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Plant Growth-Promoting Rhizobacteria (PGPR) and Their Action Mechanisms in Availability of Nutrients to Plants

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Abstract

One of the main obstacles to plant growth is the lack of the availability of nutrient elements in many agricultural environments in the world, especially the tropics where soils can be extremely low in nutrients. Using different mechanisms of action, plant growth-promoting rhizobacteria (PGPR) participate in geochemical nutrition cycles and determine their access to plants and the microbial community of the soil. Use of these bacteria as bio-inoculants will increase the availability of nutrient elements in soil, help to minimize the chemical fertilizer application, reduce environmental pollution, and promote sustainable agriculture. Considering comprehensive reviews previously published on plant growth enhancement mechanisms, this review focuses on what is known about the action mechanisms underlying the increase of the availability of nutrient elements as an effect of microbial colonization especially PGPR. In this chapter, some of the most important mechanisms and processes regarding the effects of PGPR on the availability and hence uptake of nutrient elements by plant are reviewed. The awareness of such mechanisms can be important for the selection and hence production of microbial inoculums, which are appropriate for biological fertilization as substituting or decreasing the need of using chemical fertilizers in crops. In this review, special consideration is given to the role of PGPR in the availability of nitrogen (N), phosphorus (P), potassium (K), and sulfur (S) as macronutrients and iron (Fe) and manganese (Mn) as micronutrients.

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9.1 Introduction

Many of the plant-related microorganisms are known for their ability to promote plant growth (Compant et al. 2010). Plants produce a wide range of organic compounds between 6% and 21% of the carbon fixed including sugars (such as glucose, xylose, fructose, maltose, sucrose, and ribose), organic acids (such as citric, malic, lactic, succinic, oxalic, and pyruvic acids), amino acids, fatty acids, nucleotides, putrescine, and vitamins, which can be used as nutrients or signals by microbial populations. These signal molecules can also be used to link plants and microbes (Lugtenberg 2015). Plant-associated microorganisms, on the other hand, regulate the growth and morphogenesis of plant or activate plant immunity by releasing small molecules or volatile compounds and phytohormones (Ortíz-Castro et al. 2009). Symbionts, pathogens, epiphytes, or endophytes are four ways in which microorganisms are associated with plants (Iniguez et al. 2005). The microorganisms can colonize different parts of the plant, which are grouped into three groups based on their colonization area: rhizosphere (in the vicinity of root) microorganisms, rhizoplane (on the surface of root) microorganisms, and endophytic microorganisms. Endophytes are plant-associated microorganisms that are isolated from the tissues that reside without damage to the host (Andrews and Harris 2000), while those isolated from rhizoplane and phylloplane surfaces are called epiphytes (Azevedo et al. 2000; Petrini et al. 1989; Sturz et al. 2000). There are three basic types of ecological based microbial interactions: the neutral, negative, and positive interaction that is commonly found between microorganisms and plants (Whipps 2001). Most microorganisms are commensals in which the microorganisms interact safely with host plants that have no significant effects on the overall host's growth and physiology (Beattie 2007). In negative interactions, phytopathogenic microorganisms produce phytotoxic substances such as hydrogen cyanide (HCN) or ethylene, which negatively affects plant growth and physiology (Khalid et al. 2004). In contrast to these deleterious microorganisms, some of these microorganisms can promote plant growth and development either directly or indirectly (Glick 2012a, 2014, 2015a, b). Soil bacteria that are useful for plant growth by colonizing the plant root are commonly referred to as plant growth-promoting rhizobacteria (PGPR) (Hayat et al. 2010). Majority of credible group of PGPRs belong to genera *Frankia*, *Acinetobacter*, *Arthrobacter*, *Azotobacter*, *Azospirillum Streptomyces* spp., *Bacillus*, *Enterobacter*, *Burkholderia*, *Bradyrhizobium*, *Rhizobium*, *Serratia*, *Thiobacillus*, and *Pseudomonas* (Dimkpa et al. 2009; Gray and Smith 2005; Vessey 2003). It has been reported that PGPRs are beneficial to plants in various ways (Hayat et al. 2010; Lugtenberg and Kamilova 2009; Paul 2012). Although the precise mechanisms of stimulating plant growth remain largely speculative, a possible explanation includes (i) improving soil structure and bioremediating the polluted soils by sequestering toxic heavy metal species and degrading xenobiotic compounds; (ii) improving abiotic stress resistance; (iii) biological nitrogen fixation (BNF); (iv) producing numerous plant growth regulators, like abscisic acid (ABA), gibberellic acid (GA), cytokinins (CK), and auxin, *i.e.*, indole-3-acetic acid (IAA); (v) solubilization and mineralization of nutrients, particularly mineral phosphate; (vi) protecting plants from phytopathogens by controlling or inhibiting them like antibiotic production, production of siderophores, induction of systemic resistance, chelation of available Fe in the rhizosphere, synthesis of extracellular enzymes to hydrolyze the fungal cell wall, and competition for niches within the rhizosphere; (vii) producing siderophores; and (viii) reducing the level of ethylene in the root of developing plants by production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Braud et al. 2009; Hayat et al. 2010).

In all, plants require 17 essential elements, 14 of which are taken up in inorganic forms by the roots. The absence or paucity of any one of these essential elements will commonly lead to plant death or inability to complete its life cycle. In the presence of nutrient deficiencies, even at asymptomatic levels, performance of crop, yield, and quality of crop are often at risk (Jewell et al. 2010). Since the nutrients in soils are generally bound to inorganic and organic soil constituents, or alternatively present as insoluble precipitates, plenty of nutrients are not available to plants for root absorption. PGPR play an essential role in the environment by contributing to the release of key nutrients from primary minerals that are required not only for their own nutrition but also for that of plants (Uroz et al. 2009). Use of these bacteria as bio-inoculants will increase the availability of nutrients in soil, help to minimize the chemical fertilizer application, reduce environmental pollution, and promote sustainable agriculture. PGPR have been proved to be vital for circulation of plant nutrients in many ways. Researchers are studying these microbes for the past 30 years to understand the action mechanisms employed by PGPR to support plant growth. Awareness of the mechanisms operated by these bacteria in promoting plant growth is a prerequisite for the development of new management strategies for sustainable agriculture. In the following, some of the most important mechanisms and processes regarding the effects of PGPR on the availability and hence uptake of nutrient elements are reviewed.

9.2 Action Mechanisms of PGPR of Providing Nutrients for Plants

PGPR enhance plant growth and health by the beneficial mechanisms which are direct or indirect. Any mechanism that protects the plant against infections (biological stress) or helps the plant grow healthy under abiotic stress is considered as indirect mechanics, whereas any mechanism that directly increases plant growth through the provision of nutrients or the production of growth regulators is considered as a direct mechanism (Goswami et al. 2016). This section focuses on plant growth promotion by PGPR directly. Generally, modes of action of PGPR of providing nutrients for plants are as below.

9.2.1 Increasing Nutrient Supply of Plants

In the absence of a nutrient in the soil, PGPR can provide the nutrient for plants, such as nitrogen (N) by fixing atmospheric nitrogen (N_2) (Fig. 9.1a). In the rhizosphere, there are microorganisms able to fix N_2 forming specialized structures (*e.g., Rhizobium* and related genera) or simply establishing associative relationships (*e.g., Azospirillum* and *Acetobacter*). Furthermore, some bacteria (*e.g.,* ammonifiers and nitrifiers) convert organic N compounds into inorganic forms (*i.e.,* NH_4^+ and NO_3^-) that are available for root uptake.

9.2.2 Increasing Nutrient Availability to Plants

A large proportion of nutrients are unavailable for the root uptake by plants because the nutrients in soils are generally bound to organic and inorganic soil constituents, or alternatively present as insoluble precipitates. Therefore, in these conditions, there are these nutrients in soil but their solubility is low and PGPR enhance the availability of these nutrients to plants by different mechanisms such as enhancing the solubility of phosphorus (P) and iron (Fe) (Fig. 9.1b). On the other hand, the increase of PGPR-derived ion concentration would help the uptake of nutrients by roots because one of the mechanisms of ion transport to plant roots is diffusion movement, which is caused by differences in concentration.

9.2.3 Enhancing Plant's Greater Access to Soil Nutrients

In these conditions, there is nutrient in soil and its solubility is also high but plants do not have any or more access to it. Therefore, PGPR enhance the access of plants to the nutrient and more uptake of it by increasing the root growth of plant by different mechanisms. The most important mechanisms involved in root elongation by bacteria are the production of IAA and ACC deaminase (Fig. 9.1c). Since one of the mechanisms of ion transport to plant roots is root interception (growth of roots throughout the soil mass), which is a physical contact resulted by root growth, it may be concluded that PGPR by IAA production and subsequently increased root length can enhance plant's greater access to soil nutrients. Therefore, a good root system is a prerequisite for nutrient acquisition. It is a commonplace that the contact between the nutrient and the root of the plant may be necessary before it may be taken up. However, both availability and efficiency largely depend on the contact between nutrients and the root. In general, it has well been known that many PGPR may reduce the growth rate of the primary root (Dobbelaere et al. 1999), increase the number and/or length of lateral roots (Chamam et al. 2013; Combes-Meynet et al. 2011), and stimulate root hair elongation in vitro (Contesto et al. 2008; Dobbelaere et al. 1999). Consequently, the uptake of minerals and water, and thus the growth of the whole plant, can be increased. Some of these effects, including increased root and shoot biomass, are also documented for PGPR-inoculated plants

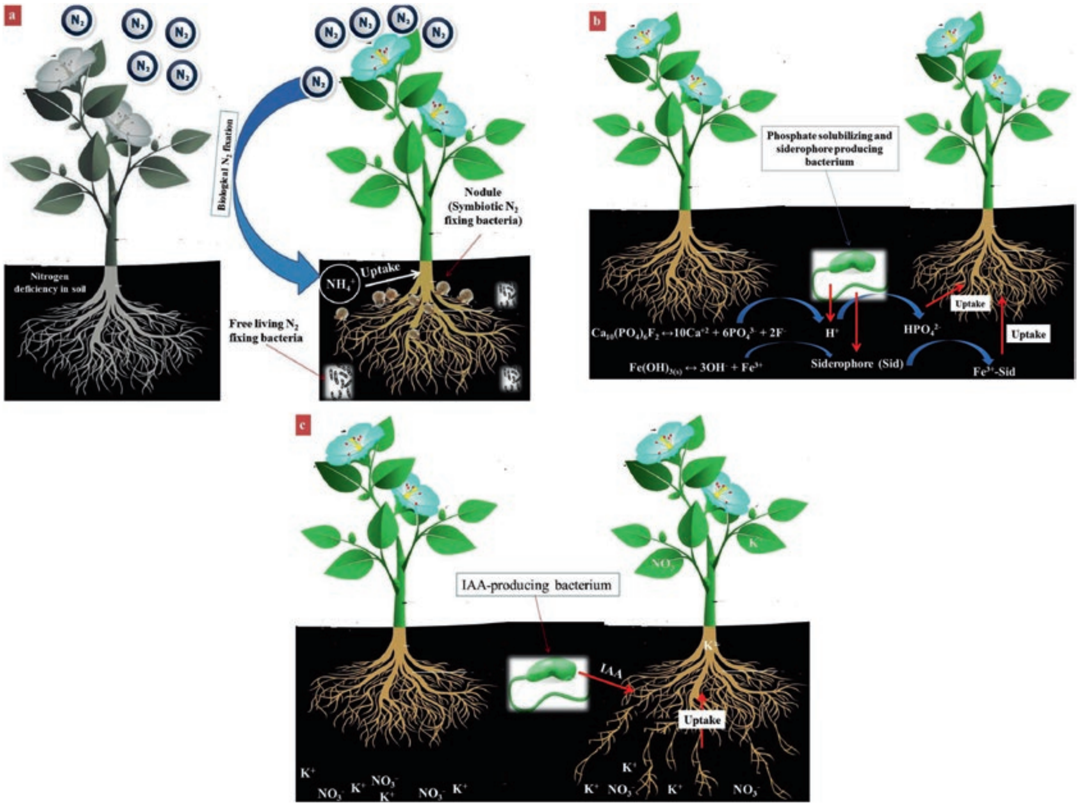

Fig. 9.1 Modes of action of PGPR of providing nutrients for plants. (**a**) Bacteria can provide the nutrients in soil which is lacking, (**b**) bacteria can increase insoluble nutrients availability to plants, and (**c**) bacteria can enhance plant greater access to soil nutrients

growing in soil (El Zemrany et al. 2006; Veresoglou and Menexes 2010; Walker et al. 2012).

9.3 Essential Plant Nutrients

Only 17 elements have been found to be absolutely essential for plant growth and metabolism that plants require to complete in their life cycle, based upon the criteria for essentiality of an element. These elements are further divided into two broad categories on the basis of their quantitative requirements: (i) macronutrients including carbon (C), hydrogen (H), oxygen (O_2), nitrogen (N), phosphorus (P), potassium (K), sulfur (S), calcium (Ca), and magnesium (Mg) and (ii) micronutrients or trace elements including manganese (Mn), iron (Fe), copper (Cu), molybdenum (Mo), zinc (Zn), nickel (Ni), chlorine (Cl), and boron (B). Among the essential elements mentioned above, O_2, H, and C are mainly obtained from CO_2 and H_2O, while the others are absorbed from the soil as mineral nutrition. Crop nutrition is affected by several factors. These factors can be internal or genetic factors (plant factors) and external factors (soil factors). Both types play significant roles in the nutrition processes that we can observe in crops. Availability of the nutrients is the resultant of a complex of soil factors. Among soil factors, soil pH is one of the most important factors affecting nutrient availability in the soil, which may either increase or decrease nutrient availability (Fig. 9.2). As shown in Fig. 9.2, maximum availability for the majority of nutrients is at pH = 6.5 (soils with pH levels higher or lower than 6.0 and 7.0), *i.e.,* under slightly acidic conditions. Among nutrient elements, N, K, and S solubility are less affected by pH, but still are to some extent. P, however, is affected. For example, at acidic pH, phosphate ions react with aluminum (Al) and Fe and they become less soluble compounds and these ions also react rapidly with Ca and Mg to form the same less soluble compounds at alkaline pH greater than pH 7.5. Availability of microelements increases with acidity, with the exception of molybdenum. The effect of soil pH on chloride availability is also neutral. In addition to pH, the availability of S, Fe, and Mn is also affected by redox reactions. In this review, special consideration is given to the role of PGPR in the availability of N, P, K, and S as macronutrients and Fe and Mn as micronutrients.

9.3.1 Nitrogen (N)

N is an essential element in plant development and a limiting nutrient for both natural and agricultural ecosystems. Although there are about 78% N_2 in the atmosphere, this form of N is not available to plants. Since there is a triple bond between the two N atoms, making the molecule almost inert, N2 cannot be directly assimilated by living cells. However, certain bacteria genera acquired an enzyme complex that uses N2 and converts it into organic N-containing molecules in the cytoplasm. Ammonium (NH_4^+) and nitrate (NO_3^-) are the predominant inorganic forms of N in soils. Plants absorb the available N in the soil through their roots in the form of NH_4^+ and NO_3^-.

