad and Khan, 2011l; Ahemad and Khan, 2010g), insecticides (Ahemad and Khan 2011h,k), fungicides (Ahemad and Khan, 2012f; Ahemad and Khan, 2011j), salinity (Mayak et al., 2004) etc.

Although, the mechanisms of rhizobacteria-mediated plant growth promotion are not completely identified, the so-called plant growth promoting rhizobacteria however, have been reported to exhibit the above mentioned properties to expedite the plant growth and development (Khan et al., 2009; Zaidi et al., 2009). The present review is an effort to elucidate the concept of rhizobacteria in the current scenario and their underlying mechanisms of plant growth promotion with recent updates. The latest paradigms of a wide range of applications of these beneficial rhizobacteria in different agro-ecosystems have been presented explicitly to garner broad perspectives regarding their functioning and applicability.

2. Rhizosphere

The narrow zone of soil directly surrounding the root system is referred to as rhizosphere (Walker et al., 2003), while the term 'rhizobacteria' implies a group of rhizosphere bacteria competent in colonizing the root environment (Kloepper et al., 1991). In addition to providing the mechanical support and facilitating water and nutrient uptake, plant roots also synthesize, accumulate, and secrete a diverse array of compounds (Walker et al., 2003). These compounds secreted by plant roots act as chemical attractants for a vast number of heterogeneous, diverse and actively metabolizing soil microbial communities. The chemicals which are secreted by roots into the soils are generally called as root exudates. The exudation of a wide range of chemical compounds (Table 1) modifies the chemical and physical properties of the soil and thus, regulates the structure of soil microbial community in the immediate vicinity of root surface (Dakora and Phillips, 2002). In fact, some of the exudates act as repellants against microorganisms while others act as attractants to lodge the microbes. The composition of these exudates is dependent upon the physiological status and species of plants and microorganisms (Kang et al., 2010). Moreover, these exudates also promote the plant-beneficial symbiotic interactions and inhibit the growth of the competing plant species (Nardi et al., 2000). Also, microbial activity in the rhizosphere affects rooting patterns and the supply of available nutrients to plants, thereby modifying the quality and quantity of root exudates. A fraction of these plant-derived small organic molecules is further metabolized by microorganisms in the vicinity as carbon and nitrogen sources, and some microbe-oriented molecules are subsequently re-taken up by plants for growth and development (Kang et al., 2010). Indeed, carbon fluxes are critical determinants of rhizosphere function. It is reported that approximately 5–21% of photosynthetically fixed carbon is

Table 2 Growth promoting substances released by PGPR.

PGPR	Plant growth promoting traits	References
Pseudomonas putida	IAA, siderophores, HCN, ammonia, exo-polysaccharides, phosphate solubilization	Ahemad and Khan (2012a,c) and Ahemad and Khan (2011c)
Pseudomonas aeruginosa	IAA, siderophores, HCN, ammonia, exo-polysaccharides, phosphate solubilization	Ahemad and Khan (2012e), Ahemad and Khan (2011a,k) and Ahemad and Khan (2010d)
Klebsiella sp.	IAA, siderophores, HCN, ammonia, exo-polysaccharides, phosphate solubilization	Ahemad and Khan (2011b,f,g)
Enterobacter asburiae	IAA, siderophores, HCN, ammonia, exo-polysaccharides, phosphate solubilization	Ahemad and Khan (2010a,b)
Rhizobium sp. (pea)	IAA, siderophores, HCN, ammonia, exo-polysaccharides	Ahemad and Khan (2012b), Ahemad and Khan (2011i), Ahemad and Khan (2010c) and Ahemad and Khan (2009b)
Mesorhizobium sp.	IAA, siderophores, HCN, ammonia, exo-polysaccharides	Ahemad and Khan (2012d), Ahemad and Khan (2010e,h) and Ahemad and Khan (2009a)
Acinetobacter spp.	IAA, phosphate solubilization, siderophores	Rokhbakhsh-Zamin et al. (2011)
Rhizobium sp.(lentil)	IAA, siderophores, HCN, ammonia, exo-polysaccharides	Ahemad and Khan (2011e,j) and Ahemad and Khan (2010f,g)
Pseudomonas sp. A3R3	IAA, siderophores	Ma et al. (2011a)
Psychrobacter sp. SRS8	Heavy metal mobilization	Ma et al. (2011b)
Bradyrhizobium sp.	IAA, siderophores, HCN, ammonia, exo-polysaccharides	Ahemad and Khan (2012f) and Ahemad and Khan (2011d,h,l)
Pseudomonas aeruginosa 4EA	Siderophores	Naik and Dubey (2011)
Bradyrhizobium sp. 750, *Pseudomonas* sp., *Ochrobactrum cytisi*	Heavy metal mobilization	Dary et al. (2010)
Bacillus species PSB10	IAA, siderophores, HCN, ammonia	Wani and Khan (2010)
Paenibacillus polymyxa	IAA, siderophores	Phi et al. (2010)
Rhizobium phaseoli	IAA	Zahir et al. (2010)
Stenotrophomonas maltophilia	Nitrogenase activity, phosphate solubilization, IAA, ACC deaminase	Mehnaz et al. (2010)
Rahnella aquatilis	Phosphate solubilization, IAA, ACC deaminase	Mehnaz et al. (2010)
Pseudomonas aeruginosa, *Pseudomonas fluorescens*, *Ralstonia metallidurans*	Siderophores	Braud et al. (2009)
Proteus vulgaris	Siderophores	Rani et al. (2009)
Pseudomonas sp.	Phosphate solubilization, IAA, siderophore, HCN, biocontrol potentials	Tank and Saraf (2009)
Azospirillum amazonense	IAA, nitrogenase activity	Rodrigues et al. (2008)
Mesorhizobium sp.	IAA, siderophores, HCN, ammonia	Wani et al. (2008)
Pseudomonas sp.	ACC deaminase, IAA, siderophore	Poonguzhali et al. (2008)
Serratia marcescens	IAA, siderophore, HCN	Selvakumar et al. (2008)
Pseudomonas fluorescens	ACC deaminase, phosphate solubilization	Shaharoona et al. (2008)
Acinetobacter sp., *Pseudomonas* sp.	ACC deaminase, IAA, antifungal activity, N_2- fixation, phosphate solubilization	Indiragandhi et al. (2008)
Enterobacter sp.	ACC deaminase, IAA, siderophore, phosphate solubilization	Kumar et al. (2008)
Burkholderia	ACC deaminase, IAA, siderophore, heavy metal solubilization, phosphate solubilization	Jiang et al. (2008)
Pseudomonas jessenii	ACC deaminase, IAA, siderophore, heavy metal solubilization, phosphate solubilization	Rajkumar and Freitas (2008)
Pseudomonas aeruginosa	ACC deaminase, IAA, siderophore, phosphate solubilization	Ganesan (2008)
Pseudomonas sp.	ACC deaminase, IAA, siderophore, heavy metal solubilization, phosphate solubilization	Rajkumar and Freitas (2008)
Azotobacter sp., *Mesorhizobium* sp., *Pseudomonas* sp., *Bacillus* sp.	IAA, siderophore, antifungal activity, ammonia production, HCN	Ahmad et al. (2008)
Bradyrhizobium sp.	IAA, siderophores, HCN, ammonia	Wani et al. (2007a)
Rhizobium sp.	IAA, siderophores, HCN, ammonia	Wani et al. (2007b)
Mesorhizobium ciceri, *Azotobacter chroococcum*	IAA, siderophores	Wani et al. (2007c)
Pseudomonas, *Bacillus*	Phosphate solubilization, IAA and siderophores	Wani et al. (2007c)
Klebsiella oxytoca	IAA, phosphate solubilization, nitrogenase activity	Jha and Kumar (2007)

Table 2 (*Continued*)

