

Enhanced Phosphorus Fertilizer Use Efficiency with Microorganisms

Hassan Etesami

Abstract

Phosphorus (P) is an essential nutrient in plant development and growth, and its deficiency is one of the major factors limiting crop yields worldwide. Although soils generally possess a large amount of total P (400–1000 mg kg⁻¹), only a small ratio (1.00-2.50%) is immediately available for uptake of plants since 75–90% of added P is precipitated by metal-cation (calcium, iron, and aluminum) complexes and quickly becomes fixed in soils. The nature of calcareous soils in the arid and semiarid regions of the world has made P use efficiency (PUE) low (10-25%) in this land. For this reason, farmers have added a significant amount of these chemical fertilizers to the cultivated land to achieve the desired result every year. Low-use efficiency of the P fertilizers and their continuous long-term use have led to environmental pollution. The use of chemical P fertilizers cannot be omitted at this time without intensely diminishing food production. However, it is known that the compound use of phosphate-solubilizing microorganisms (PSMs) and chemical P fertilizers can reduce the negative impacts of overuse of these fertilizers and improve PUE in an efficient and environmentally prudent manner. Among the PSMs, it can be mentioned arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR). AMF increase the growth, yield, and absorption of nutrients in the plant mostly by increasing the effective absorptive area of the roots by formation of an extensive extraradical hyphal network, and PGPR also contribute directly to increasing the solubilization of insoluble P compounds in the soil and thereby plant growth through mechanisms like producing organic and inorganic acids, increasing root surface area, and improving beneficial symbiosis with host plants at different stages of plant growth. In addition, it is known that the plants inoculated with a combination

H. Etesami (🖂)

Agriculture & Natural resources Campus, Faculty of Agricultural Engineering & Technology, Department of Soil Science, University of Tehran, Tehran, Iran e-mail: hassanetesami@ut.ac.ir

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of PGPR and AMF can express synergistic effect to augment plant growth indices while maintaining safe natural resources such as P stocks. This chapter is a critical summary of the efforts in using phosphate-solubilizing bacteria (PSB) and phosphate- solubilizing-AMF for augmenting the use efficiency of P fertilizers.

Keywords

Arbuscular mycorrhizal fungi \cdot Bio-fertilizer \cdot Compound use \cdot Fertilizer use efficiency \cdot PGPR \cdot Sustainable agriculture

Abbreviations

ACC	1-Aminocyclopropane-1-carboxylate
AMF	Arbuscular mycorrhizal fungi
СК	Cytokinins
GAs	Gibberellins
IAA	Indole-3-acetic acid
NFR	N ₂ -fixing rhizobia
Ν	Nitrogen
Р	Phosphorus
PGP	Plant growth promoting
PGPEB	Plant growth-promoting endophytic bacteria
PGPR	Plant growth-promoting rhizobacteria
PSB	Phosphate-solubilizing bacteria
PSF	Phosphorus-solubilizing fungi
PSMs	Phosphate-solubilizing microorganisms
PUE	P use efficiency
RP	Rock phosphate
TCP	Tricalcium phosphate

8.1 Introduction

Soil is one of the largest vital systems in the planet Earth and will face major challenges in the coming decades. By 2050, the human population is expected to exceed 9.7 billion (Nations 2015), which will result in up to 50% increase in food and fuel demand. Given this issue, supplying food will face a huge challenge for many parts of the world. In general, with the growing world population, more food is needed to be produced via intensive agriculture, which requires large quantities of fertilizer (Fallah Nosratabad et al. 2017; Vitousek et al. 1997; Ashoka et al. 2017). Chemical fertilizers are essential components of modern agriculture because they provide

necessary plant macro- and micronutrients (Adesemoye and Kloepper 2009; Martinez 2010; Kumar et al. 2017b). Phosphorus (P) fertilizers are one of these fertilizers. Phosphorus is a necessary nutrient and the most limiting element after nitrogen (N) for plants. Phosphorus plays several key roles in the plant, including participation in energy transfer reactions, root expansion, root and stem strength, flower and seed formation, photosynthesis, molecular nitrogen (N₂) fixation in legumes, product quality, resistance to plant diseases, deformation of sugar into starch, and transfer of genetic traits in plants (Cockefair 1931). In addition, P is part of the protein of cells and plays a special role as part of the nucleus protein, cell membrane, and nucleic acids (Cockefair 1931; Theodorou and Plaxton 1993). Accordingly, sufficient P nutrition is necessary for proper growth and yield of all plants (Cockefair 1931).