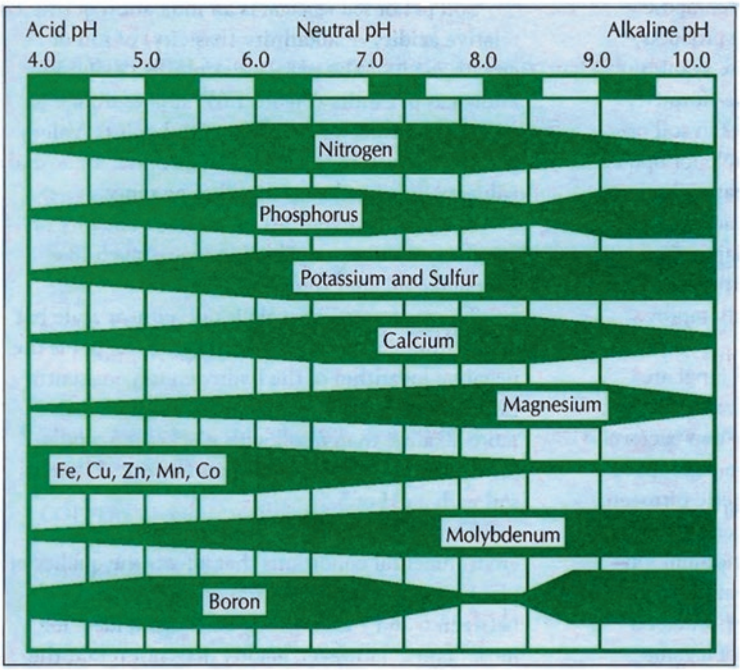

Fig. 9.2 Availability ranges of nutrient elements depending on soil pH

9.3.1.1 N_2-Fixing Bacteria (NFB)

Biological nitrogen fixation (BNF) is the process by which N_2 is reduced to ammonia by a specialized group of microorganisms called diazotrophs. All the nitrogen-fixing organisms are prokaryotes (archaebacteria and eubacteria). Diazotrophic bacteria possessing the trait of N_2 fixation are classified into three subgroups: symbiotic, free living, and associative. Root/legume-associated symbiotic bacteria possess the specificity and infect the roots to produce nodule. Several types of symbiotic biological N_2-fixing associations are known. The most prominent among them is the legume-bacteria (strains of *Rhizobium*) relationship. The amount of N_2 fixed by legumes into usable N can be substantial (176×10^{12} g year^{-1}). The legume host plant provides the bacteria with their necessary carbohydrates and possibly all the other nutrients they require in the exchange for the fixed N_2 by the bacteria. In this biological process, nodule-forming rhizobia inhabit the roots of leguminous plants and through a symbiotic relationship convert atmospheric N_2 to a form the plant can use (Fig. 9.1a). The total BNF is estimated to be twice as much as the total nitrogen fixation by nonbiological processes (80×10^{12} g year^{-1}). Associative nitrogen-fixing bacteria are a wide variety of the diazotrophs that form associative and/or endophytic relationships with a wide variety of plant roots including those of cereals and colonize the root surface of nonleguminous plants but do not inhabit specialized growth structures on their host plants (Franche et al. 2009). This relationship is described as a nonspecific and loose symbiosis. In other words, associative nitrogen fixation is commonly defined as nitrogen fixation by a free-living diazotroph under the direct influence of a host (Dalton and Kramer 2006). These bacteria do not possess specificity to plants such as *Azospirillum, Burkholderia, Enterobacter, Gluconoacetobacter, Herbaspirillum, Azoarcus* spp., *and Klebsiella* (Dalton and Kramer 2006). Due to a very close relationship established between associative NFB and plants, the fixed N_2 (some excess N) by these bacteria can also be taken up by the plant and the microbes can utilize plant-derived carbon compounds to fuel the nitrogen fixation reaction. Furthermore, plants may provide suitable conditions for protecting the nitrogenase complex from exposure to oxygen. Generally, these bacteria can make only a small contribution to the nitrogen nutrition of the plant because nitrogen fixation is an energy-expensive process, and large amounts of organic nutrients are not continuously available to microbes in the rhizosphere. Bacterial genera such as *Klebsiella*, *Azotobacter*, *Azoarcus*, *Bacillus*, *Enterobacter*, *Xanthobacter*, *Beijerinckia*, *Achromobacter* spp., *Arthrobacter* spp., *Clostridium* spp., *Corynebacterium* spp., *Herbaspirillum* spp., *Pseudomonas* spp., *Rhodopseudomonas*, *Rhodospirillum*, *Azomonas*, and *Derxia* (Saharan 2011; Saxena and Tilak 1998) are examples of the NFB that live independently of other organisms (any plant species). These bacteria are also named as free-living nitrogen-fixing bacteria. Almost all of the nitrogen fixed by free-living NFB is used by these bacteria.

9.3.1.2 Action Mechanisms of Bacteria in Providing N for Plant

Biological N_2 Fixation (BNF)

Many associated bacteria can fix N_2 so that they could provide N to the plant. N_2-fixing PGPR can increase plant N uptake by different processes. The N cycle is biologically influenced. PGPR have a central role in almost all aspects of N availability. In terms of availability of N to plants, some bacteria (diazotrophs) can convert N_2 into ammonia by the process termed biological nitrogen fixation (BNF) and using a complex enzyme system known as nitrogenase. Mechanism of BNF has been well known and documented (Franche et al. 2009; Santi et al. 2013). In nitrogen fixation process, 16 moles of ATP and a supply of electrons and protons (hydrogen ions) are needed to produce two ammonia molecules from a mole of N_2 gas (the equation below). Nitrogenase enzyme catalyzes the nitrogen fixation reaction:

$$\mathrm{N_2} + 8\mathrm{H}^+ + 8\mathrm{e}^- + 16\mathrm{Mg}\quad ATP \rightarrow 2NH_3 + \mathrm{H_2} + 16\mathrm{Mg}\quad ADP + 16\mathrm{P_i}$$

In addition to rhizobial bacteria associated with legume plants, numerous nitrogen-fixing species have also been identified that are able to colonize the root surface and, in some cases, the root interior of a variety of pasture grasses and cereal crops (non-leguminous plants) (Franche et al. 2009).

Mineralization of Organic Nitrogenous Compounds

Another mechanism of bacteria in making N available to plant is mineralization of organic forms of N in soil (Fig. 9.3). Many bacteria degrade organic matter and release fixed N for reuse by other organisms (nonlegume plant). Each part of a legume crop that remains after harvest (*e.g.,* roots, leaves, and nodules) can supply N to the soil system during the decomposition of plant materials. In addition, these plants do not use the entire N they receive from the atmosphere and return extra N to the soil. During the decomposition of plant matter, dead bacteria, and root exudates including N, organic N is once again converted to inorganic ammonium and released into the soil. The process that converts organic N to ammonium is called mineralization (conversion of organic N to inorganic forms) and plays a significant role in the management of N. The first step of mineralization is called aminization, in which microorganisms including bacteria break down complex proteins to simpler amino acids, amides, and amines. Ammonification is the second step of

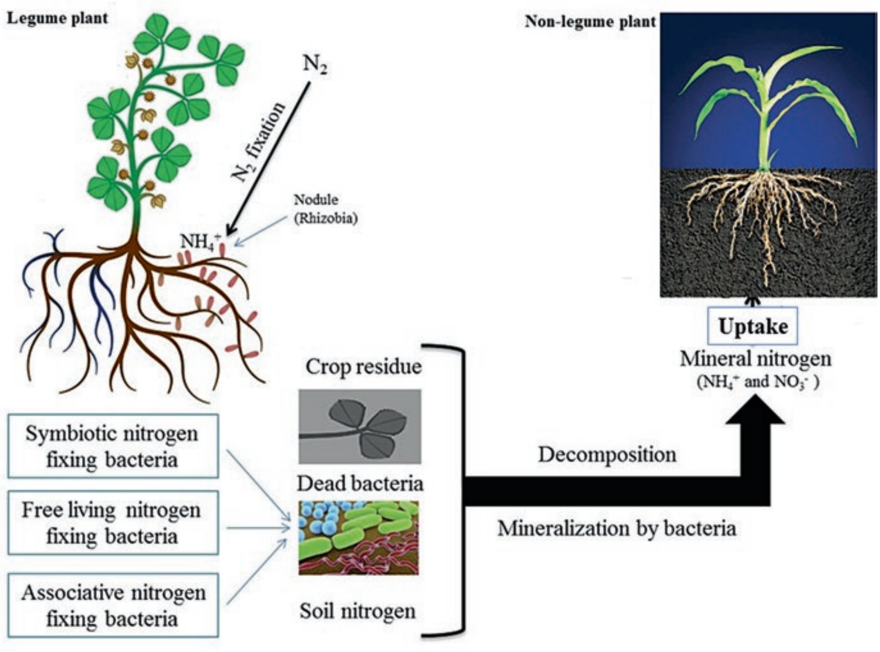

Fig. 9.3 Mechanisms increasing the availability of N in the rhizosphere to leguminous and nonleguminous plants. In legumes and a few other plants, the bacteria live in small growths on the roots called nodules. Within these nodules, nitrogen fixation is done by the bacteria, and the NH_3 produced is absorbed by the plant. Almost all of the nitrogen fixed goes directly into the leguminous plant. Little leaks into the soil for a neighboring nonlegume plant. However, other plants (nonleguminous plants) benefit from nitrogen fixing bacteria when the bacteria die and release nitrogen to the environment, or when the bacteria (associative and free living) live in close association with the plant, or by the release of ammonium or simple organic nitrogen compounds through the decomposition of organic matter obtained from vegetation (roots, leaves, fruits) of leguminous plants

mineralization in which amino (NH_2) groups are converted to ammonium. Again, microorganisms, including bacteria, do this. The two steps of nitrification (conversion of ammonium to nitrate) are also performed by microbial activity. *Nitrosomonas* (obligate autotrophic bacteria) convert ammonium to nitrite. *Nitrobacter* species perform the second step of nitrification, which converts nitrite to nitrate. This step quickly converts ammonium into nitrite, and thus nitrite concentration in soils is usually low.

Immobilization of Soluble Inorganic N

Immobilization, or the temporary tying up of inorganic N by soil microorganisms decomposing plant residues, is not strictly a loss process. A large proportion of the total fixed N will be locked up in the biomass or in the dead remains of organisms. Immobilized N will be unavailable to plants for a time, but will eventually become available as residue decomposition proceeds and populations of microorganisms decline. Therefore, it may be concluded that PGPR by immobilization of inorganic N (NO_3^-) can make more N available for plants because immobilization decreases the loss of soluble NO_3^-, which is highly mobile and is easily lost from the soil system by leaching and denitrification (conversion of NO_3^- to N gases).

Increased Root System of Plant

Nutrient presence in soil and its solubility may be high, but still plants do not have any access to it due to limitations in root growth or activities. Since essential nutrients are absorbed from the soil by the root, a good root growth is a prerequisite for increasing plant growth (Mills et al. 1996). Root hairs, along with the rest of the root surface, are the major sites of water and nutrient uptake. In an important analysis and review of the literature, Kuzyakov and Xu (2013) argued that microorganisms were more effective than roots at obtaining nutrients from the soil. Thus microorganisms win in the competition for nitrogen against roots. However, over the duration of the growing season, as root biomass increases it will outcompete microorganisms. Key to this dynamic is the high turnover rate of microbes consumed by the soil food web, in contrast to the continuously increasing root surface for membrane transport and overall biomass. PGPR increase root system of plants by production of IAA and ACC deaminase. Rhizobacterium-mediated root proliferation has been well proved (Diby et al. 2005). Plants treated with PGPR have better root with a subsequent increase of nutrient and water uptake. Promotion of root growth results in a larger root surface and can, therefore, have positive effects on water acquisition and nutrient uptake (Diby et al. 2005b; Paul and Sarma 2006) that is expected to move nutrient (*e.g.,* N) from soil to root (mechanism of mass flow in ion transport to plant roots). Phytohormone IAA, whose biosynthesis requires L-tryptophan (L-Trp) as a precursor, is primarily involved in stimulating the proliferation of lateral roots in plants; thereby root surface area is increased and they absorb more water and soil minerals (Egamberdieva and Kucharova 2009; Lugtenberg and Kamilova 2009). Under both biotic (*e.g.,* phytopathogen attacks) and abiotic (*e.g.,* heavy metals, flooding, and salinity) stresses, plant produces ethylene up to the level that is inhibitory to root growth (Arshad et al. 2007; Chen et al.

2013; Khalid et al. 2006; Nadeem et al. 2009). An enzyme ACC deaminase produced by many soil microflora including PGPR (He et al. 2010; Kumar et al. 2009) degrades ACC (an immediate precursor for ethylene in plants) and decreases the ethylene biosynthesis in plant tissues (Saleem et al. 2007; Shaharoona et al. 2007; Zahir et al. 2009). Many PGPR produce IAA and enzyme ACC deaminase that undoubtedly affect root growth, leading to the formation of root systems with increased exploratory capacity. Plant growth-promoting non-rhizobial bacteria can help the fixation of N by enhancing the capacity of rhizobial bacteria to colonize plant roots and increasing the number of nodules (Masciarelli et al. 2014). In addition, IAA-producing PGPRs by increasing root exudates can have a positive role in N_2 fixation. It has been reported that the phenolics and aldonic acids that are directly secreted by the roots of N_2-fixing legumes act as the main signal for the bacteria that form root nodules where N_2 is reduced to ammonia (Dakora and Phillips 2002). Overall, IAA and ACC deaminase-producing PGPR increase root surface area and length (Potters et al. 2009, 2007; Ryan et al. 2008; Vessey 2003) and thus increase the access of plants to nutrients and water absorption.

IAA Production

A member of the group of phytohormones, IAA is usually considered to be the most important native auxin. Almost most rhizospheric bacteria (usually more than 80% of bacteria) have the ability to produce this hormone (Khalid et al. 2004). At present, IAA-producing PGPR are the most well-studied phytohormone producers (Spaepen et al. 2007; Tsavkelova et al. 2006). The majority of root-related bacteria, which have a positive effect on plant growth, produce IAA (Hayat et al. 2010). An increase in the number of lateral roots and root hairs causes addition of root surface available for nutrients and water uptake (Fig. 9.1c). Higher water and nutrient uptake by inoculated roots causes an improved water status of plant, which in turn could be the main factor enhancing plant growth (Dalla Santa et al. 2004; Egamberdieva 2009; Egamberdieva and Kucharova 2009; Mostajeran et al. 2002). Inoculation of various plant species with such bacteria leads to increased root growth and/or enhanced formation of lateral roots and root hairs (Dimkpa et al. 2009) that can result in enhanced uptake of nutrients such as N. In addition to the production of IAA, GA and other growth regulators produced by PGPR can support increased root length, root surface area, and number of root tips, leading to enhanced uptake of nutrients (Egamberdieva and Kucharova 2009). By increasing nutrient availability via mechanisms such as producing plant growth-promoting (PGP) products, the symbiotic, free-living, and associative NFB and other PGPR can also enhance plant growth directly. The production of IAA appears to be widespread in associative NFB and has since been confirmed in a number of other genera including *Azospirillum*, *Herbaspirillum*, and *Pseudomonas* (Pedraza et al. 2004). Although the growth-promoting effects of *Azospirillum* have been well documented, the exact mechanism of growth promotion goes beyond nitrogen fixation to include nitrate reduction, phytohormone production, production of undefined signal molecules that can interfere with plant metabolism, and enhancement of mineral uptake by plants in response to root elongation (Okon and Itzigsohn 1995). Morphological plant root changes have been observed repeatedly upon *Azospirillum* inoculation and have been attributed to the production of PGP substances, CK and GA, with auxin production being quantitatively the most important (Spaepen et al. 2008). Specific evidence for the interference of IAA produced by *Azospirillum* in root development was obtained in many cases. In a study (El-Khawas and Adachi 1999), the inoculation of IAA-producing *A. brasilense* to the roots of rice resulted in an increase in root length, root surface, root dry matter, and development of lateral roots and root hair in comparison with uninoculated roots. Similarly, IAA-producing *A. brasilense* Cd induced many roots and increased root length of soybean plants (Molla et al. 2001). More direct evidence for the importance of IAA was provided when several IAA-attenuated mutants were compared with their parental wild types for their effect on plant growth. A mutant of *A. brasilense* with low production of phytohormones, but high N_2-fixing activity, did not enhance root growth over uninoculated controls (Kundu et al. 1997).