PGPR	Plant growth promoting traits	References
Bacillus spp., *Pseudomonas* spp., *Azotobacter* spp., *Rhizobium* spp.	IAA, ammonia production	Joseph et al. (2007)
Pseudomonas fluorescens	Induced systemic resistance, antifungal activity	Saravanakumar et al. (2007)
Pseudomonas chlororaphis	Antifungal activity	Liu et al. (2007)
Baciilus subtilis	Antifungal activity	Cazorla et al. (2007)
Gluconacetobacter diazotrophicus	Zinc solubilization	Saravanan et al. (2007)
Brevibacillus spp.	Zn resistance, IAA	Vivas et al. (2006)
Bacillus subtilis	IAA, phosphate solubilization	Zaidi et al. (2006)
Pseudomonas sp., *Bacillus* sp.	IAA, siderophore, phosphate solubilization	Rajkumar et al. (2006)
Pseudomonas putida	Antifungal activity, siderophore, HCN, phosphate solubilization	Pandey et al. (2006)
Bravibacterium sp.	Siderophore	Noordman et al. (2006)
Xanthomonas sp. RJ3, *Azomonas* sp. RJ4, *Pseudomonas* sp. RJ10, *Bacillus* sp. RJ31	IAA	Sheng and Xia (2006)
Bacillus sp.	P-solubilization	Canbolat et al. (2006)
Bradyrhizobium japonicum	IAA	Shaharoona et al. (2006)
Pseudomonas putida	Siderophores, Pb and Cd resistence	Tripathi et al. (2005)
Pseudomonas fluorescens PRS_9, *Pseudomonas fluorescens* GRS_1	IAA, siderophores, phosphate solubilization	Gupta et al. (2005)
Variovorax paradoxus, *Rhodococcus* sp., *Flavobacterium*	IAA and siderophores	Belimov et al. (2005)
Sphingomonas sp, *Mycobacterium* sp, *Bacillus* sp, *Rhodococcus* sp, *Cellulomonas* sp., *Pseudomonas* sp.	IAA	Tsavkelova et al. (2005)
Pseudomonas fluorescens	IAA, siderophores, antifungal activity	Dey et al. (2004)
Bacillus, *Azospirillum* sp.	IAA, P-solubilization	Yasmin et al. (2004)
Azospirillum brasilense, *Azospirillum amazonense*	IAA, P solubilization, nitrogenase activity, antibiotic resistance	Thakuria et al. (2004)
Pseudomonas fluorescens	IAA, phosphate solubilization	Jeon et al. (2003)
Rhizobium, Bradyrhizobium	HCN, siderophore, Siderophore, IAA, P-solubilization	Deshwal et al. (2003)
Bacillus, Pseudomons, Azotobacter, Azospirillum, Rhizobium	P-solubilization and IAA	Tank and Saraf (2003)
Mesorhizobium, Bradyrhizobium sp.	Siderophore	Khan et al. (2002)
Azotobacter chroococcum	Gibberellin, kinetin, IAA	Verma et al. (2001)
Azotobacter chroococcum	P-solubilization	Kumar et al. (2001)
Rhizobium meliloti	Siderophore	Arora et al. (2001)
Kluyvera ascorbata	Siderophore	Burd et al. (2000)
Kluyvera ascorbata	ACC deaminase, siderophores, metal resistance	Genrich et al. (1998)
Bradyrhizobium, Rhizobium	Siderophore	Duhan et al. (1998)
Bradyrhizobium, Rhizobium	IAA	Antoun et al. (1998)
Rhizobium ciceri	Siderophopre	Berraho et al. (1997)
Bradyrhizobium japonicum	Siderophore	Wittenberg et al. (1996)
Rhizobium leguminosarum	Cytokinin	Noel et al. (1996)
Rhizobium, Bradyrhizobium	P-solubilization	Abd-Alla (1994)

transported to the rhizosphere through root exudation (Marschner, 1995). Thus, the rhizosphere can be defined as any volume of soil specifically influenced by plant roots and/or in association with roots hairs, and plant-produced materials (Dessaux et al., 2009). Largely, three separate but interacting components are recognized in the rhizosphere: the rhizosphere (soil), the rhizoplane, and the root itself. Of these, the rhizosphere is the zone of soil influenced by roots through the release of substrates that affect microbial activity. The rhizoplane, on the other hand, is the root surface including the strongly adhering soil particles while the root itself is a component of the system, because many micro-organisms (like endophytes) also colonize the root tissues (Barea et al., 2005). Microbial colonization of the rhizoplane and/or root tissues is known as root colonization, whereas the colonization of the adjacent volume of soil under the influence of the root is known as rhizosphere colonization (Barea et al., 2005; Kloepper et al., 1991; Kloepper, 1994).

3. Plant growth promoting rhizobacteria

The plant growth promoting rhizobacteria (PGPR), are characterized by the following inherent distinctiveness's: (i) they must be proficient to colonize the root surface (ii) they must survive, multiply and compete with other microbiota, at least for the time needed to express their plant growth promotion/protection activities, and (iii) they must promote plant growth (Kloepper, 1994). About 2–5% of rhizobacteria, when reintroduced by plant inoculation in a soil containing competitive microflora, exert a beneficial effect on plant growth and are termed as plant growth promoting

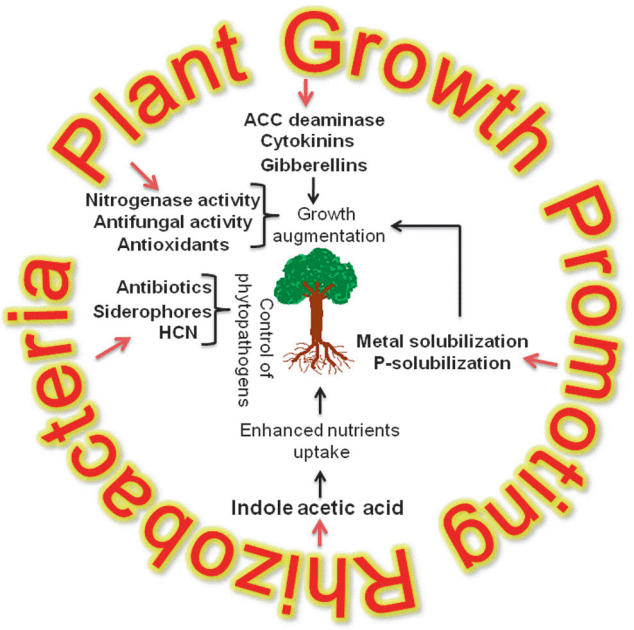

Figure 1 Mechanism of plant growth promotion by rhizobacteria.

rhizobacteria (Kloepper and Schroth, 1978). In accordance with Vessey (2003), soil bacterial species burgeoning in plant rhizosphere which grow in, on, or around plant tissues stimulate plant growth by a plethora of mechanisms are collectively known as PGPR (plant growth promoting rhizobacteria).

Alternatively, Somers et al. (2004) classified PGPR based on their functional activities as (i) biofertilizers (increasing the availability of nutrients to plant), (ii) phytostimulators (plant growth promotion, generally through phytohormones), (iii) rhizoremediators (degrading organic pollutants) and (iv) biopesticides (controlling diseases, mainly by the production of antibiotics and antifungal metabolites) (Antoun and Prévost, 2005). Furthermore, in most studied cases, a single PGPR will often reveal multiple modes of action including biological control (Kloepper, 2003; Vessey, 2003). Furthermore, Gray and Smith (2005) have recently shown that the PGPR associations range in the degree of bacterial proximity to the root and intimacy of association. In general, these can be separated into extracellular (ePGPR), existing in the rhizosphere, on the rhizoplane, or in the spaces between cells of the root cortex, and intracellular (iPGPR), which exist inside root cells, generally in specialized nodular structures (Figueiredo et al., 2011). Some examples of ePGPR are like, *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcous*, *Pseudomonas* and *Serratia* etc. (Bhattacharyya and Jha, 2012). Similarly, some examples of the iPGPR are *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium* and *Rhizobium* of the family *Rhizobiaceae*. Most of rhizobacteria belonging to this group are Gram-negative rods with a lower proportion being Gram-positive rods, cocci or pleomorphic (Bhattacharyya and Jha, 2012). Moreover, numerous actinomycetes are also one of the major components of rhizosphere microbial communities displaying marvelous plant growth