There are large amounts of P in the form of apatite minerals, which are the original source of all P, complexes of iron(III) phosphate (FePO₄), aluminum phosphate $(AIPO_4)$ and calcium phosphate $(Ca_3(PO_4)_2)$, and P adsorbed on clay particles in the soil. In addition, organic P, which originates from organic sources like microbial residues, manures, and plant tissues (as inositol phosphatases (phytate), phosphoesters, phospholipids and nucleic acids (phosphodiesters), and phosphotriesters), accounts for up to 30-65% of total P in soils (Islam and Hossain 2012; Rodríguez and Fraga 1999). Despite the high amount of P in the soil (400–1000 mg kg⁻¹), only a very low concentration of P (1.00–2.50%) is available to plants (Chen et al. 2008; Meena and Meena 2017). Since mineral and organic P are immobilized and mostly unavailable, many soils are actually P-deficient (Adesemoye and Kloepper 2009; Dey 1988; Meena and Lal 2018). Phosphorus is absorbed by the roots of plants from the soil solution mainly as orthophosphate ions ($H_2PO_4^-$ and HPO_4^{2-}). Phosphorus in pH 5.5–7 is relatively available to plant, respectively, at soil pH less than 5.5 and more than 7, due to the high reactivity of P with some metal complexes such as Fe, Al, and Ca resulting in the precipitation or adsorption of between 74 and 90% of P in the soil (Gyaneshwar et al. 2002; Leytem and Mikkelsen 2005; Yadav et al. 2018a). In general, the solubility of these P compounds (Ca–P, Fe–P, and Al–P), as well as organic P, is extremely low, and only very small amounts of soil P are in solution at any one time. In addition to soil pH, the amount of plant available P in the soil is controlled by other factors such as Ca ion concentration, soil organic matter content, type and amount of clay, soil moisture, soil texture, secretion, and density of root (Al-Rohily et al. 2013; Meena and Yadav 2015).

In order to compensate for the shortage of P, large quantities of phosphate fertilizers are added to the soil by farmers annually. The majority of P fertilizers are absorbed by solid particles and stored in a solid phase of soil (Fallah Nosratabad et al. 2017; Leytem and Mikkelsen 2005; Buragohain et al. 2017; Kumar et al. 2017a). In calcareous soils, such as Iran's soils, which have evolved in dry and semiarid climates, high pH, high calcium carbonate content, the low amounts of organic matter, and low soil moisture (drought stress) have caused the amount of plant available P to be less than the amount of P needed to provide the optimal growth of most agricultural products (Al-Rohily et al. 2013; Leytem and Mikkelsen 2005; Meena et al. 2015d). The use of chemical fertilizers containing this nutrient, especially superphosphates, which are one of the common ways of compensating for the deficiency of this nutrient in soil, is not very effective in calcareous and alkaline soils because most of the P in the fertilizer, after entering the soil, gradually turns into insoluble form and is stored in a plant nonavailable form in the soil (Leytem and Mikkelsen 2005; Yadav et al. 2017c; Dadhich and Meena 2014).

Although the application of chemical fertilizers including P fertilizers, as the best means to resolve P deficiency in crop plants (Etesami and Maheshwari 2018; Meena and Yadav 2014); Dhakal et al. 2015), initially has had an impact on the increase in yield, the excessive use of these inputs has led to a reduction in soil fertility, environmental degradation, and unexpected harmful environmental effects such as surface runoff of P, changes in the food web, eutrophication of aquatic ecosystems, and reduction in biodiversity (Adesemoye and Kloepper 2009; Verma et al. 2015c). In addition, the use efficiency of chemical fertilizers is now theoretically up to its highest level, which means that more use of chemical fertilizers can hardly increase yields. It has been known that the use efficiency of P fertilizers in calcareous and alkaline soils does not exceed 20%. Sometimes up to 90% of applied P in soil is precipitated by metal complexes in the soil (Gyaneshwar et al. 2002; Meena et al. 2015e; Yadav et al. 2018b).