Bacterial IAA, by loosening plant cell walls (Chaintreuil et al. 2000; Chi et al. 2005; James et al. 2002; Sevilla et al. 2001), can also promote an increase in root exudation (carbon exudation) that provides additional nutrients to support the growth of rhizosphere bacteria. Due to IAA bacterial derived root exudation, the increased microbial population enhances microbial respiration and subsequently reduces oxygen. Reduced oxygen supply in the root zone has been shown to enhance nitrogenase activity in rhizosphere organisms (Döbereiner et al. 1972). In addition, the correlation of nitrogenase activity and photosynthate flux indicates that carbon exudates are a major regulatory factor in diazotrophic activity in the rhizosphere (Dalton and Kramer 2006). Bacterial IAA is also involved in many processes of nodule formation by rhizobia in legume plants. Founder cell specification, nodule initiation and differentiation (IAA accumulation), nodule numbers, vascular bundle formation, and cell division and differentiation are some of the processes of nodule formation mediated by bacterial IAA. These three latter events are more necessary for nodule formation (Glick 2012b; Theunis 2005). In addition, IAA-producing bacteria, by increasing the root system, provide more active sites for more bacteria colonization. As an example, Parmar and Dadarwal (1999) reported that increased root growth provides more active sites and provides access to nodulation for rhizobia in chickpea plant. In another study, the presence of PGPR in the vicinity of the root can improve the ability of rhizobia to compete with indigenous populations to nodulation. Therefore, it is suggested to pay more attention in selecting microbial inoculants with high phytohormone production to potentially increase the uptake of N. In addition to hormone production, associative fixing bacteria may also benefit hosts plants in a variety of ways including improved nutrient cycling or uptake (especially through production of siderophores for iron uptake) (Dobbelaere et al. 2003). Bacterial IAA production also stimulates the activity of the enzyme ACC deaminase involved in the degradation of the ethylene precursor ACC (Glick 2005). In general, IAA and ACC deaminase work in concert to stimulate root elongation (Etesami et al. 2015a, 2014).

ACC Deaminase Activity

PGPR contain the enzyme ACC deaminase; it can act to modulate the level of ethylene in plants (Glick 2014; Singh et al. 2011). This enzyme is responsible for the

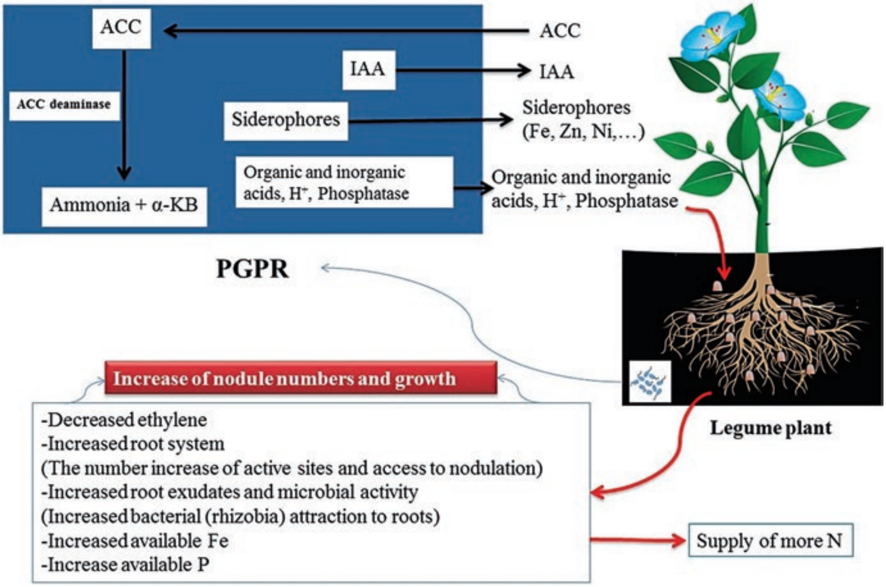

Fig. 9.4 Mechanisms by which PGPR may affect nodule number and nitrogen fixation in a legume plant

cleavage of the plant ethylene precursor, ACC, into ammonia and α-ketobutyrate (Glick et al. 2007). Plants that are inoculated with bacteria that produce enzyme ACC deaminase can adjust their ethylene levels and thus help the wider root system (Arshad et al. 2007; Safronova et al. 2006; Stearns et al. 2005). The ACC deaminase trait has been extensively studied in PGPR (Glick 2005) such as the genera *Achromobacter*, *Acidovorax*, *Alcaligenes*, *Enterobacter*, *Klebsiella*, *Methylobacterium*, *Pseudomonas*, *Rhizobium*, and *Variovorax* (Esquivel-Cote et al. 2010). In general, ACC deaminase-containing PGPRs may act as a sink for ACC. It has been well known that under stressful conditions, nodulation, nitrogenase activity, N_2 fixation, and total N content in legume plants are reduced. One of the main reasons for this decrease may be due to the production of stress-induced ethylene. Ethylene inhibits the elongation of infection threads and, consequently, the formation of nodules in most legumes (Sugawara et al. 2006). Extra ethylene production can also inhibit root prolongation, growth of lateral roots, and root hair growth (Belimov et al. 2009; Mayak et al. 2004; Saleem et al. 2007), which subsequently result in decrease in the nodule number of root. Fe deficiency also decreases nodule mass and particularly leghemoglobin content, number of bacteroids, and nitrogenase activity (Garcia et al. 2015; Tang et al. 1990). The deficiency of P supply and availability also remains a severe limitation of N_2 fixation and symbiotic interactions (Pereira and Bliss 1989). It has been well known that PGPR can alleviate the effect of these stresses on legume plant and increase N_2 fixation by different ways (Fig. 9.4).

9.3.2 Phosphorus (P)

After N, the essential mineral element that most frequently limits the growth of plants is phosphorus (P), which is taken up only in monobasic ($H_2PO_4^-$) or dibasic (HPO_4^{2-}) soluble forms. P is found mainly in inorganic fractions, which are either adsorbed into the soil's inorganic surfaces or found as sparingly available precipitates, and in organic forms that are either adsorbed, incorporated within biomass, or associated with soil organic matter (Richardson and Simpson 2011). Even in soils with abundant P ranging from 400 to 1200 mg kg^{-1} of soil, usually only about 1% of the soil P is actually in a readily available, soluble form, and over 90% is generally bound tightly to soil particles and inorganic minerals such as apatite, hydroxyapatite, and oxyapatite or appear as one of several organic forms including inositol phosphate (soil phytate), phosphomonoesters, and phosphotriesters (Khan et al. 2007b), which require mineralization before they become plant available (Jewell et al. 2010). P is an integral part of various biochemical substances such as nucleic acids, phospholipids, nucleotides, and phosphoproteins. Calcium concentration, soil pH, proportion of organic matter, type and proportion of clay, soil moisture, soil texture, root density, and exudates are among the parameters that have been able to influence the availability of soil P to the plant (Barber 1995). Parameters including high soil pH, high soil $CaCO_3$, low soil organic matter, and drought decrease P availability to plants in the calcareous soils of Iran, with arid and semiarid climates. As previously mentioned, the soil pH for optimum P availability is 6.5. P reactions in soil are pH dependent. At high or neutral pH, phosphate is converted to less soluble compounds such as dicalcium phosphate dihydrate or octacalcium phosphate. In some cases it may eventually convert to hydroxyapatite. P may react with Al and Fe to form low-solubility Fe- and Al-phosphates such as strengite and varescite under acidic conditions. The limitation in bioavailability of P from the soil along with the fact that this element is essential for plant growth suggests that the inability to obtain sufficient amount of P restricts plant growth (Khan et al. 2007b). Plants are well adapted to the uptake of P from low-concentration soil solution under low-P conditions (Jungk 2001). Plants have been demonstrated to alter the rhizosphere with specific exudates, commonly organic acids or enzymes, to improve the availability of nutrients such as phosphate (Hong et al. 2008; Park et al. 2007; Xiao et al. 2007). Furthermore, by inhibiting primary root growth, promoting lateral root growth, and enhancing root hair development and cluster root formation, which all promote P acquisition by plants, plants adjust their root architecture to low-P conditions (Jain et al. 2007; Ma et al. 2003; Niu et al. 2013; Osmont et al. 2007). Lateral roots have been known to play an important role in the absorption of P via different ways such as solubilizing insoluble P (Lynch 2007) and increasing the absorptive surface of the root system (Pérez-Torres et al. 2008) and soil exploration (Zhu et al. 2005).

9.3.2.1 Phosphate-Solubilizing Bacteria (PSB)

It has been known that strategies mentioned above are often not efficient enough to meet the needs of the plants growing especially in calcareous and alkaline soils. Therefore, using phosphate-solubilizing bacteria (PSB) for providing accessible forms of P for plants is necessary when it is scant or unavailable in soils. The conversion of insoluble phosphate compounds (both organic and inorganic) in a form accessible to the plant is an important trait of PSB. Solubilization of insoluble P by microorganisms was reported by Pikovskaya (1948). In soil, PSB constitute 1–50% of the total respective population. PSB have been isolated, using serial plate dilution method or by enrichment culture technique, from almost all areas, including from rhizosphere and non-rhizosphere soils, rhizoplane, phyllosphere, and rock P deposit area soil and even from stressed soils (Zaidi et al. 2009).

The ability to solubilize insoluble inorganic phosphate compounds such as hydroxyapatite, tricalcium phosphate, rock phosphate, and dicalcium phosphate has been reported in PGPR strains belonging to various genera (Khan et al. 2009b; Ramaekers et al. 2010). A significant number of microbial species show the capacity of solubilizing P; these include actinobacteria, bacteria, fungi, and even algae. The solubilization of insoluble phosphates has been reported in most known bacterial genera (*e.g.*, *Streptomyces* sp., *Agrobacterium* sp., *Azospirillum brasilense*, *Bacillus* sp., *B. circulans*, *B. cereus*, *B. fusiformis*, *B. pumilus*, *B. megaterium*, *B. mycoides*, *B. polymyxa*, *B. coagulans*, *B. subtilis*, *Rhodococcus*, *Klebsiella*, *Vibrio proteolyticus*, *Alcaligenes* sp., *Aerobacter aerogenes*, *Achromobacter* sp., *Enterobacter, Thiobacillus ferrooxidans*, *T. thiooxidans*, *Xanthomonas* sp., *Actinomadura oligospora*, *Brevibacterium* sp., *Citrobacter* sp., *Arthrobacter*, *Serratia*, *Chryseobacterium*, *Gordonia*, *Phyllobacterium*, *Xanthobacter agilis*, *Delftia* sp., *Azotobacter*, *Xanthomonas*, *Pantoea*, *Pseudomonas* sp., *P putida*, *P. striata*, *P. fluorescens*, *P. calcis*, *Flavobacterium* sp., *Nitrosomonas* sp., *Erwinia* sp., *Micrococcus* sp., and *Nitrobacter* sp.) (Sharma et al. 2013). By mobilizing inorganic and organic P, symbiotic nitrogenous rhizobia like *Rhizobium leguminosarum* bv. *Trifolii* and *Rhizobium* species nodulating *Crotalaria* species also improved plant P nutrition (Abril et al. 2007; Sridevi et al. 2007; Zaidi et al. 2009). Of the bacterial genera mentioned above, *Pseudomonas and Bacillus* were reported as the most important bacterial genera that were able to effectively solubilize insoluble phosphates.

9.3.2.2 Action Mechanisms of P Solubilization by PSB

Solubilization and mineralization of P in rhizosphere are the most common modes of action implicated in PGPR that increase the nutrient availability to the host plant (Glick 2012a; Rashid et al. 2004b). PGPR play an important role in all three major components of the soil P cycle (*i.e.,* dissolution–precipitation, sorption–desorption, and mineralization–immobilization). An example is the PSB, which dissolve various sparingly soluble P sources such as $Ca_3(PO_4)_2$ (Rodriguez et al. 2004) and $Zn_3(PO_4)_2$ (Saravanan et al. 2007) by lowering pH of the rhizosphere soil and making P available for plant uptake. By solubilizing and mineralizing reactions, and immobilizing P into microbial biomass and/or forming sparingly available forms of inorganic and organic soil P, PSB and their interactions in soil play a critical role in mediating the distribution of P between the available pool in soil solution and the total soil P. Overall, phosphate-solubilizing PGPRs can either convert these insoluble phosphates into available forms through acidification, chelation, exchange reactions, release of complexing or mineral dissolving compounds (*e.g.,* organic acid anions, protons, hydroxyl ions, CO_2), secretion of siderophores, IAA production, ACC deaminase activity, and release of organic acids (Chung et al. 2005; Glick 2012a) or mineralize organic phosphates by secreting a variety of different extracellular phosphatases, catalyzing the hydrolysis of phosphoric esters (Gyaneshwar et al. 2002; Van Der Heijden et al. 2008). Each organism can act in one or more than one way to bring about the solubilization of insoluble P. Though it is difficult to pinpoint a single mechanism, production of organic acids and consequent pH reduction appear to be of great importance. In the following section, different mechanisms involved in the solubilization and mineralization of insoluble P by PSB are discussed.

Production of Organic Acids

One of the most known mechanisms of P solubilization by PSB is associated with the production of organic and inorganic acids and proton excretion. H^+ excretion is originated from NH_4^+ assimilation by plant and PSB (Parks et al. 1990). For some microorganisms, NH_4^+-driven proton release seems to be the sole mechanism to promote P solubilization. An HPLC analysis of the culture solution of *Pseudomonas* sp., in contrast to the expectation, did not detect any organic acid while solubilization occurred (Illmer and Schinner 1995). According to these authors, probable cause for the dissolution of phosphate without acid production is the release of protons originated from assimilation of NH_4^+.

Organic acids (*e.g.,* acid, oxalic acid, citric acid, lactic acid, tartaric acid, and aspartic) are the product of the microbial metabolism, mostly by oxidative respiration or by fermentation of organic carbon sources (*e.g.,* glucose) (Trolove et al. 2003) or by oxidation of the soil organic matter or being added as manure. Furthermore, PGPR (*e.g.,* IAA producers) can enhance the amount of root exudates. Root exudates include a huge diversity of organic nutrients (*i.e.,* organic acids, phytosiderophores, sugars, vitamins, amino acids, nucleosides, mucilage) and signals that attract microbial populations, especially PSB able to metabolize plant-exuded compounds and proliferate in this microbial habitat (Badri and Vivanco 2009; Drogue et al. 2013; Khan et al. 2007a; Pothier et al. 2007; Sharma et al. 2013).

Organic acids produced by PSB and plant decrease the rhizosphere pH favoring the solubility of precipitated P forms. Organic anions produced by PSB can also compete with phosphates for fixation sites or even replace phosphate (anion exchange of phosphate) sorbed on the surfaces of soil clays (kaolinite, goethite, montmorillonite, and amorphous Al oxides). They also can enhance the chelation of the cations (Al^{3+}, Fe^{3+}, and Ca^{2+}) bound to P or the formation of soluble complexes with metal ions associated with insoluble P avoiding thus the precipitation of phosphate (Osorio Vega 2007; Rashid et al. 2004a; Whitelaw 1999) and thus P is released. The monovalent anion phosphate $H_2PO_4^-$ is a major soluble form of inorganic phosphate, which usually occurs at lower pH. However as the pH of the soil environment increases the divalent and trivalent forms of Pi (HPO_4^{-2} and HPO_4^{-3}, respectively) occur. Thus, the synthesis and discharge of organic acid by the phosphate-solubilizing PGPR strains into the surrounding environment acidify the cells and their surrounding environment that ultimately leads to the release of P ions from the P mineral by H^+ substitution for the cation bound to phosphate (Goldstein 1994). When phosphate-solubilizing PGPRs are inoculated to neutral or alkaline soils, the acid production decreases the rhizosphere pH, favoring thus the solubility of calcium phosphates and apatites (Fig. 9.5a). If the activity of H^+ increases in the reactants of the reactions of the solubility of dicalcium phosphate and hydroxyapatite, these reactions proceed. In addition, the sequestering of Ca^{2+} by organic anions or other chelating agents such as siderophores favors the reactions. In acid soils, the minerals variscite and strengite control the solubility of phosphate. The presence of organic acids assists the formation of complexes with Al^{3+} and Fe^{3+} ions, which in turn facilitates the dissolution of these minerals. If Fe^{3+} and Al^{3+} are sequestered via chelation with organic anions, the reactants of the reactions of the solubility of strengite and variscite proceed to the right (Fig. 9.5b).