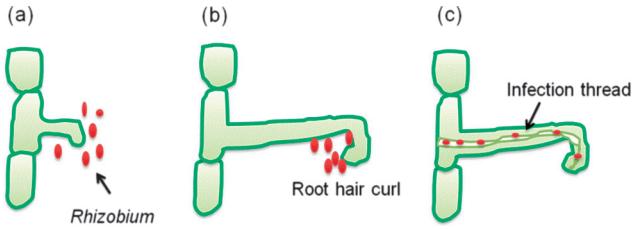

Figure 2 The nodulation process (a) Interaction of rhizobial rhicadhesin with host lectins and rhizobial attachment with root cells. (b) Excretion of nod factors by rhizobia causes root hair curling. (c) Rhizobia penetrate root hair and form an infection thread through which they penetrate the cortical cells and form bacteroid state thereby nodules are formed.

beneficial traits (Bhattacharyya and Jha, 2012; Merzaeva and Shirokikh 2006). Among them, *Micromonospora* sp., *Streptomyces* spp., *Streptosporangium* sp., and *Thermobifida* sp., which have shown an enormous potential as biocontrol agents against different root fungal pathogens, are worthy of mention (Bhattacharyya and Jha, 2012; Franco-Correa et al., 2010).

4. Mechanisms of plant growth promotion

According to Kloepper and Schroth (1981), PGPR mediated plant growth promotion occurs by the alteration of the whole microbial community in rhizosphere niche through the production of various substances (Table 2) (Kloepper and Schroth, 1981). Generally, PGPR promote plant growth directly by either facilitating resource acquisition (nitrogen, phosphorus and essential minerals) or modulating plant hormone levels, or indirectly by decreasing the inhibitory effects of various pathogens on plant growth and development in the forms of biocontrol agents (Glick, 2012) (Fig. 1).

4.1. Direct mechanisms

4.1.1. Nitrogen fixation

Nitrogen (N) is the most vital nutrient for plant growth and productivity. Although, there is about 78% N_2 in the atmosphere, it is unavailable to the growing plants. The atmospheric N_2 is converted into plant-utilizable forms by biological N_2 fixation (BNF) which changes nitrogen to ammonia by nitrogen fixing microorganisms using a complex enzyme system known as nitrogenase (Kim and Rees, 1994). In fact, BNF accounts for approximately two-thirds of the nitrogen fixed globally, while the rest of the nitrogen is industrially synthesized by the Haber–Bosch process (Rubio and Ludden, 2008). Biological nitrogen fixation occurs, generally at mild temperatures, by nitrogen fixing microorganisms, which are widely distributed in nature (Raymond et al., 2004). Furthermore, BNF represents an economically beneficial and environmentally sound alternative to chemical fertilizers (Ladha et al., 1997).

Nitrogen fixing organisms are generally categorized as (a) symbiotic N_2 fixing bacteria including members of the family rhizobiaceae which forms symbiosis with leguminous plants (e.g. rhizobia) (Ahemad and Khan, 2012d; Zahran, 2001) and non-leguminous trees (e.g. *Frankia*) and (b) non-symbiotic (free living, associative and endophytes) nitrogen fixing forms

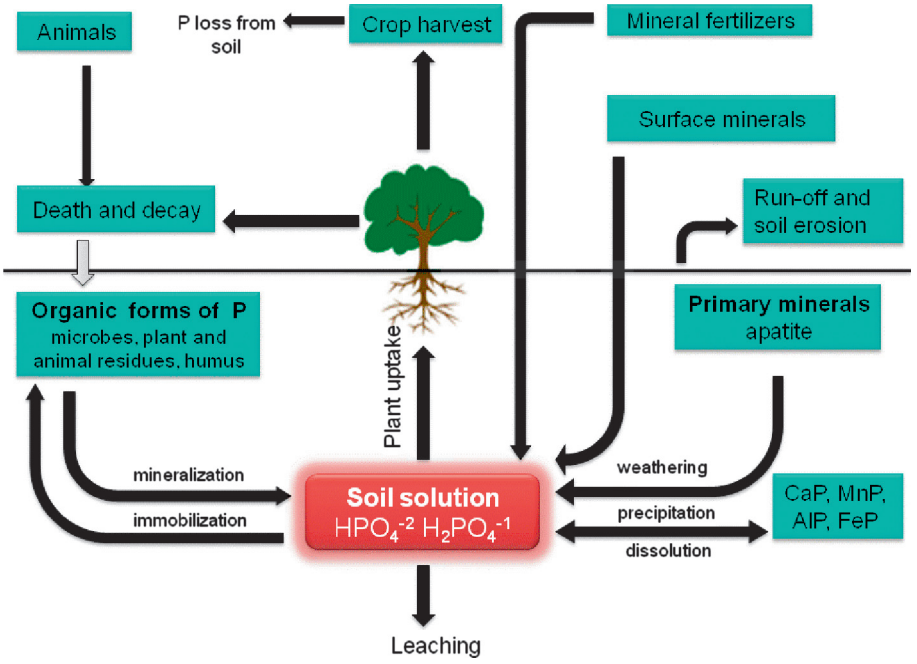

Figure 3 Movement of phosphorus in soils.

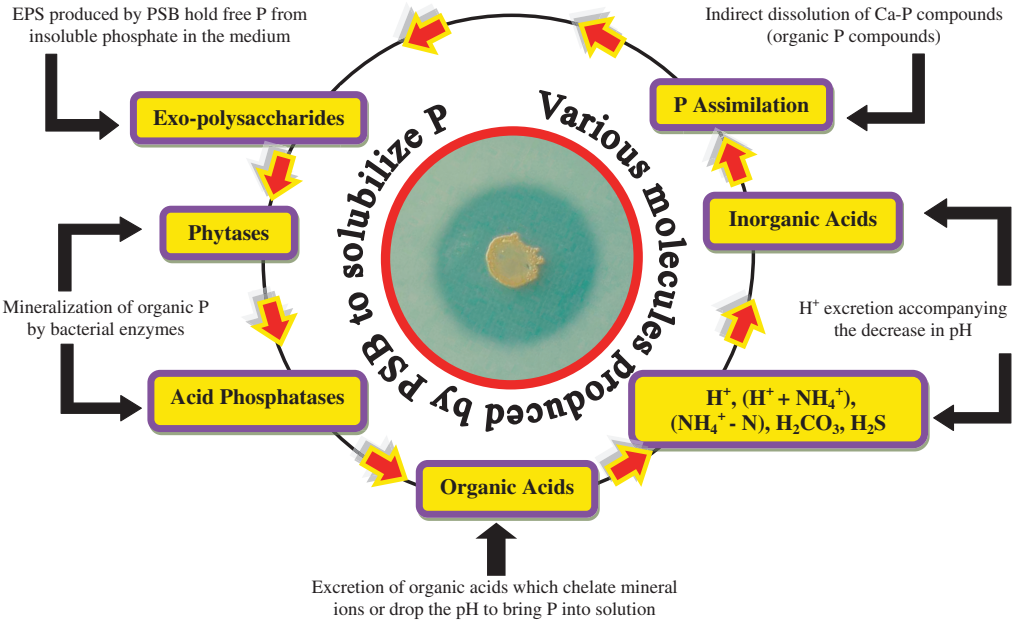

Figure 4 Various organic/inorganic substances produced by PSB responsible for phosphate solubilization in soils.

such as cyanobacteria (*Anabaena*, *Nostoc*), *Azospirillum*, *Azotobacter*, *Gluconoacetobacter diazotrophicus* and *Azocarus* etc. (Bhattacharyya and Jha, 2012). However, non-symbiotic nitrogen fixing bacteria provide only a small amount of the fixed nitrogen that the bacterially-associated host plant requires (Glick, 2012). Symbiotic nitrogen fixing rhizobia within the rhizobiaceae family (α-proteobacteria) infect and establish symbiotic relationship with the roots of leguminous plants. The establishment of the symbiosis involves a complex interplay between host and symbiont (Giordano and Hirsch, 2004) resulting in the formation of the nodules wherein the rhizobia colonize as intracellular symbionts (Fig. 2). Plant growth-promoting rhizobacteria that fix N_2 in non-leguminous plants are also called as diazotrophs capable of forming a non-obligate interaction with the host plants (Glick et al., 1999). The process of N_2 fixation is carried out by a complex enzyme, the nitrogenase complex (Kim and Rees, 1994). Structure of nitrogenase was elucidated by Dean and Jacobson (1992) as