Although most plants (P-efficient plants) have evolved diverse array of strategies to uptake sufficient P under P- restricting conditions and cope with P-stressed conditions (i.e., carbon metabolism, modifications to root morphology, exudation of organic and inorganic acids, protons, and enzymes of acid phosphatase, membrane structure, etc.) (Islam and Hossain 2012; Karthikeyan et al. 2002; Lambers et al. 2006, 2015; Mudge et al. 2002), studies have shown that this strategy cannot meet the plant's need for this nutrient (Etesami and Beattie 2017; Meena et al. 2016a).

The phosphorus mobility in soil is very low and cannot respond to the rapid absorption of P by plant. This leads to the emergence and development of phosphate-depleted areas adjacent to the contact surface of roots with soil. Therefore, the plant needs an auxiliary system that can easily go beyond these P-depleted areas and, by developing a wide network around the root system, receive P from a larger volume of adjacent soil (Etesami and Beattie 2017; Lambers et al. 2006; Varma et al. 2017a; Datta et al. 2017a).

Biological fertilizers are considered to be the most effective plant assistants for the supply of P at the optimal level, which are prepared based on the selection of a variety of useful soil microorganisms (Etesami and Maheshwari 2018; Meena et al. 2018b). Today, biological fertilizers are considered as a supplement for chemical fertilizers aimed at increasing soil fertility and producing agricultural products in sustainable agriculture (Adesemoye and Kloepper 2009; Sihag et al. 2015; Kumar et al. 2018a). Biological fertilizers have significant advantages in comparison with chemical substances, including that they do not produce toxic substances in the food cycle, have self-replicating properties, and cause soil physical and chemical properties to be improved (Al Abboud et al. 2014; Singh et al. 2016; Yadav et al. 2017b). Generally, the microorganisms used to produce biological fertilizers originate from soil and are active in most soils. However, in many cases, their quantity and quality are not optimal, and therefore the use of their inoculations is necessary. In these biological fertilizers, the cell population density is such that it can provide up to more than one million living cells for each inoculated plant, while naturally there is no such number of bacteria, especially in the plant's rhizosphere (Etesami and Maheshwari 2018; Nosratabad et al. 2017; Meena et al. 2015c).

The role of phosphate-solubilizing microorganisms (PSMs) is well-known in solubilizing insoluble phosphates and increasing its availability to plants (Sharma et al. 2013; Kumar et al. 2018b). Although there are several PSMs in the soil, usually this number of bacteria is not noticeable in comparison with other common bacteria and is located in the rhizosphere of different plants (Rodríguez and Fraga 1999). Less than 10% of all microorganisms in the soil are able to dissolve insoluble phosphates (Gupta et al. 1998). Therefore, the amount of P released by these bacteria is not usually sufficient to increase the growth of the plants. Therefore, inoculation of plants with specific bacteria with a much larger population than that found in the soil is necessary to benefit from the P-solubilizing properties of those bacteria in increasing plant growth and yield considerably (Etesami and Maheshwari 2018; Meena et al. 2016b).

PGPR (plant growth-promoting rhizobacteria), the bacteria that colonize plant roots and promote plant growth, and AMF (arbuscular mycorrhizal fungi), which are composed of a group of root obligate biotrophs (obligate symbiosis) that barter mutual benefits with about 80% of plants, augment the availability of micro- and macronutrients to growing plants by influencing solubility or uptake conditions (i.e., augmenting the solubility of P and Fe) (Berruti et al. 2016; Vessey 2003). Under conditions of nutritional deficiencies, these microorganisms augment the availability of micro- and macronutrients by different ways. Tolerance to nutrient deficiency stress can be explained by nutrient mobilization in the rhizosphere and via generation of phytohormones especially IAA (indole-3-acetic acid), ACC (1-aminocyclopropane-1-carboxylate) deaminase activity, siderophore production, and phosphate solubilization (Etesami and Beattie 2017; Glick 2014). Plantassociated beneficial microorganisms can be applied to make better the ability of crop plants to withstand and produce yield in nutrient-poor growth environments (Etesami 2018b; Etesami and Maheshwari 2018). As an example, PGPR- IAAinduced changes in root architecture might lead to an enlargement in total root surface area, consequently improving micro- and macronutrients and water uptake, which may have positive effects on plant growth in a general sense (Etesami et al. 2015a; Etesami and Alikhani 2016a; Etesami and Maheshwari 2018; Glick 2012; Somers et al. 2008).