Production of Inorganic Acids

PSB have also been shown to solubilize insoluble phosphates by producing inorganic acids (*e.g.,* HCl) (Kim et al. 1997). Bacteria of the genera *Nitrosomonas* and *Thiobacillus* species (microbial sulfur oxidation) and other bacteria can also dissolve phosphate compounds by producing nitric and sulfuric acids, and carbonic acid formed as a result of the decomposition of organic residues, respectively (Azam and Memon 1996), decreasing soil pH. Therefore, elemental sulfur can be inoculated with *Thiobacillus* to enhance the P solubility of apatite, and hence plant biomass (Stamford 2003). However, the effectiveness of inorganic acids is lower than that of organic acids in solubilizing insoluble phosphates (Kim et al. 1997). The other mechanism is the production of H_2S, which reacts with ferric phosphate to yield ferrous sulfate with concomitant release of phosphate (Swaby and Sperber 1958). Overall, acidification does not seem to be the only mechanism of solubilizing insoluble phosphates by phosphate-solubilizing PGPRs because the ability to reduce PH in some cases is not related to the ability to solubilize P minerals (SubbaRao 1982).

Production of IAA and ACC Deaminase

PGPR can enhance the capacity of plants to acquire P from soil through increased root growth either by hormonal stimulation of root growth, branching, or root hair development (*e.g.,* production enzymes that alter plant ethylene precursors, such as ACC deaminase or production of IAA) or by an extension of existing root systems (Hayat et al. 2010; Richardson et al. 2009). ACC deaminase can affect plant root growth by degrading the precursor for the production of the stress hormone, ethylene. Increased level of ethylene production in plant can decrease root growth. As a consequence, the enzymes can also indirectly influence P effect on root growth as well as its uptake by plant, because ethylene can adjust root architectural response to P availability in the soil. Under stresses such as P deficiency, the increased

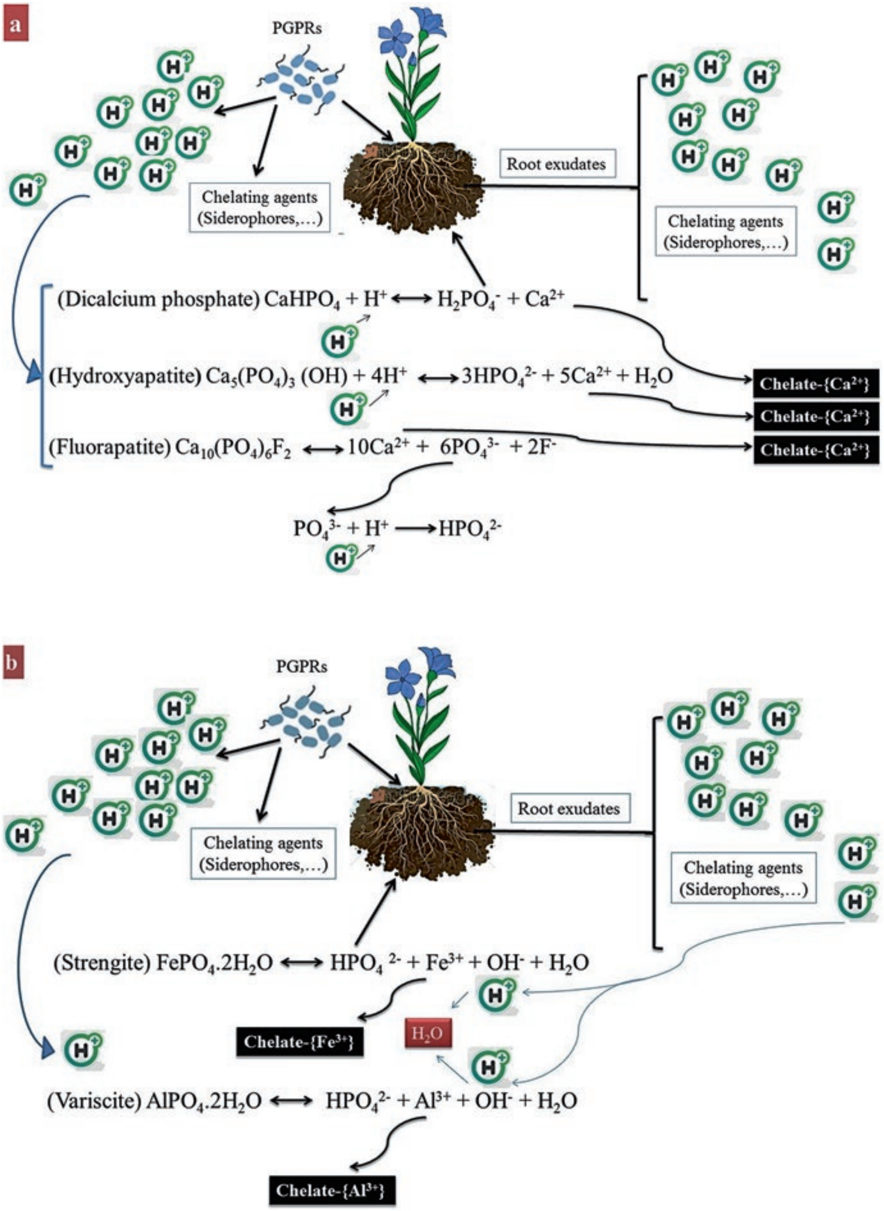

Fig. 9.5 (**a**) Role of PGPR in enhancing the capacity of plants to acquire P from soil through alteration of sorption equilibria that may result in increased net transfer of orthophosphate ions into soil solution. Organic anions and protons are particularly effective in solubilizing precipitated forms of P (e.g., Ca phosphates under alkaline conditions and (**b**) Fe and Al under acidic conditions), chelating metal ions that are commonly associated with complexed forms of soil P (as is for the role of siderophores in mediating Fe availability)

production of stress can adversely affect plant response to P and decrease the number of root hairs (Borch et al. 1999).

Bacterial IAA can increase the root exudates and root system. Organic acids (*e.g.,* gluconic and citric acid) found in the root exudates in turn result in acidification of the rhizosphere (Amir and Pineau 2003; Dakora and Phillips 2002; Jones et al. 2003). In addition, production of CO_2 by respiration processes (due to release of carbohydrates, amino acids, lipids, and vitamins by roots and subsequently stimulation of microorganisms in the soil), pump of H^+ in nutrient uptake by plant and microbes, organic matter decomposition, and N_2 fixation by the symbiosis *Rhizobium* legume (Marschner and Rimmington 1988) are some of the responsible mechanisms for acidification of rhizosphere than the bulk soil. By the complexation of essential ions, the organic acids play an important role in the increase of mobility of the elements for plant uptake. Acid pH is common for the rhizosphere environment due to proton extrusion through the root cell membrane (Spaepen et al. 2007). The acidification can also contribute to plant growth by mobilizing nutrients such as P and micronutrient. Increase in the acidity of the surrounding soil can occur by releasing proton and organic acids from the seeds and roots and absorbing nutrient ions by the plant (Hartmann et al. 2008). Altered root morphology of inoculated plants may enhance P uptake. In addition, the prevalence of root hair and lengths is also associated with an increase in the absorption of relatively immobile elements such as P. A large number of phosphate-solubilizing PGPR (Ahemad 2012; Ahemad and Khan 2010; He et al. 2010; Misra et al. 2012; Oves et al. 2013) in soils have been reported to secrete IAA that is absorbed by plant roots to increase the endogenous pool of plant IAA (Glick et al. 2007). Datta et al. (1982) reported that a P-solubilizing and IAA-producing strain of *B. firmus* increased the grain yield and P uptake of rice in a P-deficient soil amended with rock phosphate.

In general, stimulation of root growth or greater elongation of root hairs by specific microorganisms may enhance plant P nutrition indirectly by allowing greater exploration of soil, rather than by direct increase in the availability of soil P. It is presumed that the supply and availability of P to the root surface are influenced by the root and microbial processes. According to the materials listed above, it may be suggested that IAA-producing PGPR (due to having a role in enhancing root exudates and root surface area) can also solubilize insoluble phosphates similar to phosphate-solubilizing bacteria (Fig. 9.6) (Dobbelaere et al. 1999; Lambrecht et al. 2000; Steenhoudt and Vanderleyden 2000).

Production of Siderophores

Siderophores are complexing agents that have a high affinity for Fe(III) and are produced by almost all microorganisms in response to Fe deficiency. Siderophores, in the case of iron deficiency, act as a solubilizing agent for Fe from organic compounds or minerals. Some of the produced siderophores (~500 known siderophores) are exclusively used by microbial species and strains that produce them and some of them are used by a wide variety of plants and microorganisms (Crowley 2006). The ability to produce siderophores by phosphate-solubilizing PGPR is well established (Caballero-Mellado et al. 2007; Hamdali et al. 2008; Vassilev et al. 2006). The

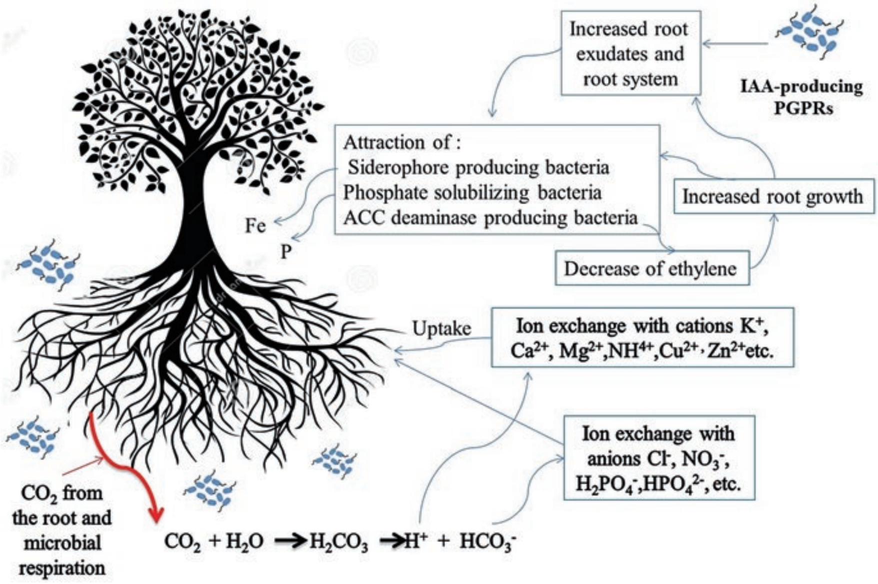

Fig. 9.6 The schematic representation of role of IAA-producing PGPR in the availability of nutrient elements (e.g., P) to plant by affecting plant (root) growth and hence plant root exudates

siderophores can increase the availability of P for plants either by chelating cations (*e.g.,* Ca^{2+}, Fe^{+3}, and Al^{3+}) forming precipitations with P or by exchange of ligands. Considering the dominance of mineral dissolution over ligand exchange by organic acid anions as a P-solubilizing mechanism (Parker et al. 2005), the potential role of siderophores in enhancing the availability of P should be clear (Sharma et al. 2013).

Production of Exopolysaccharides (EPS)

The role of exopolysaccharides (EPS) in the microbial mediated solubilization of P has also been confirmed (Yi et al. 2008). Microbial EPS, produced by some bacteria and fungi, are polymers composed mainly of carbohydrates and secreted outside the cell wall of microbes. However, these organic compounds may be homo- or heteropolysaccharides and may also contain a number of different organic and inorganic substituents. In general, the composition and structures of EPS are very diverse (Sutherland 2001). It has been known that EPS-producing PGPR (*e.g., Enterobacter* sp., *Arthrobacter* sp., and *Azotobacter* sp.) have the ability to solubilize tricalcium phosphate (TCP) (Yi et al. 2008). However, more studies are needed to understand the relationship between phosphate solubilization and EPS production (Sharma et al. 2013).

Mineralization of Organic P

In addition to mechanisms involved in releasing P from inorganic compounds, the release of phosphatase enzymes that mineralize organic P compounds has also been

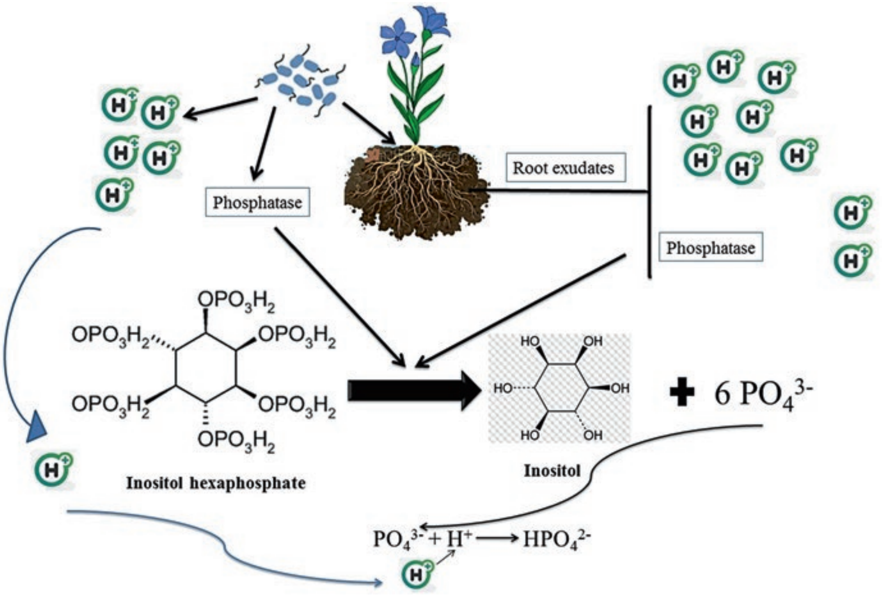

Fig. 9.7 The role of PGPR in the release of phosphatase enzymes mineralizing organic P compounds and releasing inorganic P (HPO_4^{2-})

suggested as another mechanism involved (Fig. 9.7). Organic P solubilization is also called mineralization of organic P. Mineralization of soil organic P plays an imperative role in P cycling of a farming system. Organic P may constitute 4–90% of the total soil P (Khan et al. 2009b). Organic P of organic compounds can be released in soil by enzymes of phosphatase. Phosphate-solubilizing PGPR similarly produce a range of phosphatases and when cultured in laboratory media have the capacity to utilize P from various forms of organic P that occur in soil. These enzymes, depending on their pH, are divided into acid and alkaline phosphatase, both of which can be produced by phosphate-solubilizing PGPR depending on the external conditions (Jorquera et al. 2008; Kim et al. 1998). So it is clear that alkaline phosphatases usually dominate in neutral and alkaline soils, while acid phosphatases are abundant in acidic soils (Renella et al. 2006). Although the roots of plants can produce acid phosphatase, they rarely produce large quantities of alkaline phosphatase, suggesting that this is a potential niche for phosphate-solubilizing PGPR (Criquet et al. 2004). It is also difficult to differentiate between root- and phosphate-solubilizing PGPR-produced phosphatases (Richardson et al. 2009); however, some evidence suggests that microbial phosphatases have a higher affinity for phosphorus compounds than plant phosphates and are also effective in releasing orthophosphate from soil organic P (Tarafdar et al. 2001). NSAPs (nonspecific acid phosphatases) dephosphorylate phospho-ester or phosphoanhydride bonds of organic matter. Among the variety of phosphatase enzyme classes released by phosphate-solubilizing PGPR, phosphomonoesterases (often just called phosphatases) are the most abundant and best studied (Nannipieri et al. 2011). Inositol phosphate is a dominant form of organic phosphorus found in many soils (Turner 2006). Phytases specifically cause release of P from phytate degradation. Phytate in its original form is the main source of the inositol and the main form of P stored in plant seeds and pollen, and the main component of P is organic matter (Richardson et al. 1994). Bünemann (2008) reported that up to 60% of the total organic P may typically be hydrolyzed by phosphatases with highest amounts being released by phytases (monoester phosphatases active against phytate). Phosphonatases and C–P lyases also can cleave the C–P bond of organophosphonates (Rodríguez et al. 2006).