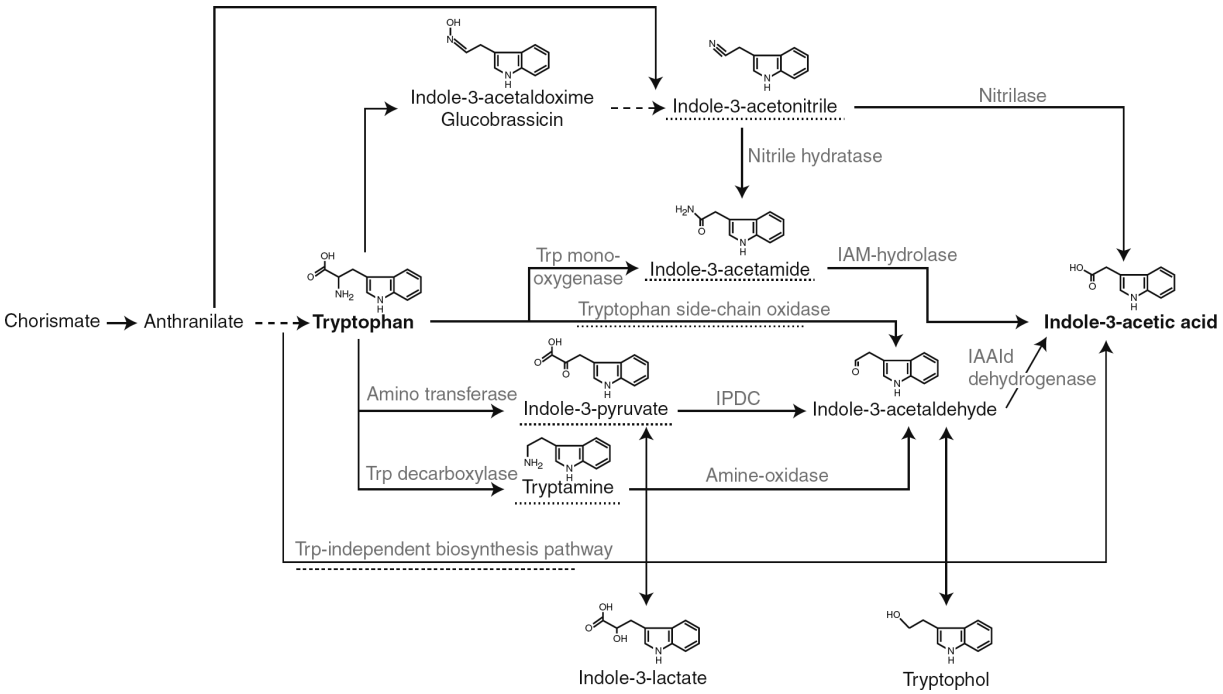

Figure 5 Overview of the different pathways to synthesize IAA in bacteria. The intermediate referring to the name of the pathway or the pathway itself is underlined with a dashed line. IAAld, indole-3-acetaldehyde; IAM, indole-3-acetamide; IPDC, indole-3-pyruvate decarboxylase; Trp, tryptophan (Adapted from Spaepen et al. (2007)).

a two-component metalloenzyme consisting of (i) dinitrogenase reductase which is the iron protein and (ii) dinitrogenase which has a metal cofactor. Dinitrogenase reductase provides electrons with high reducing power while dinitrogenase uses these electrons to reduce N_2 to NH_3. Based on the metal cofactor three different N fixing systems have been identified (a) Mo-nitrogenase, (b) V-nitrogenase and (c) Fe-nitrogenase. Structurally, N_2-fixing system varies among different bacterial genera. Most biological nitrogen fixation is carried out by the activity of the molybdenum nitrogenase, which is found in all diazotrophs (Bishop and Jorerger, 1990).

The genes for nitrogen fixation, called *nif* genes are found in both symbiotic and free living systems (Kim and Rees, 1994). Nitrogenase (*nif)* genes include structural genes, genes involved in activation of the Fe protein, iron molybdenum cofactor biosynthesis, electron donation, and regulatory genes required for the synthesis and function of the enzyme. In diazotrophs, *nif* genes are typically found in a cluster of around 20–24 kb with seven operons encoding 20 different proteins (Glick, 2012). The molybdenum nitrogenase enzyme complex has two component proteins encoded by the *nifDK* and the *nifH* genes. The *NifDK* component is a heterotetrameric ($\alpha_2\beta_2$) protein formed by two αβ dimers related by a twofold symmetry. NifDK carries one iron molybdenum cofactor (FeMo-co) within the active site in each α-subunit (NifD) (Rubio and Ludden, 2008). The symbiotic activation of *nif*-genes in the *Rhizobium* is dependent on low oxygen concentration, which in turn is regulated by another set of genes called *fix*-genes which are common for both symbiotic and free living nitrogen fixation systems (Kim and Rees, 1994; Dean and Jacobson, 1992). Since nitrogen fixation is a very energy demanding process, requiring at least 16 mol of ATP for each

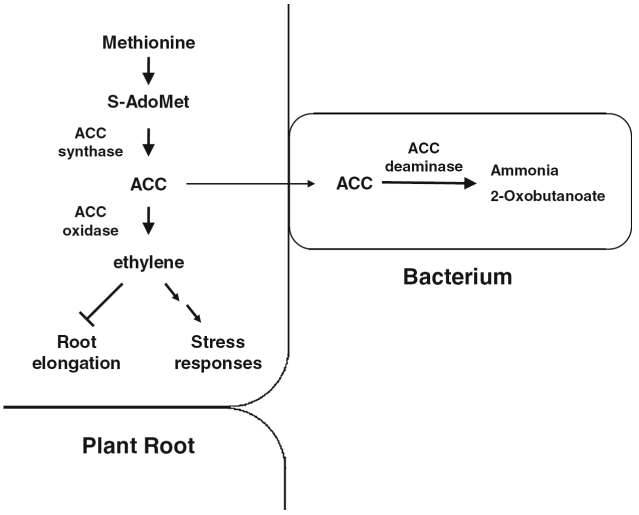

Figure 6 A possible mechanism of how stress controller bacteria reduce ethylene levels in the plant root using bacterial ACC deaminase. ACC synthesized in plant tissues by ACC synthase is thought be exuded from plant roots and be taken up by neighboring bacteria. Subsequently, the bacteria hydrolyze ACC to ammonia and 2-oxobutanoate. This ACC hydrolysis maintains ACC concentrations low in bacteria and permits continuous ACC transfer from plant roots to bacteria. Otherwise, ethylene can be produced from ACC and then cause stress responses including growth inhibition. S-AdoMet: S-adenosyl-L-methionine; ACC: 1-aminocyclopropane-1-carboxylate (Adapted from Kang et al. (2010)).

Table 3 Examples of plant growth promoting rhizobacteria tested for various crop types.