There are several reports that show the potential of various bacterial strains to solubilize insoluble inorganic phosphates such as TCP (tricalcium phosphate), dicalcium phosphate (CaHPO₄), hydroxyapatite $[Ca_5(PO_4)_3(OH)]$, and rock phosphate (phosphorite) and mineralize organic phosphates (Islam and Hossain 2012; Khan et al. 2007; Sharma et al. 2013). In addition to enhancing P availability, PSB can, through other mechanisms such as fixing atmospheric nitrogen, producing plant hormones, e.g., such as GAs (gibberellins), CK (cytokinins), and auxins (i.e., IAA), and synthesizing the enzyme ACC deaminase, which lessens plant levels of ethylene, thereby diminishing environmental stresses (abiotic and biotic stresses)

on plants, sequestering Fe for plants by production of siderophores, and antifungal activity, improve plant growth (Bianco and Defez 2010; Chabot et al. 1996; Duarah et al. 2011; Hamdali et al. 2008; Islam and Hossain 2012; Naik et al. 2008; Thakuria et al. 2004; Yildirim et al. 2011; Zaidi et al. 2006; Varma et al. 2017b).

The availability of macronutrient elements including P can be a major restriction to plant growth in many agricultural environments of the world, especially the tropics where soils are highly low in macro- and micronutrients (Etesami and Maheshwari 2018). PGPR and AMF take part in the geochemical cycling of microand macronutrients and determine their availability for plants and soil microbial community by different action mechanisms (Adesemoye et al. 2008; Desai et al. 2016; Sofi et al. 2018). In this chapter, a summary of the efforts in using PSB and phosphate-solubilizing-AMF for increasing the use efficiency of P fertilizers is discussed. Review of the literature shows that the PSMs as both co-inoculation and single inoculation can take advantage of plant uptake of P and thereby augment the use efficiency of applied chemical P fertilizers.

8.2 Plant–Microbe Interactions

Long ago, the study of the interactions between plant and their associated microorganisms (whether beneficial microorganisms or harmful microorganisms) has been very interesting for microbiologists and botanists. The knowledge gained from this research could lead to the development of novel agricultural applications. Plant communities affect soil microorganisms via interactions inside the rhizosphere, the region of soil where microbial communities are directly influenced by plant root systems and exudates (Fig. 8.1) (Berg and Smalla 2009; Buée et al. 2009).

The rhizosphere is a rich niche for diverse microorganisms compared to surrounding bulk soils (Bais et al. 2006). Microbial root colonization often initiates with the recognition of specific compounds in the root exudates by microorganisms. These compounds probably have also major roles in belowground community interactions (Compant et al. 2010). Plant roots secrete a wide range of organic compounds between 6% and 21% of the carbon fixed including sugars (i.e., glucose, xylose, fructose, maltose, sucrose, and ribose), organic acids (i.e., citric, malic, lactic, succinic, oxalic, and pyruvic acids), putrescine, amino acids, fatty acids, nucleotides, and vitamins (Etesami and Maheshwari 2018; Meena et al. 2015a), which can be used as nutrients or signals by microbial populations. These signal molecules can also be used for cross talk between the plant and microbes (Lugtenberg 2015). From the other point of view, plant-associated microorganisms release some metabolites like phytohormones, small molecules, or volatile compounds, which may operate directly or indirectly to actuate plant immunity or adjust plant growth and morphogenesis (Ortíz-Castro et al. 2009).