Immobilization of Inorganic P

Phosphate-solubilizing PGPR decompose organic amendments added to soil (*e.g.,* manures and plant residues) and mineralize organic P along with that of soil organic matter. However, in the long run, all of the microbial phosphorus is potentially available to plants, and it has been suggested that the immobilization of phosphorus in biomass is an important mechanism for regulating the supply of P in soil solution (Seeling and Zasoski 1993) and for maintaining it in labile forms that are protected (in a temporal sense) from reactions with soil (Olander and Vitousek 2004). In general, PGPR in the presence of labile C serve as a sink for P, by rapidly immobilizing it even in low-P soils; therefore phosphate-solubilizing PGPR become a source of P to plants upon its release from their cells. Release of P immobilized by phosphate-solubilizing PGPR primarily occurs when cells die due to changes in environmental conditions, starvation, or predation. Environmental changes, such as drying–rewetting or freezing–thawing, can result in so-called flush events, a sudden increase in available P in the solution due to an unusually high proportion of microbial cell lysis (Butterly et al. 2009). According to the theory of sink, phosphate-solubilizing PGPR remove and assimilate phosphorus from the liquid and thus activate the indirect dissolution of calcium phosphate compounds by sequentially removing P from the liquid medium. For instance, the P content in the biomass of *Pseudomonas* sp. and *P. aurantiogriseum* was similar to that observed in non-phosphate-solubilizing PGPR (Illmer et al. 1995) which can be explained by the fact that the P content in biomass of organisms is consistently correlated with the decomposition of P containing organic substrates (Dighton and Boddy 1989).

9.3.2.3 Promotion of Plant Growth by PSB

Besides making soluble P accessible for uptake by plants, there have been a number of reports on plant growth promotion by these microorganisms (Sharma et al. 2013). There are studies showing that phosphate-solubilizing microorganisms under controlled conditions and, in some cases, in field conditions have increased plant P nutrition and subsequently plant growth (Gyaneshwar et al. 2002; Harvey et al. 2009; Jakobsen et al. 2005; Khan et al. 2009a, 2007a; Whitelaw 1999; Zaidi et al. 2009). Following inoculation of *Ricinus communis* and *Helianthus annuus* with P-solubilizing *Psychrobacter* sp. SRS8 (Ma et al. 2010), wheat with P-solubilizing *Pseudomonas* sp. (Babana and Antoun 2006), and peanut with P-solubilizing *Pantoea* J49 (Taurian et al. 2010), an increase in growth and P uptake of these plants over

Table 9.1 Plant growth-promoting substances released by PSB

Bacterial isolates	PGP traits	References
Pseudomonas aeruginosa strain OSG41	Production of IAA and siderophores	Oves et al. (2013)
Pseudomonas sp.	Production of IAA	Singh et al. (2013)
Acinetobacter haemolyticus RP19	Production of IAA	Misra et al. (2012)
Pseudomonas putida	Production of IAA and siderophores	Ahemad and Khan (2011b, 2012c, d)
Pseudomonas fluorescens strain Psd	Production of IAA and siderophores	Upadhyay and Srivastava (2010)
Bacillus thuringiensis	Production of IAA	Sandip et al. (2011)
Pseudomonas aeruginosa	Production of IAA and siderophores	Ahemad and Khan (2010b, 2011a, d, 2012a)
Pseudomonas sp. TLC 6-6.5-4	Production of IAA and siderophore	Li and Ramakrishna (2011)
Bacillus sp.	Production of IAA	Karuppiah and Rajaram (2011)
Klebsiella sp.	Production of IAA and siderophores	Ahemad and Khan (2011c, e, 2012b)
Enterobacter asburiae	Production of IAA and siderophores	Ahemad and Khan (2010a)
Bacillus species PSB10	Production of IAA and siderophores	Wani and Khan (2010)
Arthrobacter sp. MT16, *Microbacterium* sp. JYC17, *Pseudomonas chlororaphis* SZY6, *Azotobacter vinelandii* GZC24, and *Microbacterium lactium* YJ7	Production of ACC deaminase, IAA, and siderophore	He et al. (2010)
Pseudomonas sp.	Production of IAA and siderophore	Tank and Saraf (2009)
Enterobacter aerogenes NBRI K24 and *Rahnella aquatilis* NBRI K3	Production of ACC deaminase, IAA, and siderophore	Kumar et al. (2009)
Enterobacter sp.	Production of ACC deaminase, IAA, and siderophore	Kumar et al. (2008)
Burkholderia	Production of ACC deaminase, IAA, and siderophore	Jiang et al. (2008)
Pseudomonas aeruginosa	Production of ACC deaminase, IAA, and siderophore	Ganesan (2008)

uninoculated plants was observed. In addition to solubilizing P, phosphate-solubilizing PGPR also promote plant growth through N_2 fixation (He et al. 2010), lowering ethylene levels (Jiang et al. 2008; Kumar et al. 2009), siderophore production (Ahemad and Khan 2012a, b), and phytohormone secretion (Misra et al. 2012; Oves et al. 2013) (Table 9.1).

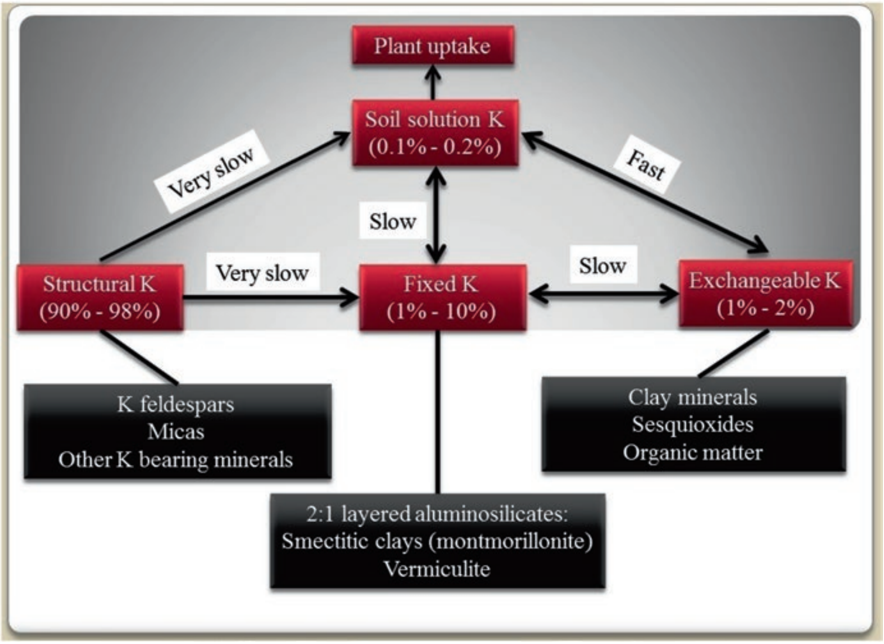

Fig. 9.8 Forms of potassium (K) in the soil and their plant availability

9.3.3 Potassium (K)

Potassium (K), one of the most important macronutrients, plays an important role in plant growth that is required in adequate quantities for all crops to achieve their maximum yield. K together with N and P forms the NPK chemical fertilizer used in both intensive and extensive agriculture. Non-exchangeable K, exchangeable K, mineral non-exchangeable K, and K in soil solution (water-soluble K) are four forms of K in the soil (Fig. 9.8). Although K deposits are generally large in soil, most soil K is not directly available for plant capture (Zörb et al. 2014). Mineral form makes up more than 90–98% of soil K (Sparks 1987), which is tightly bound, and most of it is unavailable for plant uptake. The potassium present in the soil solution is absorbed by the plants. Owing to soil erosion, introduction of high-yielding crop varieties and hybrids during green revolution, low application of K fertilizer, imbalanced fertilizer application, intensive cropping, runoff, leaching, and presence of insoluble K sources, the K availability to plants is decreasing (Xiafang and Weiyi 2002; Zörb et al. 2014). As a consequence, K deficiency is becoming one of the major constraints in crop production, and therefore many crops do respond to K fertilization in soils. In this situation, the role of PGPR is gaining importance in modern agriculture for sustainable crop production, which can enhance K availability in soil by their activities. The use of K-solubilizing microorganisms is one of the effective technologies to fulfill the K requirement of crops.

9.3.3.1 KSB (Potassium-Solubilizing Bacteria)

Soil bacteria, fungi, and actinobacteria are important in the cycling of mineral elements. Among these microbes, bacteria are the important players in this system. The bacteria involved in the solubilization of K from K-bearing minerals are called KSB (potassium-solubilizing bacteria). Potassium-solubilizing PGPRs have the ability to convert insoluble/mineral K into available K in soil making them available to the plants (Diep and Hieu 2013; Gundala et al. 2013; Keshavarz Zarjani et al. 2013; Zeng et al. 2012). KSB play an important role in the natural K cycle (Meena et al. 2014; Parmar and Sindhu 2013; Sindhu et al. 2014b). A wide range of bacteria including *Pseudomonas*, *Burkholderia*, *Acidithiobacillus ferrooxidans*, *Enterobacter hormaechei, Paenibacillus glucanolyticus, Arthrobacter* spp.*, Paenibacillus mucilaginosus, P. glucanolyticus, Bacillus mucilaginosus*, *B. edaphicus*, and *B. circulans* have been reported to release K from K-bearing minerals (Basak and Biswas 2009; Keshavarz Zarjani et al. 2013; Li et al. 2006; Lian et al. 2002; Prajapati et al. 2013; Sangeeth et al. 2012; Sheng 2005; Sheng and He 2006; Uroz et al. 2007; Zhang et al. 2013).

9.3.3.2 Action Mechanisms of KSB in the Availability of K

The K-bearing minerals are a major source of insoluble K in soils (Mengel and Kirkby 2001). The minerals are biotite, feldspar, mica, vermiculite, muscovite, orthoclase, illite/smectite, etc. These minerals supply slowly available K to plants. Clay minerals are selective for K ions and release K slowly from the lattice wedge sites (Mengel and Kirkby 2001). It has been known that KSB by converting mineral K into available K have a significant role in providing K to plants. At this time, there is little information on the mechanisms used by KSB to solubilize K. The K solubilization is a complex phenomenon affected by many factors, *e.g.*, amount of mineral, microorganisms involved, nutritional status of soil, soil mineral type, size of mineral, and environmental factors (Sindhu et al. 2016). Like the basic mechanism of PGPR for solubilizing P, potassium-solubilizing PGPR also solubilize K through the production of organic acids. Extracellular polysaccharides, production of capsular polysaccharides, hydroxyl anion, siderophores, organic ligands, extracellular enzymes, and formation of biofilms on the rhizospheric mineral surfaces are also involved in dissolution of minerals to release K (Balogh-Brunstad et al. 2008; Barker et al. 1998; Basak and Biswas 2012; Das and Pradhan 2016; Keshavarz Zarjani et al. 2013; Liermann et al. 2000; Liu et al. 2006; Meena et al. 2015; Parmar and Sindhu 2013; Sheng and He 2006; Singh et al. 2015; Uroz et al. 2009; Vandevivere et al. 1994). In general, some of the direct mechanisms used by KSB (Fig. 9.9) include (i) acidolysis, (ii) chelation, (iii) oxidation, and (iv) production of carbon dioxide (CO_2), explained separately in the following sections.

Acidolysis

Acidolysis is defined as decomposition resulting from the interaction of a compound and an acid. The major mechanism involved in mineral weathering is acidification. Although K appears to be less affected directly by soil pH, lowering the pH is one of the mechanisms for KSB to solubilize K. Minerals are known to be

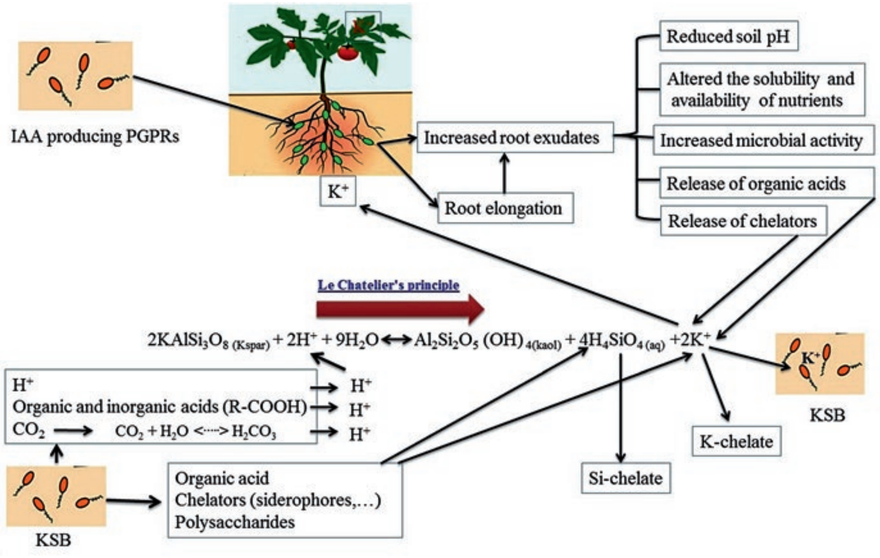

Fig. 9.9 The role of IAA producing and K solubilizing PGPR in the availability of K to plant by different mechanisms

susceptible to various biological by-products of bacterial metabolism, including protons, organic acids, and more complex molecules (Uroz et al. 2009). K-bearing mineral weathering in the rhizosphere is a proton attack as a result of microbial production of organic and inorganic acids, followed by removal of the products of weathering (cations dissolved from the mineral) by the production of complex-forming agents (organic acids, extracellular polymeric substances, siderophores, etc.) and/or by cellular cation uptake (Shelobolina et al. 2012), which induces the releasing of K. According to Le Chatelier's principle, after removal of the products of weathering by the production of complex-forming agents or by cellular cation uptake, the equilibrium shifts to the left to produce more K (Fig. 9.9).

Acidity in soils can be generated from several sources. K-solubilizing PGPR can also have a significant role in acid production. CO_2 is released from decomposition of soil organic matter (SOM) by soil microorganisms and respiration from plant roots and soil fauna. After being hydrated, CO_2 is converted into carbonic acid ($CO_2 + H_2O \leftrightarrow H_2CO_3$) (Fig. 9.9). In addition, decomposition of organic materials and sulfide oxidation by microorganisms result in the production of organic acids and sulfuric acid, respectively. Nitric and nitrous acids are also produced by nitrifying bacteria. The hydrogen ion released by these acids can react with aluminosilicate minerals (feldspars, micas, clays, etc.). For example, hydrogen ion can convert K feldspar (a primary mineral) into kaolinite, a secondary mineral (Fig. 9.9). As a result of this reaction and the breakdown of K-feldspar, H^+ is used up and K^+ is released to solution, a kind of ion-exchange reaction.

In general, such acidolysis by organic acids produced by KSB can either directly dissolve the mineral K as a result of slow releases of exchangeable K or readily available exchangeable K or chelate by both Al and Si ions associated with K mineral (Römheld and Kirkby 2010). For example, KSB had the ability to weather phlogopite through acidic dissolution and aluminum chelation of the crystal network (Abou-el-Seoud and Abdel-Megeed 2012; Meena et al. 2014). Increasing evidence also exists for a mechanism of direct silicate precipitation by bacteria via metal sorption at the cell membrane (Konhauser and Ferris 1996; Urrutia and Beveridge 1994).

As mentioned above, bacterial IAA increases root system and promotes an increasing amount of root exudation. The IAA-derived root system increase enhances the bacterial effect on mineral mobilization due to increased surface area for reactivity and helps improve nutrient uptake and mobilization of minerals (Gahoonia et al. 1997). Some of the roles of bacterial mediated root exudation in weathering K-bearing minerals include the following: (i) root exudation of high concentrations of organic acid anions can lower rhizosphere pH (Dakora and Phillips 2002); (ii) root exudates help by indirectly providing the substrates for the production of weathering metabolites by bacteria (Gahoonia et al. 1997); and (iii) root exudates include complex-forming agents (organic acids, extracellular polymeric substances, siderophores, etc.) (Shelobolina et al. 2012).