PGPR	Plant	Conditions	Results of addition of bacteria to plants	Reference
Pseudomonas putida, Azospirilium, Azotobacter	Artichoke (*Cynara scolymus*)	In vitro	Phosphate solublizing bacteria along with nitrogen fixing bacteria led to significant increase in radicle and shoot length, shoot weight, coefficient of velocity of germination, seedling vigority index, and significant decrease in mean time of germination	Jahanian et al. (2012)
Pseudomonas sp. PS1	Greengram (*Vigna radiata* (L.) wilczek)	Pots	Significantly increased plant dry weight, nodule nubers, total chlorophyll content, leghaemoglobin, root N, shoot N, root P, shoot P, seed yield and seed protein	Ahemad and Khan (2012e), Ahemad and Khan (2011k) and Ahemad and Khan (2010d)
Bradyrhizobium MRM6	Greengram (*Vigna radiata* (L.) wilczek)	Pots	When herbicide tolerant Rhizobium strain MRP1 was used with herbicide, it increased the growth parameters at all tested concentrations of herbicides (quizalafop-p-ethyl and clodinafop)	Ahemad and Khan (2012f) and Ahemad and Khan (2011h,l)
Pseudomonas sp. A3R3	*Alyssum serpyllifolium, Brassica juncea*	Pots	Increased significantly the biomass (*B. juncea*) and Ni content (*A. serpyllifolium*) in plants grown in Ni-stressed soil	Ma et al. (2011a)
Pseudomonas sp.	Soybean, wheat	Fields	Significantly increased soil enzyme activities, total productivity, and nutrient uptake	Sharma et al. (2011)
Psychrobacter sp. SRS8	*Ricinus communis, Helianthus annuus*	Pots	Stimulated plant growth and Ni accumulation in both plant species with increased plant biomass, chlorophyll, and protein content	Ma et al. (2011b)
Rhizobium strain MRP1	Pea (*Pisum sativum*)	Pots	Significantly increased the growth, symbiotic properties (nodulation and leghaemoglobin content), amount of N and P nutrients in plant organs, seed yield and seed protein of pea plants	Ahemad and Khan (2011i), Ahemad and Khan (2010c) and Ahemad and Khan (2009b)
Rhizobium phaseoli	*Vigna radiata* L.	Pots	In the presence of tryptophan, Rhizobium mitigated the adverse effects of salinity and increased the plant height, number of nodules per plant, plant biomass, grain yield, and grain nitrogen concentration significantly.	Zahir et al. (2010)
Bacillus species PSB10	Chickpea (*Cicer arietinum*)	Pots	Significantly improved growth, nodulation, chlorophyll, leghaemoglobin, seed yield and grain protein; reduced the uptake of chromium in roots, shoots and grains	Wani and Khan (2010)
Mesorhizobium strain MRC4	Chickpea (Cicer arietinum)	Pots	Significantly increased symbiotic properties (nodulation and leghaemoglobin content), root N, shoot N, root P, shoot P, seed yield and seed protein	Ahemad and Khan (2010e,h) and Ahemad and Khan (2009a)
Rhizobium strain MRL3	Lentil (*Lens esculentus*)	Pots	Significantly increased symbiotic properties (nodulation and leghaemoglobin content), root N, shoot N, root P, shoot P, seed yield and seed protein	Ahemad and Khan (2011j), Ahemad and Khan (2010f,g)

Table 3 (*Continued*)

PGPR	Plant	Conditions	Results of addition of bacteria to plants	Reference
Bradyrhizobium sp. 750, *Pseudomonas* sp., *Ochrobactrum cytisi*	*Lupinus luteus*	Fields	Increased both biomass, nitrogen content, accumulation of metals (improved phytostabilisation potential)	Dary et al. (2010)
Paenibacillus polymyxa	Pepper	Gnotobiotic conditions	Significantly increased the biomass of plants and elicited induced systemic resistance against bacterial spot pathogen *Xanthomonas axonopodis* pv. *vesicatoria* untreated plants.	Phi et al. (2010)
Pseudomnas putida strain R-168, *Pseudomonas fluorescens* strain R-93, *Pseudomonas fluorescens* DSM 50090, *Pseudomonas putida* DSM291, *Azospirillum lipoferum* DSM 1691, *Azospirillum brasilense* DSM 1690	Maize (*Zea mays* L.)	Fields	Plant height, seed weight, number of seed per ear and leaf area, shoot dry weight significantly increased	Gholami et al. (2009)
Pseudomonas sp. SRI2, *Psychrobacter* sp. SRS8, *Bacillus* sp. SN9	*Brassica juncea*, *Brassica oxyrrhina*	Pots	Increased the biomass of the test plants and enhanced Ni accumulation in plant tissues	Ma et al. (2009a)
Psychrobacter sp. SRA1, *Bacillus cereus* SRA10	*Brassica juncea*, *Brassica oxyrrhina*	Pots	Enhanced the metal accumulation in plant tissues by facilitating the release of Ni from the non-soluble phases in the soil	Ma et al. (2009b)
Achromobacter xylosoxidans strain Ax10	*Brassica juncea*	Pots	Significantly improved Cu uptake by plants and increased the root length, shoot length, fresh weight and dry weight of plants	Ma et al. (2009c)
Pseudomonas aeruginosa, Pseudomonas fluorescens, Ralstonia metallidurans	Maize	Pots	Promoted plant growth, facilitated soil metal mobilization, enhanced Cr and Pb uptake	Braud et al. (2009)
Klebsiella pneumonia	*Triticum aestivum*	Pots	Significantly increased the root length and shoot length	Sachdev et al. (2009)
Pseudomonas sp.	Chickpea	Pots	Enhanced fresh and dry weight of plants even at 2 mM nickel concentration	Tank and Saraf (2009)
Azospirillum amazonense	Rice (*Oryza sativa* L.)	Greenhouse	Grain dry matter accumulation (7–11.6%), the number of panicles (3–18.6%) and nitrogen accumulation at grain maturation (3.5–18.5%) increased	Rodrigues et al. (2008)
Pseudomonas species	Rice (Oryza sativa), maize (Zea mays)	In vitro	Pseudomonad isolated from rice showed a higher ability to control bacterial and fungal root pathogens than that obtained from maize	Lawongsa et al. (2008)
Pseudomonas aeruginosa strain MKRh3	Black gram	Pots	Plants showed lessened cadmium accumulation, extensive rooting, and enhanced plant growth	Ganesan (2008)

Table 3 (*Continued*)

PGPR	Plant	Conditions	Results of addition of bacteria to plants	Reference
Mesorhizobium sp. RC3	Chickpea (Cicer arietinum)	Pots	Increased the dry matter accumulation, number of nodules, seed yield and grain protein by 71%, 86%, 36% and 16%, respectively, compared to noninoculated plants. Nitrogen in roots and shoots increased by 46% and 40%, respectively, at 136 mg Cr/kg	Wani et al. (2008)
Pseudomonas aeruginosa	Indian mustard and pumpkin	Pots	Stimulated plant growth, reduced Cd uptake	Sinha and Mukherjee (2008)
Bacillus weihenstephanensis strain SM3	*Helianthus annuus*	Pots	Increased plant biomass and the accumulation of Cu and Zn in the root and shoot systems, also augmented the concentrations of water soluble Ni, Cu and Zn in soil with their metal mobilizing potential	Rajkumar et al. (2008)
Azospirillum brasilense Sp245	Common bean (*Phaseolus vulgaris* L.)	Greenhouse	Root growth increased	Remans et al. (2008)
Bacillus sp. *Paenibacillus* sp.	Rice	Pots	Promoted significantly the root and shoot growth	Beneduzi et al. (2008)
Bacillus edaphicus	Indian mustard (*Brassica juncea*)	Pots	Stimulated plant growth, facilitated soil Pb mobilization, enhanced Pb accumulation	Sheng et al. (2008)
Bacillus subtilis, Pseudomonas aeruginosa	*Solanum lycopersicum* L. (tomato), *Abelmoschus esculentus* (okra), *Amaranthus* sp. (African spinach)	Greenhouse	Dry biomass increased 31% for tomato, 36% for okra, and 83% for African spinach	Adesemoye et al. (2008)
Pseudomonas tolaasii ACC23, *Pseudomonas fluorescens* ACC9, *Alcaligenes* sp. ZN4, *Mycobacterium* sp. ACC14	*Brassica napus*	Pots	Protected canola plant against the inhibitory effects of cadmium	Dell'Amico et al. (2008)
Azotobacter chroococcum, Azospirillum lipoferum	Cotton (*Gossypium hirsutum* L.)	Fields	Seed yield (21%), plant height (5%) and microbial population in soil (41%) increased over their respective controls while boll weight and staple length remained statistically unaffected	Anjum et al. (2007)
Bradyrhizobium sp. (vigna) RM8	Greengram (*Vigna radiate*)	Pots	Enhanced the nodule numbers by 82%, leghaemoglobin by 120%, seed yield by 34%, grain protein by 13%, root N by 41% and shoot N by 37% at 290 mg Ni/kg soil	Wani et al. (2007a)