Recent advance in plant-microorganism interaction research revealed that plants are able to shape their rhizosphere and endorhiza microbiome (Berendsen et al. 2012). Under stress conditions, stressed plants can require the presence of associated microorganisms for their growth and establishment in different ecosystems

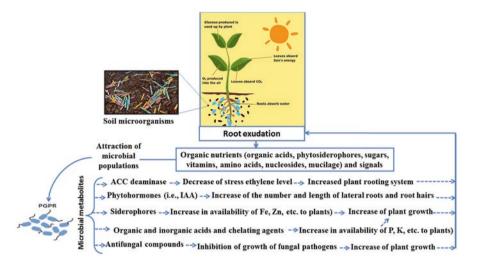


Fig. 8.1 A diagrammatic representation of how interactions occur between plants and their associated bacteria. Up to 40% of photosynthetically fixed carbon is secreted into the rhizosphere by plants. These carbon materials attract microbial populations, especially those able to metabolize plant-exuded compounds and proliferate in this microbial habitat. Microorganisms can use these compounds as substrates, resulting in an increased microbial biomass and activity around the roots, the so-called rhizosphere effect. Plants can influence bacterial gene expression, especially genes encoding plant-beneficial traits, by releasing these root exudates. Root exudation-mediated plantassociated PGPR can modulate root development and growth through the production of phytohormones (indole-3-acetic acid, IAA), 1-aminocyclopropane-1-carboxylate (ACC) deaminase, siderophores, organic and inorganic acids, etc. The PGPR result in a reduction of the growth rate of primary root and an increase of the number and length of lateral roots and root hairs. PGPR also modify root physiology by changing gene transcription and metabolite biosynthesis in plant cells and thereby increase root exudations, resulting in the microbial activity, and this process continues in a cycle

(Hardoim et al. 2008; Kakraliya et al. 2018). Symbiotic microorganisms exist in all plants living in the natural ecosystems. This relationship may be the key factor involved in plants' stress tolerance ability. Indeed, local adjustment of plants to their growth environment is driven by genetic differentiation in plant closely associated microorganisms (Etesami and Beattie 2018; Rodriguez and Redman 2008). It has been proven that transplanting different plant species in the absence of microorganisms is notoriously difficult, which hints at a role of microorganisms in plant growth under stressful conditions (Leifert et al. 1989).

In general, the microorganisms may affect plant growth in one of three ways. The interaction may be (1) beneficial, such as interaction between plant and AMF, PGPR, plant growth-promoting endophytic bacteria (PGPEB), and the N-fixing rhizobia (NFR), (2) harmful such as the interaction between plant and phytopathogenic microorganisms (plant disease-causing soil microorganisms), and (3) neutral for the plant, and sometimes the impact of a microorganism may vary as the soil conditions alter (Cheng et al. 2010; Yadav et al. 2017a). Majority of plants harbor a diverse community of microorganisms that can positively affect host plant

growth (Hardoim et al. 2008). In general, plant-associated beneficial microorganisms such as AMF, PGPR, and NFR possess the capacity to assist plant growth, augment nutrient availability and uptake (direct action mechanisms), and support the health of plants by decreasing the deleterious effects of various pathogens on the growth and yield of plants as biocontrol agents (indirect action mechanisms) (Etesami and Maheshwari 2018; Vessey 2003).

8.3 Limitations of Using Phosphate Fertilizers

Mineral forms of soil phosphorus are composed of P adsorbed on clay particles, apatite minerals, and complexes of Fe-P, Al-P, and Ca-P. The solubility of these P compounds, as well as organic P, is highly low, and, despite the high amount of total phosphorus in the soil, only very small amounts of soil P exist in soil solution. In other words, when soils are initially fertilized with P fertilizers, owing to the complex behavior of P in soils, only a small fraction of added P fertilizer to agricultural soils is taken up by plants. In addition to worldwide concern about the energy and costs connected with mining the phosphorite (rock phosphate) and its conveyance from manufacturing sites to farm crop fields (Sharma et al. 2013), the use efficiency of P fertilizers (recovery of fertilizer P) in calcareous and alkaline soils does not exceed 20%. Sometimes up to 90% of applied P in soil is precipitated by metal complexes in the soil (Gyaneshwar et al. 2002). The alteration of plantavailable phosphorus to less available forms in soil is the reason for the low initial efficiency of P fertilizers. Soil P availability is affected by soil pH. Phosphorus in pH 6.5 is more available to plants. In other words, pH-dependent chemical fixation determines the quantity of available P. In highly calcareous soils, soluble P readily forms insoluble minerals with calcium $(Ca_3(PO_4)_2)$, which is indeed a problem (Bertrand et al. 2003). Soils with high clay content, particularly those dominated by Al- and Fe oxide minerals (Fe₂O₃ and Al₂O₃), retain P most forcefully. When organic matter is accruing in soil, retention of P in organic matter (P immobilization) is also only an inefficiency process (Williams and Donald 1957).