It has been reported that solubilization of K-bearing minerals by KSB is due to the production of organic acids like citric acid, tartaric acids, 2-ketogluconic acid, oxalic acid, gluconic acid, malic acid, propionic, fumaric, glycolic, and succinic acid (Keshavarz Zarjani et al. 2013; Prajapati and Modi 2012; Prajapati et al. 2012; Sheng and He 2006; Wu et al. 2005), which convert insoluble K (*i.e.,* mica, muscovite, biotite, feldspar) to soluble form of K (soil solution form) with the net result of increasing the availability of the nutrients to the plants. Gluconic, oxalic acids, α-ketogluconic, and succinic citric are the most efficient acids released by K-solubilizing PGPR strains that are effectively involved in the solubilization of insoluble K. In addition, the various types of organic acids produced by KSB differed with different organisms (Table 9.2) (Maurya et al. 2014; Verma et al. 2014; Zhang and Kong 2014).

Chelation Process

Chelation is a type of bonding of ions and molecules to metal ions. It involves the formation or presence of two or more separate coordinate bonds between a polydentate (multiple bonded) ligand and a single central atom. Usually these ligands are organic compounds. Chelating molecules might increase the dissolution rates of cations by forming strong bonds with them or with mineral surfaces (Uroz et al. 2009). Complex-forming agents (*e.g.,* organic acids, extracellular polymeric substances, siderophores) produced by K-solubilizing PGPR or in root exudates form a complex with cations dissolved from K-bearing minerals, removing the products of weathering. According to Le Chatelier's principle, with the uptake of K by plant or K-solubilizing PGPRs and/or removal of K by forming complex, the equilibrium is disturbed and K will be drawn upon from the non-exchangeable and soil mineral

Table 9.2 Mechanisms used by KSB for K solubilization

KSB	Action mechanism	References
Enterobacter hormaechei	Organic acids	Prajapati et al. (2013)
Paenibacillus mucilaginosus	Tartaric, citric, and oxalic acids	Liu et al. (2012)
Bacillus mucilaginosus	Acidification	Abou-el-Seoud and Abdel-Megeed (2012)
Burkholderia glathei	Siderophores and organic ligands	Calvaruso et al. (2007)
Burkholderia	Acidification and complexation	Uroz et al. (2007)
Bacillus circulans	Lipo-chitooligosaccharides production	Lian et al. (2002)
Bacillus mucilaginosus	IAA production	Han and Lee (2005)
Bacillus mucilaginosus *Bacillus edaphicus*	Production of citric, tartaric, and oxalic acid	Sheng (2005)
Bacillus spp.	Gluconic acid	Gundala et al. (2013)
Bacillus mucilaginosus	Polysaccharides	Liu et al. (2006)
Bacillus edaphicus	Production of organic acids like oxalic acid and tartaric acids and production of capsular polysaccharides (CPS)	Sheng and He (2006)
Rhizobium tropici	Production of tartaric acids and extracellular polysaccharides	Wang et al. (2015)
Pseudomonas aeruginosa	Acetic, citric, and oxalic acids	Badr et al. (2006)
Bacillus, Clostridium, and *Thiobacillus*	production of mucilaginous capsules containing of exopolysaccharides	Groudev (1987)
Cladosporium cladosporioides and *Penicillium* sp.	Production of protons, organic acids, siderophores, and organic ligands as chelating agents	Kumar et al. (2015), Meena et al. (2014, 2015)

fraction (Fig. 9.9). K-solubilizing PGPR secrete organic acids which act as chelating agents and quickly dissolve rock and silicon ions, ultimately releasing the K ions into the soil (Bennett et al. 1998).

Štyriakova et al. (2003) showed that K solubilization occurred by buildup of complex between organic acids and metal ions such as Fe^{2+}, Al^{3+}, and Ca^{2+}. Organic acids can either directly enhance dissolution by either a proton- or a ligand-mediated mechanism or indirectly enhance dissolution by the formation of complexes in solution with reaction products (Ullman and Welch 2002). Liu et al. (2006) demonstrated that polysaccharides strongly adsorbed the organic acids and attached to the surface of the mineral, resulting in an area of high concentration of organic acids near the mineral. It was suggested that the extracellular polysaccharides adsorbed SiO_2 and this affected the equilibrium between the mineral and fluid phases and led to the reaction toward SiO_2 and K^+ solubilization. Adhering to mineral surfaces and extracting nutrients from mineral particles by electron transfer, breaking the oxygen links, and chelating ions present in solution through their carboxyl and hydroxyl groups are some of the action mechanisms of organic acids and chelating molecules on mineral weathering (Welch et al. 2002). The latter indirectly accelerates the dissolution rate of the mineral by creating an imbalance between cation and anion concentrations in the solution. Bacterial organic acids have been found to facilitate the weathering of minerals through the formation of metal organic complexes with silicon ions to bring the K into solution, in addition to directly dissolving K from rocks (Bennett et al. 1998). According to previous discoveries, acidification does not seem to be the only solubilization mechanism, so that the ability to reduce pH in some cases is not consistent with the ability to solubilize K minerals by K-solubilizing PGPR (Liu et al. 2006; Sheng and Huang 2001; Subhashini and Kumar 2014; Zhang and Kong 2014). In general, acidolysis and complexolysis processes can be simultaneously used by K-solubilizing PGPR to impact mineral stability. *Agrobacterium* and *Bacillus* strains were described for their ability to weather phlogopite via aluminum chelation and acidic dissolution of the crystal network (Leyval and Berthelin 1989). Some of the selected examples about mechanisms used by KSB to solubilize K have been shown in Table 9.2.

Oxidation

Microbial Fe(II) oxidation as an additional mechanism of microbial weathering of K-bearing minerals having Fe (II) (e.g., biotite) in the rhizosphere has been reported, contributing to soil formation and providing K and Fe for plant nutrition (Shelobolina et al. 2012). Microbial oxidation of structural Fe (II) led to biotite changes similar to those found in nature, including a decrease in the unit cell b dimension toward dioctahedral levels and Fe and K release. Structural Fe (II) oxidation can entangle either direct enzymatic oxidation, followed by solid-state mineral transformation, or indirect oxidation as a result of forming aqueous Fe, followed by electron transfer from Fe (II) in the mineral to Fe (III) in solution. These cells indirectly attack biotite through oxidation of the sorbed Fe (II) in indirect oxidation that was generated because of electron exchange between structural Fe (II) and surface Fe (III) in the biotite (Shelobolina et al. 2012).

Production of CO_2

The weathering of K-bearing minerals may be the result of carbonic acid formation from the respiratory CO_2 release of the microorganisms and its subsequent reaction with water (Barker et al. 1998). Bacterial IAA can attract more rhizosphere bacteria in the rhizosphere by increasing more amount of root exudation, resulting in more production of CO_2. In addition, CO_2 can directly release K from K-bearing minerals (Rosenqvist et al. 2014). For example, CO_2 can convert K feldspar into muscovite and release K (Fig. 9.10). In general, K-solubilizing PGPR can dissolve K-bearing minerals by production of organic acids, IAA, siderophore, and polysaccharides. Previous studies showed K-solubilizing PGPR with other PGP traits. For example, Zhao et al. (2008) isolated bacterial strains with multiple beneficial activities such as IAA production, K solubilization, and siderophore production. Prajapati et al. (2013) reported that inoculation with IAA-producing PGPR strain *Enterobacter hormaechei* enhanced the root and shoot length of okra and mobilized K efficiently in plant when feldspar was added to the soil. The plants with more fibrous, branching roots increase nutrient (K)-absorbing surface. Nadeem et al. (2009) reported that ACC deaminase-containing rhizobacteria improved the uptake of K in maize

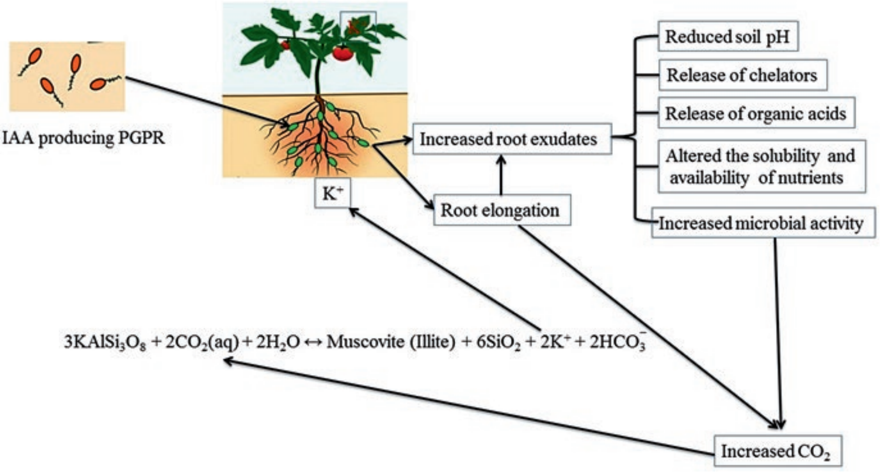

Fig. 9.10 The direct role of CO_2 in releasing K from K-bearing minerals

under salinity stress. They observed that these strains were strong colonizers of plant roots. The increased colonization by the K-solubilizing PGPR made the plants capable to explore more soil that might have improved the uptake of K indirectly. Previous studies showed that the solubilization and release of K through organic acids by K-solubilizing PGPR resulted in plant growth promotion leading to enhanced yield and production, which have been well reviewed (Ahmad et al. 2016; Bahadur et al. 2014; Das and Pradhan 2016; Meena et al. 2016; Sharma et al. 2016; Sindhu et al. 2014a, 2016; Velázquez et al. 2016; Zahedi 2016). The above discussion shows that bacterial strains have a number of potential mechanisms to solubilize K from insoluble sources and the contribution of these mechanisms in weathering of K-bearing minerals is variable. Among these mechanisms, the production of organic acids is one of the major mechanisms used by K-solubilizing PGPR. It has also been observed that K solubilization by the bacteria is affected by a large number of soil and environmental factors (Uroz et al. 2009).

9.3.3.3 KSB and Increased Availability of K and Other Nutrients

As discussed above, the production of organic acids is one of the major mechanisms used by KSB to solubilize K-bearing minerals and release K. The availability of some plant nutrients is also greatly affected by soil pH. Therefore, these bacteria can also provide the availability of nutrients such as P, Fe, Zn, Cu, and Mn. According to Prajapati et al. (2013), K-solubilizing PGPR can not only activate the insoluble K mineral but also change that into available P, Zn, and Fe. Sheng (2005) and Sheng et al. (2008) showed that inoculation of cotton and rape plants with the K-solubilizing PGPR strain *Paenibacillus edaphicus* NBT enhanced the N and P content in both plants and soil. Increases ranging from 26% to 30% were found in both plants when illite was added to soil as a source of insoluble K. The plant dry weight and the uptake of both K and N by tobacco seedlings enhanced significantly with respect to uninoculated controls mainly when the strain inoculated was *Klebsiella variicola* XF11 (Zhang and Kong 2014). Lin et al. (2002) indicated significant increases in K and P uptake in tomato plants inoculated with silicate-dissolving bacterium (*B. mucilaginosus*) compared with the non-inoculated plants. K-solubilizing PGPR also resulted in increased biomass and enhanced contents of P and K in sorghum plants than uninoculated control (Zheng and Tu 2005). Inoculation of K-solubilizing PGPR combined with K- and P-bearing minerals caused increase in dry matter yield of sorghum plants along with P and K uptake and also improved fertility in three different soils, i.e., clay, sandy, and calcareous soils (Badr et al. 2006). The organic acids and siderophores generated by PGPR could play a crucial role in the solubilization of elements such as K, Si, and Fe from the liquid medium containing acid-leached soil, muscovite, and biotite (Liu et al. 2006). In general, the K-solubilizing PGPR contribute to exudation of soluble compounds, decomposition of soil organic matter, and mobilization and mineralization of other nutrients (Abhilash et al. 2013; Archana et al. 2013; Diep and Hieu 2013; Rajawat et al. 2012; Zeng et al. 2012).

9.3.4 Sulfur (S)

Sulfur (S), an essential macronutrient required for growth, is increasingly becoming a limitation to crop yield and quality as a result of a reduction in atmospheric S levels due to the increasing use of low-S fuels and enhanced emission controls and crop varieties removing S from soil more rapidly (Fowler et al. 2005; Irwin et al. 2002). Since crop plants have become increasingly dependent on the soil to supply the S, these changes have had an important effect on agriculture. S is needed for the synthesis of proteins and a number of essential vitamins and cofactors and also is a constituent of the essential amino acids cysteine, cystine, and methionine. In agricultural soils, most of the soil S (>95%) is present in an organic form (Gahan and Schmalenberger 2014) as a heterogeneous mixture of forms, partly included in microbial biomass and partly in the soil organic matter. In addition, S present in soil is approximately 95% organically bound largely in one of the two major forms: sulfate esters and carbon-bonded S (sulfonates or amino acid sulfur) (Kertesz and Mirleau 2004). Sulfonates and sulfate esters are not directly available to plants which depend upon microorganisms in rhizosphere and soil for mobilizing these organic forms (Kertesz et al. 2007). S occurs in a variety of oxidation states with three oxidation states of −2 (sulfide and reduced organic sulfur), 0 (elemental sulfur), and +6 (sulfate) being the most significant in nature. Plants obtain S in the form of sulfate (SO_4^{2-}), which is the dominant plant-available source of S and constitutes less than 5% of the total soil S (Autry and Fitzgerald 1990), while to a lesser extent atmospheric reduced S may be utilized (Leustek et al. 2000). Chemical or biological agents help transformation of S from one state to another. A biogeochemical cycle which characterizes these transformations includes many oxidation-reduction reactions.

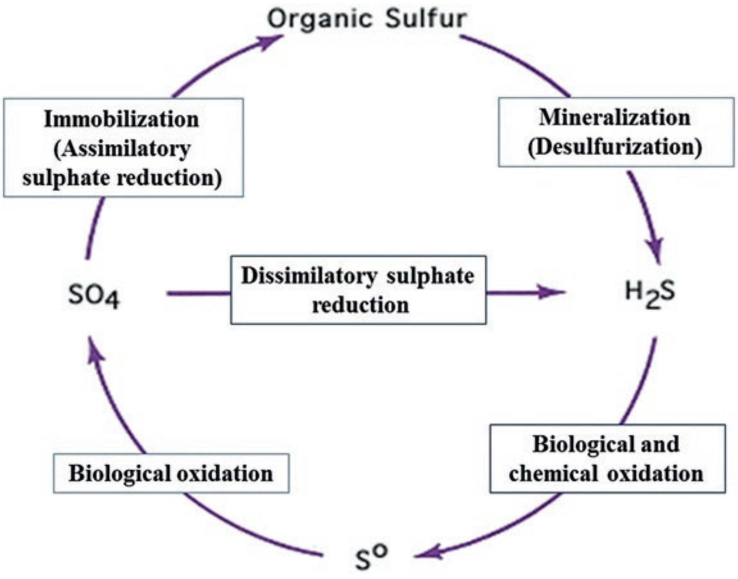

Fig. 9.11 The major processes of transformation involved in the cycling of S in soil

9.3.4.1 Action Mechanisms of Sulfur (S) Availability by PGPR

Similar to some other nutrients, S is also subjected to biological alterations in soil by the soil bacteria. The major processes of transformation involved in the cycling of S in soil are (i) mineralization of organic S to the inorganic form (H_2S), (ii) immobilization or assimilation of S into organic compounds by plants or microorganisms, (iii) oxidation of S and inorganic S compounds, and (iv) reduction of S and incompletely oxidized inorganic compounds of S (Fig. 9.11). Due to having indirect and direct functions in these processes, microorganisms especially bacteria can increase the availability of S to plants, which are explained as follows.