Table 3 (*Continued*)

PGPR	Plant	Conditions	Results of addition of bacteria to plants	Reference
Rhizobium sp. RP5	Pea (*Pisum sativum*)	Pots	Enhanced the dry matter, nodule numbers, root N, shoot N, leghaemoglobin, seed yield, and grain protein by 19%, 23%, 26%, 47%, 112%, 26%, and 8%, respectively, at 290 mg Ni/kg	Wani et al. (2007b)
Pseudomonas putida CC-R2-4, *Bacillus subtilis* CC-pg104	*Lectuca sativa* L.	Gnotobiotic conditions	Significant increase in shoot length and root length achieved through encapsulated inoculant	Rekha et al. (2007)
Methylobacterium oryzae, Berkholderia sp.	*Lycopersicon esculentom*	Gnotobiotic conditions, pots	–	Madhaiyan et al. (2007)
Bacillus spp.	Barley (*Hordeum vulgare*)	Greenhouse	Increased root weight up to 16.7% and shoot weight up to 347%	Canbolat et al. (2006)
Sinorhizobium sp. Pb002	*Brassica juncea*	Microcosms	Increased the efficiency of lead phytoextraction by *B. juncea* plants	Di Gregorio et al. (2006)
Brevibacillus	*Trifolium repens*	Pots	Enhanced plant growth and nutrition of plants and decreased zinc concentration in plant tissues	Vivas et al. (2006)
Xanthomonas sp. RJ3, *Azomonas* sp. RJ4, *Pseudomonas* sp. RJ10, *Bacillus* sp. RJ31	*Brassica napus*	Pots	Stimulated plant growth and increased cadmium accumulation	Sheng and Xia (2006)
Pseudomonas sp, *Bacillus* sp.	Mustard	Pots	Stimulated plant growth and decreased Cr (VI) content	Rajkumar et al. (2006)
Ochrobactrum, Bacillus cereus	Mungbean	Pots	Lowers the toxicity of chromium to seedlings by reducing Cr (VI) to Cr (III)	Faisal and Hasnain (2006)
Pseudomonas jessenii PS06, *Mesorhizobium ciceri* C-2/2	*Cicer arietinum* (chickpea)	Greenhouse, fields	The co-inoculation treatment increased the seed yield (52% greater than the uninoculated control treatment) and nodule fresh weight	Valverde et al. (2006)
Azotobacter chroococcum HKN-5, *Bacillus megaterium* HKP-1, *Bacillus mucillaginosus* HKK-1	*Brassica Juncea*	Greenhouse	Protected plant from metal toxicity, stimulated plant growth	Wu et al. (2006)
Bacillus subtilis SJ-101	*Brassica Juncea*	Growth chamber	Facilitated Ni accumulation	Zaidi et al. (2006)
Pseudomonas putida KNP9	Mung bean	Greenhouse	Stimulated the plant growth, reduced Pb and Cd uptake	Tripathi et al. (2005)
Rhizobacterial strains A3 and S32	*Brassica juncea*	Pots	Promoted the plant growth under chromium stress	Rajkumar et al. (2005)
Pseudomas fluorescens	Soybean	Greenhouse	Increased plant growth	Gupta et al. (2005)
Ochrobactrum intermedium	Sunflower	Pots	Increased plant growth and decreased Cr(VI) uptake	Faisal and Hasnain (2005)
Variovox paradoxus, Rhodococcus sp, *Flavobacterium*	*Brassica juncea*	In vitro	Stimulating root elongation	Belimov et al. (2005)
Azospirillum brasilense, Bacillus pantothenticus, Pseudomonas pieketti	Rice (Oryza sativa)	Micro-plots	Increased rice grain yield maximum up to 76.9%	Thakuria et al. (2004)
Pseudomonas fluorescens PGPR1, PGPR2, PGPR4	Peanut (*Arachis hypogaea* L.)	Pots, fields	Significantly enhanced pod yield, haulm yield and nodule dry weight over the control	Dey et al. (2004)
Unidentified PGPR isolate	Wheat	Gnotobiotic conditions	Increases in root elongation (up to 17.3%), root dry weight (up to 13.5%), shoot elongation (up to 37.7%) and shoot dry weight (up to 36.3%) in inoculated wheat seedlings	Khalid et al. (2004)

Table 3 (*Continued*)

PGPR	Plant	Conditions	Results of addition of bacteria to plants	Reference
Pseudomonas fluorescens Avm, *Rhizobium leguminosarum* bv *phaseoli* CPMex46	Alfalfa	Growth chamber	Improved Cu and Fe translocation from root to shoot	Carrillo-Castaneda et al. (2003)
Enterobacter sakazakii 8MR5, *Pseudomonas* sp. 4MKS8, *Klebsiella oxytoca* 10MKR7	*Zea mays* L. (maize)	Pots	Inoculation increased growth parameters	Babalola et al. (2003)
Pseudomonas sp.	Soybean, mungbean, wheat	Pots	Promotes growth of plants	Gupta et al. (2002)
Enterobacter cloacae	*Brassica napus*	Pots	Both root and shoot length significantly increased.	Saleh and Glick (2001)
Brevundimonas Kro13	–	Culture media	Sequestered cadmium directly from solution	Robinson et al. (2001)
Kluyvera ascorbata SUD165	Indian mustard, canola, tomato	Growth chamber	Both strains decreased some plant growth inhibition by heavy metals, No increase of metal uptake with either strain over non-inoculated plants	Burd et al. (2000)
Pseudomonas putida	*Vigna radiata* L. (mungbean)	Pots	The ethylene production inhibited in the inoculated plants	Mayak et al. (1999)

mole of reduced nitrogen, it would be advantageous if bacterial carbon resources were directed toward oxidative phosphorylation, which results in the synthesis of ATP, rather than glycogen synthesis, which results in the storage of energy in the form of glycogen (Glick, 2012). For instance, treatment of legume plants with rhizobia having a deleted gene for glycogen synthase resulted in a considerable augmentation in both the nodule number and plant dry weight with reference to treatment with the wild-type strain (Marroqui et al., 2001).

4.1.2. Phosphate solubilization

Phosphorus (P), the second important plant growth-limiting nutrient after nitrogen, is abundantly available in soils in both organic and inorganic forms (Fig. 3) (Khan et al., 2009). Despite of large reservoir of P, the amount of available forms to plants is generally low. This low availability of phosphorous to plants is because the majority of soil P is found in insoluble forms, while the plants absorb it only in two soluble forms, the monobasic ($H_2PO_4^-$) and the diabasic (HPO_4^{2-}) ions (Bhattacharyya and Jha, 2012). The insoluble P is present as an inorganic mineral such as apatite or as one of several organic forms including inositol phosphate (soil phytate), phosphomonesters, and phosphotriesters (Glick, 2012). To overcome the P deficiency in soils, there are frequent applications of phosphatic fertilizers in agricultural fields. Plants absorb fewer amounts of applied phosphatic fertilizers and the rest is rapidly converted into insoluble complexes in the soil (Mckenzie and Roberts, 1990). But regular application of phosphate fertilizers is not only costly but is also environmentally undesirable. This has led to search for an ecologically safe and economically reasonable option for improving crop production in low P soils. In this context, organisms coupled with phosphate solubilizing activity, often termed as phosphate solubilizing microorganisms (PSM), may provide the available forms of P to the plants and hence a viable substitute to chemical phosphatic fertilizers (Khan et al., 2006). Of the various PSM(s) inhabiting the rhizosphere, phosphate-solubilizing bacteria (PSB) are considered as promising biofertilizers since they can supply plants with P from sources otherwise poorly available by various mechanisms (Fig. 4) (Zaidi et al., 2009). Bacterial genera like *Azotobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas*, *Rhizobium* and *Serratia* are reported as the most significant phosphate solubilizing bacteria (Bhattacharyya and Jha, 2012). Typically, the solubilization of inorganic phosphorus occurs as a consequence of the action of low molecular weight organic acids which are synthesized by various soil bacteria (Zaidi et al., 2009). Conversely, the mineralization of organic phosphorus occurs through the synthesis of a variety of different phosphatases, catalyzing the hydrolysis of phosphoric esters (Glick, 2012). Importantly, phosphate solubilization and mineralization can coexist in the same bacterial strain (Tao et al., 2008).