Mineralization of Sulfur (S)

Plant S nutrition depends primarily on the uptake of inorganic sulfate. Due to interconversion of sulfate ester-S and carbon-bonded S to inorganic sulfate by soil microorganisms, it has been shown that the sulfate ester and sulfonate pools of soil S are also plant bioavailable (Kertesz and Mirleau 2004). Aerobic and anaerobic heterotrophic bacteria (*Pseudomonas* and *Clostridium*) release S from sulfate-esters using sulfatases ($R\text{-}O\text{-}SO_3^- + H_2O \rightarrow ROH + H^+ + SO_4^{2-}$); however, release of S from sulfonates is catalyzed by a bacterial multicomponent monooxygenase system (Gahan and Schmalenberger 2014). Splitting of the C-O bond of aliphatic sulfate esters and the O-S bond of aromatic sulfate esters is performed by the enzymes of alkylsulfatase and arylsulfatase, respectively (Kertesz 2000). Some bacteria such as *Pseudomonas, Klebsiella, Salmonella, Enterobacter, Serratia,* and *Comamonas* are able to mobilize sulfate esters (Hummerjohann et al. 2000). Sulfide can be produced by anaerobic bacteria as a result of the breakdown of proteins to amino acids and further degradation of amino acids to sulfide (R-SH → R + H_2S) (desulfurization).

Immobilization of Sulfur (S)

Sulfur (S) immobilization is microbial conversion of inorganic S compounds to organic S compounds, first to sulfate esters and subsequently to carbon-bound sulfur (Kertesz and Mirleau 2004). S is used for the biosynthesis of amino acids and proteins by bacteria (assimilatory sulfate reduction) in this process. Bacteria reduce only enough sulfates to meet their nutritional requirements for S. During the study period, soil microorganisms were capable of binding all the available sulfate into microbial biomass. In general, PGPR in the presence of labile C serve as a sink for S, by rapidly immobilizing it; therefore PGPR become a source of S to plants upon its release from their cells. Release of S immobilized by PGPR primarily occurs when cells die.

Oxidation of Sulfur (S)

Sulfur (S) oxidation is the process by which a variety of microorganisms convert hydrogen sulfide (H_2S) into elemental sulfur (S_0) by partial oxidation, or sulfate (SO_4^{2-}), which can be used by the plants, while the acidity produced by oxidation helps to solubilize plant nutrients and improve alkali soils (Wainwright 1984). Instead of H_2S, also other sulfur compounds like thiosulfate ($S_2O_3^{2-}$) and tetrathionate ($S_4O_6^{2-}$) can be converted to sulfate ($S_0 \rightarrow H_2S \rightarrow S_2O_3^{2-} \rightarrow S_4O_6^{2-} \rightarrow S_3O_6^{2-} \rightarrow SO_3^{2-} \rightarrow SO_4^{2}$). Thiobacilli (*e.g.,* bacteria of the genus *Thiobacillus*) play an important role in S oxidation in soil. *Beggiatoa, Sulfolobus*, *Thermothrix*, *Thiobacillus*, and *Thiothrix*, known as colorless sulfur-oxidizing bacteria (Janssen et al. 1998), are the most important chemolithotrophic sulfur-oxidizing bacteria (SOB). S oxidation is the most important step of S cycle, which improves soil fertility and decreases pH soil and subsequently increases the availability of micronutrients and P. Photoautotrophic or chemolithotrophic sulfide-oxidizing bacteria use sulfide as an electron donor and convert it to S or sulfate (Robertson and Kuenen 2006). The CO_2 and oxygen (aerobic species) or nitrate and nitrite (anaerobic species) are used as the terminal electron acceptors in photoautotrophic and chemolithotrophic sulfide-oxidizing bacteria, respectively. Light energy and oxidizing reactions supply directly energy needed for metabolism of photoautotrophic SOB and chemolithotrophic SOB, respectively. Among photoautotrophic sulfide-oxidizing bacteria, the green SOB like *Chlorobium*, *Prosthecochloris*, *Chloroherpeton*, *Pelodictyon,* and *Ancalochloris* and purple SOB such as *Chromatium*, *Allochromatium*, *Thioalkalicoccus*, *Thiococcus*, *Thiorhodococcus*, *Thiocystys*, and *Thiospirillum* (Tang et al. 2009) are the most frequent. In addition to being oxidized biologically, oxidation of the reduced S compound is also carried out chemically by ferric iron as the oxidizing agent, and iron-oxidizing bacteria are utilized to regenerate the ferric iron (Fe^{3+}) for further use (Pagella and De Faveri 2000).

Reduction of Sulfur (S)

In addition to reductive reactions, bacteria have also a major role in reductive reactions of the biological S cycle (Kertesz and Mirleau 2004). Sulfate, in turn, can be reduced back to sulfide by sulfate-reducing bacteria such as *Desulfovibrio* and *Desulfatomaculum* (Tang et al. 2009). Sulfate in the absence of oxygen functions as a terminal electron acceptor in metabolic pathways for anaerobic respiration and is converted to sulfide (dissimilatory sulfate reduction). Although dissimilatory sulfate reduction results in decrease of plant-available sulfate, H_2S produced by the reduction of sulfate is further oxidized by some of the green and purple phototrophic bacteria to release elemental sulfur (S_0). The latter can also be oxidized to sulfate by SOB once again.

9.4 Action Mechanisms of PGPR in Availability of Micronutrients

9.4.1 Production of Organic and Inorganic Acids

Since most of the nutrients (micronutrients especially) tend to be less available when soil pH is above 7.5 (Fig. 9.2), it seems that decreasing soil pH (a slightly acidic pH, *e.g.,* 6.5–6.8) is one of the action mechanisms of PGPR in the availability of these nutrients to plants. Due to strongly being adhered to soil particles, these metals are not easily available for uptake by plants in most of the metalliferous soils (Gamalero and Glick 2012). In this context, PGPR producing acid such as PSB, sulfur-oxidizing bacteria (SOB), and nitrifying bacteria are very promising agents. By secreting low-molecular-weight organic acids, the PGPR listed above can solubilize the insoluble and biologically unavailable metals and subsequently facilitate the bioavailability of these nutrients for plant uptake (Fig. 9.12) (Becerra-Castro et al. 2011, 2011; Li and Ramakrishna 2011; He et al. 2013).

9.4.2 Production of Chelating Agents

In addition to soil pH, chelation process can increase nutrient availability to plants by different ways (Fig. 9.13). Hence, the natural chelating agents produced by PGPR may be considered as the other action mechanism of PGPR in the availability of nutrients to plants. Hydroxamate siderophores, organic acids, and amino acids are some of the most important substances possessing this nature, which are naturally produced by soil microorganisms. These substances are essential in natural ecosystems to solubilize and transport these nutrients to plant roots. For example, iron occurs mainly as Fe^{3+} and forms insoluble hydroxides and oxyhydroxides, and thus is not easily available to both plants and microorganisms (Ahemad and Kibret 2014). Under iron-limiting conditions to acquire Fe, PGPR secrete low-molecular-weight siderophores, which are iron chelators with exceptionally strong affinity for ferric iron (Fe^{3+}) (Schalk et al. 2011). Despite their preferential affinity for Fe^{3+}, they

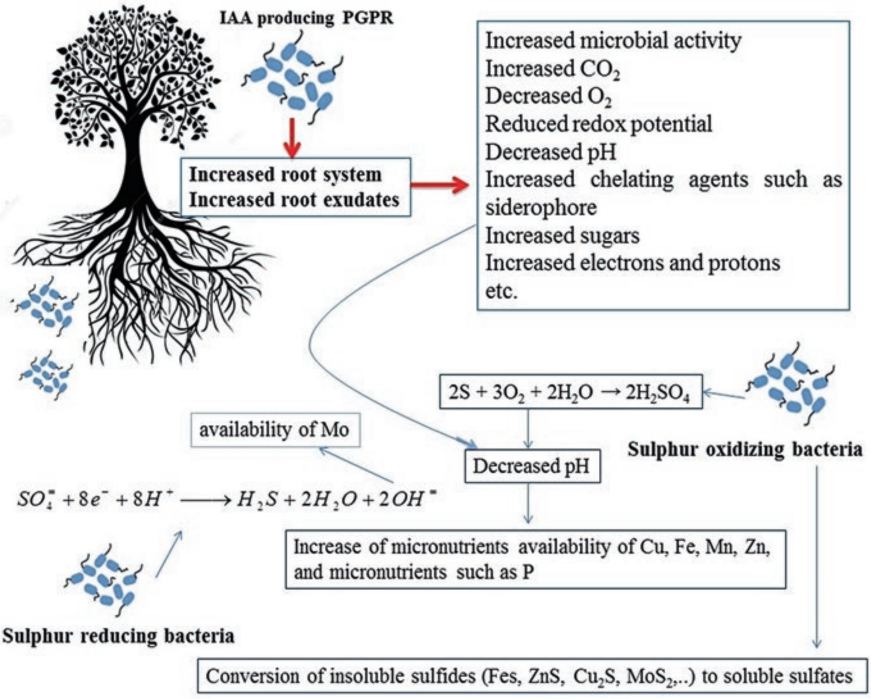

Fig. 9.12 The role of PGPR in increasing the availability of micronutrients to plant by different mechanisms

can also chelate several other metals such as Mg^{2+}, Mn^{2+}, chromium (Cr^{3+}), gallium (Ga^{3+}), cadmium (Cd), Zn^{2+}, Cu^{2+}, Ni, arsenic (As) and lead (Pb), and radionuclides, including plutonium (Pu^{4+}) with variable affinities (Nair et al. 2007; Rajkumar et al. 2010; Schalk et al. 2011). Glycolic, oxalic, malonic, tartaric, lactic, citric, α-ketogluconic, piscidic, succinic, malic, valeric, and formic are some of the known organic acids with chelating properties similar to siderophores (Panhwar et al. 2013). In addition to producing chelating agents, PGPR such as K-solubilizing PGPR can increase metal bioavailability in metal-stressed soils by producing biosurfactant, which aids in metal release from soil particles (Gamalero and Glick 2012; Singh and Cameotra 2013).

9.4.3 Production of IAA

As mentioned above, phytohormone (IAA)-producing PGPR can enhance indirectly the availability of micronutrients by improving root development and growth and root exudates. The exudates released by roots of plant also attract the wide range of PGPR with other plant growth-promoting traits such as siderophore production, phosphate solubilizing, and ACC deaminase production. These bacteria

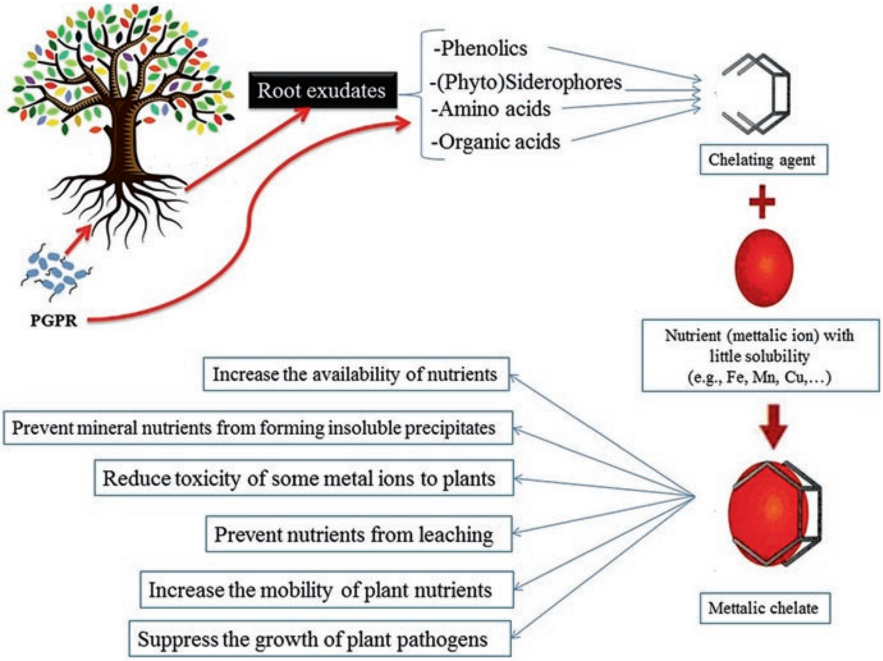

Fig. 9.13 The role of chelating agents produced by PGPR in increasing nutrient availability to plants by different ways

can also enhance the availability of micronutrients by siderophore as a chelating agent, production of acid, and decrease of ethylene and subsequent increase of root system (Fig. 9.6). Root exudates can also act as binding material/cementing agents of soil and, thus, improve soil structure and regulate and maintain the microbial population near the root surface. Microbial activity near the root surface plays an important role in the development and rooting pattern of the plant. In addition, attracted PGPR themselves also produce many exudates, which are very helpful in plant nutrition and growth. The presence of various composites of amino acids, organic acids, sugars, vitamins, purines, adenine, guanine, cytidine, uridine, enzymes (*e.g.,* phosphatase), and some gaseous molecules (*e.g.,* CO_2) in root exudates (Dakora and Phillips 2002) enhances the availability of micronutrients. A fraction of these exudates are further metabolized by PGPR in the vicinity as C and N sources, and some bacterium-oriented molecules are subsequently retaken up by plants for growth and development (Sheng and He 2006). Another nutritional effect that organic acids have in root exudates is acidification of the rhizosphere, which enhances the availability of micronutrients. In general, PGPR, especially IAA-producing bacteria, can increase the availability of micronutrients in the soil directly by the production of different compounds (such as carboxylates, phenolic compounds, etc.) or indirectly through affecting plant growth and hence the production of root exudates (Fig. 9.14) (Badri and Vivanco 2009). To understand the action

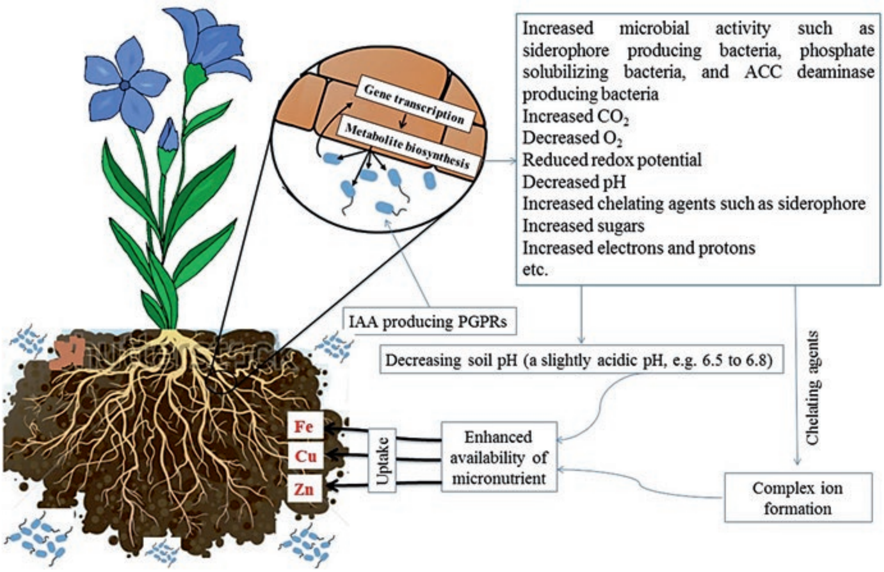

Fig. 9.14 Impact of PGPR on micronutrients acquisition and root functioning. PGPRs can modulate root development and growth through the production of phytohormones such as IAA, secondary metabolites. PGPR also influence plant nutrition via ACC deaminase, solubilization of phosphorus, or siderophore production, and modify root physiology by changing gene transcription and metabolite biosynthesis in plant cells

mechanism of PGPR in the availability of micronutrients to plant, two nutrient elements Fe and Mn are explained in more detail as follows.