Though, PSB are commonly found in most soils; their establishment and performances are severely affected by environmental factors especially under stress conditions (Ahemad and Khan, 2012a,e; Ahemad and Khan, 2010a,b). However, the beneficial effects of the inoculation with PSB used alone (Ahemad and Khan, 2012e; Ahemad and Khan, 2011k; Ahemad and Khan, 2010d; Poonguzhali et al., 2008; Chen

et al., 2008) or in combination with other rhizospheric microbes have been reported (Zaidi and Khan, 2005; Vikram and Hamzehzarghani, 2008). Besides providing P to the plants, the phosphate solubilizing bacteria also augment the growth of plants by stimulating the efficiency of BNF, enhancing the availability of other trace elements by synthesizing important plant growth promoting substances (Suman et al., 2001; Ahmad et al., 2008; Zaidi et al., 2009) (Table 2).

4.1.3. Siderophore production

Iron is a vital nutrient for almost all forms of life. All microorganisms known hitherto, with the exception of certain lactobacilli, essentially require iron (Neilands, 1995). In the aerobic environment, iron occurs principally as Fe^{3+} and is likely to form insoluble hydroxides and oxyhydroxides, thus making it generally inaccessible to both plants and microorganisms (Rajkumar et al., 2010). Commonly, bacteria acquire iron by the secretion of low-molecular mass iron chelators referred to as siderophores which have high association constants for complexing iron. Most of the siderophores are water-soluble and can be divided into extracellular siderophores and intracellular siderophores. Generally, rhizobacteria differs regarding the siderophore cross-utilizing ability; some are proficient in using siderophores of the same genus (homologous siderophores) while others could utilize those produced by other rhizobacteria of different genera (heterologous siderophores) (Khan et al., 2009). In both Gram-negative and Gram-positive rhizobacteria, iron (Fe^{3+}) in Fe^{3+}-siderophore complex on bacterial membrane is reduced to Fe^{2+} which is further released into the cell from the siderophore via a gating mechanism linking the inner and outer membranes. During this reduction process, the siderophore may be destroyed/recycled (Rajkumar et al., 2010; Neilands, 1995). Thus, siderophores act as solubilizing agents for iron from minerals or organic compounds under conditions of iron limitation (Indiragandhi et al., 2008). Not only iron, siderophores also form stable complexes with other heavy metals that are of environmental concern, such as Al, Cd, Cu, Ga, In, Pb and Zn, as well as with radionuclides including U and Np (Neubauer et al., 2000; Kiss and Farkas, 1998). Binding of the siderophore to a metal increases the soluble metal concentration (Rajkumar et al., 2010). Hence, bacterial siderophores help to alleviate the stresses imposed on plants by high soil levels of heavy metals.

Plants assimilate iron from bacterial siderophores by means of different mechanisms, for instance, chelate and release of iron, the direct uptake of siderophore-Fe complexes, or by a ligand exchange reaction (Schmidt, 1999). Numerous studies of the plant growth promotion vis-à-vis siderophore-mediated Fe-uptake as a result of siderophore producing rhizobacterial inoculations have been reported (Rajkumar et al., 2010). For example, Crowley and Kraemer (2007) revealed a siderophore mediated iron transport system in oat plants and inferred that siderophores produced by rhizosphere microorganisms deliver iron to oat, which has mechanisms for using Fe-siderophore complexes under iron-limited conditions. Similarly, the Fe-pyoverdine complex synthesized by *Pseudomonas fluorescens* C7 was taken up by *Arabidopsis thaliana* plants, leading to an increase of iron inside plant tissues and to improved plant growth (Vansuyt et al., 2007). Recently, Sharma et al. (2003) assessed the role of the siderophore-producing *Pseudomonas* strain GRP3 on iron nutrition of *Vigna radiate*. After 45 days, the plants showed a decline in chlorotic symptoms and iron, chlorophyll a and chlorophyll b content increased in strain GRP3 inoculated plants compared to control.

4.1.4. Phytohormone production

Microbial synthesis of the phytohormone auxin (indole-3-acetic acid/indole acetic acid/IAA) has been known for a long time. It is reported that 80% of microorganisms isolated from the rhizosphere of various crops possess the ability to synthesize and release auxins as secondary metabolites (Patten and Glick, 1996). Generally, IAA secreted by rhizobacteria interferes with the many plant developmental processes because the endogenous pool of plant IAA may be altered by the acquisition of IAA that has been secreted by soil bacteria (Glick, 2012; Spaepen et al., 2007). Evidently, IAA also acts as a reciprocal signaling molecule affecting gene expression in several microorganisms. Consequently, IAA plays a very important role in rhizobacteria-plant interactions (Spaepen and Vanderleyden, 2011). Moreover, down-regulation of IAA as signaling is associated with the plant defense mechanisms against a number of phyto-pathogenic bacteria as evidenced in enhanced susceptibility of plants to the bacterial pathogen by exogenous application of IAA or IAA produced by the pathogen (Spaepen and Vanderleyden, 2011). IAA has been implicated in virtually every aspect of plant growth and development, as well as defense responses. This diversity of function is reflected by the extraordinary complexity of IAA biosynthetic, transport and signaling pathways (Santner et al., 2009). Generally, IAA affects plant cell division, extension, and differentiation; stimulates seed and tuber germination; increases the rate of xylem and root development; controls processes of vegetative growth; initiates lateral and adventitious root formation; mediates responses to light, gravity and florescence; affects photosynthesis, pigment formation, biosynthesis of various metabolites, and resistance to stressful conditions. IAA produced by rhizobacteria likely, interfere the above physiological processes of plants by changing the plant auxin pool. Moreover, bacterial IAA increases root surface area and length, and thereby provides the plant greater access to soil nutrients. Also, rhizobacterial IAA loosens plant cell walls and as a result facilitates an increasing amount of root exudation that provides additional nutrients to support the growth of rhizosphere bacteria (Glick, 2012). Thus, rhizobacterial IAA is identified as an effector molecule in plant–microbe interactions, both in pathogenesis and phytostimulation (Spaepen and Vanderleyden, 2011).

An important molecule that alters the level of IAA synthesis is the amino acid tryptophan, identified as the main precursor for IAA and thus plays a role in modulating the level of IAA biosynthesis (Zaidi et al., 2009). Strangely, tryptophan stimulates IAA production while, anthranilate, a precursor for tryptophan, reduces IAA synthesis. By this mechanism, IAA biosynthesis is fine-tuned because tryptophan inhibits anthranilate formation by a negative feedback regulation on the anthranilate synthase, resulting in an indirect induction of IAA production (Spaepen et al., 2007). However, supplementation of culture media with tryptophan increases the IAA production by most of the rhizobacteria (Spaepen and Vanderleyden, 2011). Biosynthesis of tryptophan starts from the metabolic node chorismate in a five-step reaction encoded by the *trp* genes. The branch point compound chorismate is synthesized starting from phosphoenolpyruvate and erythrose 4-phosphate in the shikimate pathway, a common pathway for

the biosynthesis of aromatic amino acids and many secondary metabolites (Spaepen and Vanderleyden, 2011; Merino et al., 2008; Dosselaere and Vanderleyden, 2001). Starting with tryptophan, at least five different pathways have been described for the synthesis of IAA, and most pathways show similarity to those described in plants, although some intermediates can differ (Fig. 5) (Spaepen and Vanderleyden, 2011; Patten and Glick, 1996): (1) IAA formation via indole-3-pyruvic acid and indole-3-acetic aldehyde is found in a majority of bacteria like, *Erwinia herbicola*; saprophytic species of the genera *Agrobacterium* and *Pseudomonas*; certain representatives of *Bradyrhizobium, Rhizobium, Azospirillum, Klebsiella*, and *Enterobacter*, (2) The conversion of tryptophan into indole-3-acetic aldehyde may involve an alternative pathway in which tryptamine is formed as in pseudomonads and azospirilla and (3) IAA biosynthesis via indole-3-acetamide formation is reported for phytopathogenic bacteria *Agrobacterium tumefaciens, Pseudomonas syringae*, and *E. herbicola*; saprophytic pseudomonads like (e.g. *Pseudomonas putida* and *P. fluorescens*). (4) IAA biosynthesis that involves tryptophan conversion into indole-3-acetonitrile is found in the cyanobacterium (*Synechocystis* sp.) and (5) the tryptophan-independent pathway, more common in plants, is also found in azospirilla and cyanobacteria.