9.5 Iron (Fe)

As an essential nutrient for plants, iron (Fe) is crucial for a variety of cellular functions and essential physiological processes, including respiration and photosynthesis and a necessary cofactor for many enzymatic reactions (Zuo and Zhang 2010). Under aerobic conditions, Fe exists predominantly as Fe^{3+} and reacts to form highly insoluble hydroxides and oxyhydroxides that are basically unavailable to plants and microorganisms (Desai and Archana 2011; Zuo and Zhang 2010). High soil pH reduces while acidic soil conditions increase Fe availability. As pH increases by one unit, activity of Fe^{3+} decreases by 1000-fold. In most soils, Fe is present in large quantities, but mainly in forms that are not available to plants (Schmidt 2003; Wintergerst et al. 2007). It has been reported that most plants need the concentrations of soluble Fe at 10^{-4} to 10^{-8} M (optimal soils usually slightly acidic) for their optimal growth. However, 10^{-9} M or lower concentrations of soluble Fe (calcareous or alkaline soils with low bioavailable Fe) are insufficient for plant growth and plants may develop a Fe deficiency-associated leaf chlorosis as a disease symptom.

There are many factors that affect the availability of Fe in the soil. The availability of Fe strongly depends on soil redox potential (redox change) and pH. When decreasing redox potential and pH, availability of Fe increases. PGPR can increase the availability of Fe by decreasing soil redox potential and pH.

9.5.1 Fe Acquisition Strategies by Plants

Despite the abundance of Fe in soils, its availability for plants and microbes is low. Plants and microorganisms have evolved active strategies of Fe uptake. Mobilization of Fe is the prerequisite for uptake of Fe into the roots, which is achieved by two different strategies in the plant kingdom. These strategies are named as strategy I and strategy II. In strategy I, all plant species (monocotyledonous and dicotyledonous plants), except grasses, acidify the rhizosphere and produce organic products. In addition, Fe^{3+} is reduced into Fe^{2+} by a Fe chelate reductase enzyme, converting Fe (III) to Fe (II) (Hartmann et al. 2008). Subsequently, Fe^{2+} can be taken up by a membrane-bound Fe (II) transporter. However, strategy II grasses handle Fe deficiency by the synthesis and secretion of siderophores and uptake of them by the activation of the Fe^{3+} siderophore transporter in the plasmalemma of root cells (Altomare and Tringovska 2011; Charlson and Shoemaker 2006; Curie et al. 2001; Guerinot 2010; Wintergerst et al. 2007).

9.5.2 Action Mechanisms of PGPR in Fe Availability

It has been known that strategies I and II are often not efficient enough to meet the needs of the plants growing especially in calcareous and alkaline soils. Studies show that many IAA- and siderophore-producing PGPR strains could improve iron nutrition (Etesami et al. 2015a; Jin et al. 2006; Ramos-Solano et al. 2010).

9.5.2.1 Production of Siderophores

Most plant-associated bacteria can produce iron chelators called siderophores in response to low iron levels in the rhizosphere. Siderophores are low-molecular-weight organic compounds, which have high affinity to bind some elements such as Fe^{3+} as well as other metal ions and increase their availability (Boukhalfa and Crumbliss 2002). Several examples of increased Fe uptake in plants with concurrent stimulation of plant growth as a result of PGPR inoculations have been reported (Barzanti et al. 2007; Burd et al. 2000; Carrillo-Castañeda et al. 2002; Lemanceau et al. 2009). Many studies have demonstrated that microbial siderophores can be used as Fe source for plants with strategies I and II (Fernández and Winkelmann 2005; Jin et al. 2006; Johnson et al. 2002; Rasouli-Sadaghiani et al. 2014; Robin et al. 2008; Siebner-Freibach et al. 2003; Vansuyt et al. 2007).

According to results of previous studies, it is most probable that the bacterial siderophore is not absorbed by the plant, and iron is obtained through a reduction-based mechanism (Johnson et al. 2002). Ferric siderophores are transported into cells via specific Fe-siderophore membrane receptors, allowing siderophore release for subsequent reuse (Lemanceau et al. 2009) (Fig. 9.15). It has been found that the ability of siderophores in supplying Fe^{+3} to the root surfaces and in the intracellular spaces of root cells is the most important function of these chelating compounds in the gramineous plant nutrition. Accordingly, the higher concentrations of Fe^{+3} ions, which are available to the root phytosiderophores, enhance their subsequent absorption by plants (Sharma et al. 2003). It has been shown that ligand exchange is another theory on the supply of Fe by siderophores (Latour et al. 2009; Yehuda et al. 1996). This theory has been suggested for iron, showing that Fe supplied by siderophores interacts with phytosiderophores in a ligand exchange reaction and is finally absorbed by the phytosiderophores. This theory confirms the indirect role of siderophore in Fe uptake (Shweta et al. 2008). Among different known microbial siderophores, plants are capable of using hydroxamates, ferrichrome, rhodotorulic acid, desferrioxamine B, agrobactin, as well as catecholate-hydroxamate (Fernández and Winkelmann 2005). Generally, compared to most microorganisms, most plants can grow at very low concentrations of Fe (O'Sullivan and O'Gara 1992); therefore many plants can take up iron in the presence of siderophore-producing microorganisms. In addition to high affinity for Fe (III) ions, siderophores can also form complexes with other bivalent ions (and including phosphates and other micronutrients) that can be assimilated by the plant (Ramos-Solano et al. 2010).

9.5.2.2 Production of IAA

As previously mentioned, the production of root and microbial exudates is an important parameter determining the availability of nutrients in the rhizosphere. Organic acids present in root and microbial exudates result in acidification of the rhizosphere (Dakora and Phillips 2002), which can, in turn, contribute to plant growth by mobilizing nutrients such as Fe. Because of the function of IAA in secreting root exudates (rhizodeposits) and increasing rooting system and since these exudates are involved in acidifying rhizosphere and in providing a reducing condition required for converting Fe^{3+} to Fe^{2+}, it may be suggested that IAA-producing PGPR can also solubilize insoluble Fe sources and induce plant growth and iron uptake in a similar manner to strategy I in plants (Fig. 9.15). For example, protons and electrons are secreted within carbon compounds as undissociated acids or compounds with reducing capabilities. Some of the compounds in root exudates are able to form Fe complexes that improve availability. High-molecular-weight components (i.e., proteins, mucilage) and low-molecular-weight compounds (*i.e.,* secondary metabolites, organic acids, carbohydrates, amino acids, phenolics) are typically the dominant soluble-reduced carbon compounds in rhizodeposits (Badri and Vivanco 2009; Wen et al. 2007). The consumption of O_2, due to respiration by the root (increase of root system due to bacterial IAA) and associated microflora (increase of microflora activity due to production of more root exudates), can also result in steep redox gradients in the rhizosphere (Etesami et al. 2015a, b; Hartmann et al. 2008). Likewise, chelating agents present in root and microbial exudates such as organic acids are capable of chelating Fe^{3+} and making it available to plant roots in a similar manner to strategy II in plants (Fig. 9.15).

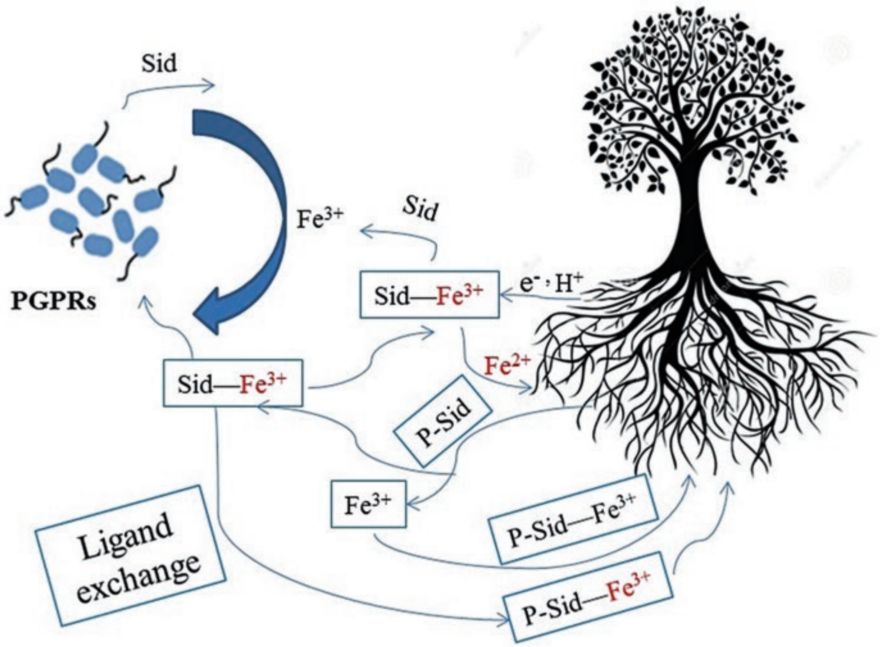

Fig. 9.15 Schematic representations of role of siderophore (Sid)-producing PGPR in enhancing iron availability for plant. In non-grass species (Strategy I), acidification of the rhizosphere occurs in part through the activity of a plasma membrane H^+-ATPase. This H^+ excretion contributes to the solubilization of Fe^{+3}, which is reduced to Fe^{+2} by the FRO_2 ferric chelate reductase, transferring electrons (e^-) from NADPH to Fe^{+3} (Lemanceau et al. 2009). In grasses, Strategy II involves the synthesis of phytosiderophores (P-Sid). P-Sid is secreted from the roots by an uncharacterized mechanism into the rhizosphere where it chelates Fe^{+3}. The Fe^{+3}–P-Sid complex is then transported into the epidermal cells of the roots. PGPRs do not take up Fe^{+3}-Sid complexes, but rather obtain iron through a reduction-based mechanism involving Fe-Sid membrane receptors, acquiring Fe^{2+} while releasing Sid for subsequent reuse. Sid increases the Fe^{+3} pools in the rhizosphere, increasing Fe^{+3} available to the root P-Sid. P-Sid that has a higher affinity for Fe^{3+} than Sid may acquire it via ligand exchange

9.6 Manganese (Mn)

As a micronutrient, manganese (Mn) is essential for many plant functions (as a component of enzymes) and is also involved in photosynthesis and root growth. Mn as free Mn^{2+} in the soil is readily available to plants, and as oxides is of low solubility. The proportion of Mn in various forms in the soil is dependent both on chemical reactions and on microbial activity. As previously mentioned (Fig. 9.2), high soil pH greatly reduces the solubility of soil Mn, and therefore its availability to roots. Thus, Mn deficiency is most likely to occur in soils that are alkaline or have been limed. Mn is a nutrient element and its availability in the rhizosphere is affected by two major factors, namely redox condition and pH. In oxidized soils, Mn is present in its oxidized form, Mn^{4+}, in the low-soluble mineral pyrolusite. It has been known that

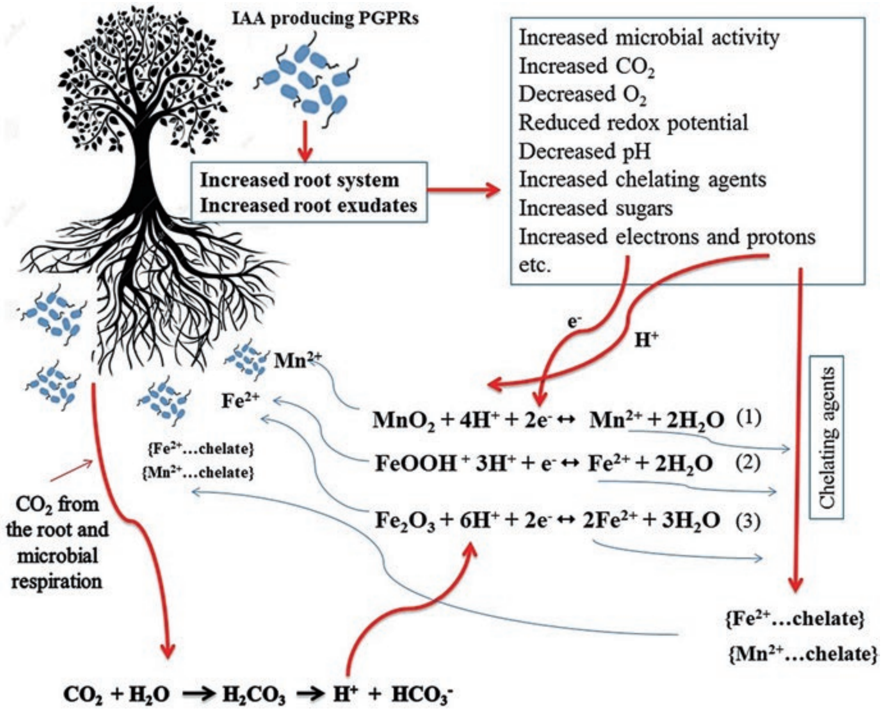

Fig. 9.16 The schematic representation of role of PGPR in the availability of Mn and Fe to plant by affecting plant (root) growth and hence plant root exudates. The electrons and protons required to the reduction of Mn and Fe in reactions (1), (2), and (3) are supplied by the decomposition of carbonaceous compounds and the proton excretion system of root cells, respectively. The roots and PGPR by producing chelating agents (phenolic compounds, organic acids) can form soluble complex with Mn, Fe, and other elements avoiding the reprecipitation of them

some PGPR can increase the availability of this element to plants. For example, PGPR such as *Bacillus*, *Pseudomonas*, and *Geobacter* could reduce oxidized Mn^{4+} to Mn^{2+}, which is the chemical form that is metabolically useful for plants (Osorio Vega 2007). These bacteria can affect Mn availability in the soil mostly by affecting plant growth and hence plant root exudates (Dutta and Podile 2010; Miransari 2011). Increased root exudates originated from bacterial activities in turn supply electrons (by the decomposition of organic molecules present in root exudates) and protons (by the proton excretion system of root cells) required for the reduction of Mn in the following reaction:

$$MnO_2 + 4H^+ + 2e^- \leftrightarrow Mn^{2+} + 2H_2O$$

Consequently, the activity of Mn reducers is highly favored in the rhizosphere (Osorio Vega 2007). By producing electron and H^+, applications of organic matter (OM) can also favor the reduction of Mn (Hue et al. 2001). Therefore, in alkaline soils where Mn usually is insoluble the rhizosphere effect and application of OM can be beneficial. In addition, roots and PGPR can produce chelating agents (phenolic compounds, organic acids) that form soluble complex with Mn, Fe, and other elements avoiding the reprecipitation of them (Fig. 9.16).

9.7 Concluding Remarks and Future Perspectives

It is evident that PGPR have a high potential to be used in the management of nutrient-deficient soils. Using PGPR to increase the availability of nutrition elements in soil is an attractive proposition for developing a more sustainable agriculture. These PGPR have an important role in the cycling of nutrient elements in soil-plant systems and it is anticipated that better understanding of their contribution to mobilizing soil nutrients and plant nutrient nutrition will provide an opportunity for developing more nutrient-efficient and sustainable agricultural systems and improved knowledge of ecosystem function. Developing the proper formulation and delivery systems to ensure survival and effective establishment of target PGPR within the rhizosphere is a main requirement for prosperous deployment of bacterial inoculants (Richardson and Simpson 2011). Increased knowledge concerning the beneficial interactions of PGPR with plants and a proper screening will be of special importance for sustainable agriculture that depends on biological processes and resources, rather than on the use of agrochemicals for maintaining soil fertility and plant health. Previous studies clearly demonstrate the presence of one or more than one type of PGP character in majority of the bacterial strains. A bacterial strain possessing multiple PGP traits is expected to indicate better response than those having single PGP characteristic. However, it would be desirable to examine whether all the traits of PGP are expressed concurrently or at different phases of growth of the bacteria. In other words, since many PGPR possess several of PGP traits simultaneously, different mechanisms at various times during the life cycle of the plant can be used. However, the exact modes by which PGPR promote plant growth at a specific step in life cycle are not fully understood (Bhattacharyya and Jha 2012), which need further studies in the future. In addition, certain issues, such as what should be an ideal and universal delivery system, how to improve the efficacy of biofertilizers, how to stabilize PGPR in soil systems, and how nutritional and root exudation aspects could be controlled in order to get maximum benefits from PGPR application, have not been well known until this moment, which are needed to be addressed by scientists in the future. Biotechnological and molecular approaches may possibly develop more understanding about PGPRs' mode of actions that will result in more successful plant–microbe interaction and prosperous application of the beneficial bacteria (Khalid et al. 2009).

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