Most *Rhizobium* species have been shown to produce IAA (Ahemad and Khan, 2012b,d,f; Ahemad and Khan, 2011e, j). Since, IAA is involved in multiple processes including cell division, differentiation and vascular bundle formation, these three processes are also essential for nodule formation. Hence, it seems likely that auxin levels in the host legume plants are necessary for nodule formation (Glick, 2012; Spaepen et al., 2007). It is also reported that the inoculation with *Rhizobium leguminosarum* bv. *viciae* wherein the IAA biosynthetic pathway had been introduced, produced potential nitrogen fixing root nodules containing up to 60-fold more IAA than nodules formed by the wild-type counterpart in *Vicia hirsute* (Camerini et al., 2008). Environmental stress factors which modulate the IAA biosynthesis in different bacteria include acidic pH, osmotic and matrix stress, and carbon limitation (Spaepen et al., 2007). Among genetic factors, both the location of auxin biosynthesis genes in the bacterial genome (either plasmid or chromosomal) and the mode of expression (constitutive vs. induced) have been shown to affect the level of IAA production. The location of auxin biosynthesis genes can affect the IAA level, as plasmids are mostly present in multiple copies. This can be illustrated by the difference in the IAA level between the rhizobacterial strains, *Pseudomonas savastanoi* pv. *savastanoi* and *P. syringae* pv. *syringae*. In the former strain, the genes for auxin biosynthesis genes are present on a plasmid, while in the latter one the corresponding genes are located on the chromosomal DNA, resulting in a lower IAA production. The IAA production in *P. syringae* pv. *Syringae* could be increased many fold by introducing a low-copy plasmid, carrying the IAA biosynthetic operon (Spaepen and Vanderleyden, 2011; Spaepen et al., 2007; Brandl and Lindow, 1997; Patten and Glick, 1996).

4.1.5. 1-Aminocyclopropane-1-carboxylate (ACC) deaminase

Generally, ethylene is an essential metabolite for the normal growth and development of plants (Khalid et al. 2006). This plant growth hormone is produced endogenously by approximately all plants and is also produced by different biotic and abiotic processes in soils and is important in inducing multifarious physiological changes in plants. Apart from being a plant growth regulator, ethylene has also been established as a stress hormone (Saleem et al., 2007). Under stress conditions like those generated by salinity, drought, water logging, heavy metals and pathogenicity, the endogenous level of ethylene is significantly increased which negatively affects the overall plant growth. For instance, the high concentration of ethylene induces defoliation and other cellular processes that may lead to reduced crop performance (Saleem et al., 2007; Bhattacharyya and Jha, 2012). Plant growth promoting rhizobacteria which possess the enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, facilitate plant growth and development by decreasing ethylene levels, inducing salt tolerance and reducing drought stress in plants (Nadeem et al., 2007; Zahir et al., 2008). Currently, bacterial strains exhibiting ACC deaminase activity have been identified in a wide range of genera such as *Acinetobacter*, *Achromobacter*, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia* and *Rhizobium* etc. (Shaharoona et al., 2007a,b; Nadeem et al., 2007; Zahir et al., 2008; Zahir et al., 2009; Kang et al., 2010). Such rhizobacteria take up the ethylene precursor ACC and convert it into 2-oxobutanoate and NH_3 (Arshad et al., 2007) (Fig. 6). Several forms of stress are relieved by ACC deaminase producers, such as effects of phytopathogenic microorganisms (viruses, bacteria, and fungi etc.), and resistance to stress from polyaromatic hydrocarbons, heavy metals, radiation, wounding, insect predation, high salt concentration, draft, extremes of temperature, high light intensity, and flooding (Glick, 2012; Lugtenberg and Kamilova, 2009). As a result, the major noticeable effects of seed/ root inoculation with ACC deaminase-producing rhizobacteria are the plant root elongation, promotion of shoot growth, and enhancement in rhizobial nodulation and N, P and K uptake as well as mycorrhizal colonization in various crops (Nadeem et al., 2007; Shaharoona et al., 2008; Nadeem et al., 2009; Glick, 2012).

4.2. Indirect mechanisms

The application of microorganisms to control diseases, which is a form of biological control, is an environment-friendly approach (Lugtenberg and Kamilova, 2009). The major indirect mechanism of plant growth promotion in rhizobacteria is through acting as biocontrol agents (Glick, 2012). In general, competition for nutrients, niche exclusion, induced systemic resistance and antifungal metabolites production are the chief modes of biocontrol activity in PGPR (Lugtenberg and Kamilova, 2009). Many rhizobacteria have been reported to produce antifungal metabolites like, HCN, phenazines, pyrrolnitrin, 2,4-diacetylphloroglucinol, pyoluteorin, viscosinamide and tensin (Bhattacharyya and Jha, 2012). Interaction of some rhizobacteria with the plant roots can result in plant resistance against some pathogenic bacteria, fungi, and viruses. This phenomenon is called induced systemic resistance (ISR) (Lugtenberg and Kamilova, 2009). Moreover, ISR involves jasmonate and ethylene signaling within the plant and these hormones stimulate the host plant's defense responses against a variety of plant pathogens (Glick, 2012). Many individual bacterial components induce ISR, such as lipopolysaccharides (LPS), flagella, siderophores, cyclic lipopeptides,

2,4-diacetylphloroglucinol, homoserine lactones, and volatiles like, acetoin and 2,3-butanediol (Lugtenberg and Kamilova, 2009).

5. Applications of PGPR as multifunctional agents

The effect of PGPR in crop productivity varies under laboratory, greenhouse and field trials. Because, soil is an unpredictable environment and an intended result is sometimes difficult to achieve. Climatic variations also have a large impact on the effectiveness of PGPR but sometimes unfavorable growth conditions in the field are to be expected as normal functioning of agriculture (Zaidi et al., 2009). Plant growth promoting traits do not work independently of each other but additively as it was suggested in the "additive hypothesis," that multiple mechanisms, such as phosphate solubilization, dinitrogen fixation, ACC deaminase and antifungal activity, IAA and siderophore biosynthesis etc. are responsible for the plant growth promotion and increased yield (Bashan and Holguin, 1997). Under both natural agro-ecological niches and controlled soil environments, significant increase in yields of different crop plants has been observed following PGPR applications (Table 3). Due to the existing reluctance worldwide to embrace foods produced by genetically modified plants, PGPR may be advantageous as a means of promoting plant growth. The wide scale application of PGPR may decrease the global dependence on agricultural chemicals. Furthermore, it is a technology which is readily accessible to farmers in both developed and developing countries (Gamalero et al., 2009).

6. Conclusion

Plant growth promoting rhizobacteria, having multiple activities directed toward plant growth promotion vis-à-vis exhibiting bioremediating potentials by detoxifying pollutants like, heavy metals and pesticides and controlling a range of phytopathogens as biopesticides, have shown spectacular results in different crop studies. The productive efficiency of a specific PGPR may be further enhanced with the optimization and acclimatization according to the prevailing soil conditions. In future, they are expected to replace the chemical fertilizers, pesticides and artificial growth regulators which have numerous side-effects to sustainable agriculture. Further research and understanding of mechanisms of PGPR mediated-phytostimulation would pave the way to find out more competent rhizobacterial strains which may work under diverse agro-ecological conditions.

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