In the near future, most countries face the energy crisis and environmental hazards due to pollutants so that the process of producing chemical fertilizers may not be easily possible. Although the available P sources in the world are so high that the risk of a critical shortage is not very serious at least until the next century, it is very likely that the excess costs of preparing and producing P fertilizers in the near future are very probable. Therefore, it is needed to reduce application of P fertilizers in agricultural land by PSMs. Mycorrhizal fungi and PSB cannot replace all P fertilizers. However, these microorganisms can reduce the plant's need for chemical P fertilizers by increasing the plant's ability to absorb more P and other mineral elements from the soil and enhancing the efficiency of P fertilizer use. As an example, research has shown that mycorrhizal fungi and PSB could supply the plant with P from an RP source in calcareous soils (Ghorchiani et al. 2018; Dhakal et al. 2016).

8.4 Strategies for Increasing Fertilizer Phosphorus Use Efficiency

Some strategies that can improve fertilizer PUE include (McLaughlin 2012) (1) altering timing of fertilizer application. In soils with high P-retention capacities like calcareous soil and acidic soil, P fertilizers must not be applied too long before planting because increase in the time of contact with soil diminishes P availability rapidly in those soils (McLaughlin 2012). It is known that the best time to apply P fertilizers in soils with high fixation capacity is at sowing. Applying small amounts and splitting applications at sowing and topdressing later in the crop growth cycle are managements that must be considered about this element in highly sandy soils, (2) altering rate of fertilizer application. The best and only way to determine the correct rate of P fertilizers to apply is based on soil testing. Adding P fertilizers to soils that contain sufficient amounts of plant-available P is wasteful and could lead to P losses to water bodies (McLaughlin 2012), (3) altering placement in the soil. Since adsorption of P is high in soils with high P retention, band placement of P is the best management practice for soluble P fertilizers because this method of fertilizer application decreases the amount of soil fertilizer contact and limits strong adsorption (McLaughlin 2012). On the other hand, the best method of fertilizer application for sparingly soluble fertilizers like reactive RP is broadcast application because this method of fertilizer application promotes dissolution in the soil, (4) picking out crop species or varieties efficient at scavenging P from soils (McLaughlin 2012). Since P is diffusion-limited in most soils, it is known that genotypes/species with efficient and extensive root systems (to access a greater soil volume) and with effective associations with mycorrhizal fungi are more efficient in taking up P from soils and thereby increase P use efficiency (Lynch 2007) and (5) different fertilizer formulations. Use of acidifying fertilizers in alkaline soils or the compound use of PSM and chemical P fertilizers improves P use efficiency. Among the strategies mentioned above, it seems that microbial mediated P management is an eco-friendly and cost-effective way for sustainable development of agricultural crop (Etesami and Maheshwari 2018; Meena et al. 2014).

8.5 Biodiversity of Phosphate-Solubilizing Microorganisms

Both fungi and bacteria play a central role in the natural P cycle and convert insoluble forms of P to available forms to plants. Diverse genera of PSMs inhabit in soil and plant rhizosphere. These microorganisms occur in both fertile and P-deficient soils (Etesami and Maheshwari 2018; Oehl et al. 2001) and were isolated from diverse environment including rhizoplane, rhizosphere, and endorhiza (endosphere) of different plants (Etesami and Alikhani 2016b; Etesami et al. 2014a, b; Islam et al. 2007; Islam and Hossain 2012; Kumar et al. 2001; Oliveira et al. 2009; Panhwar et al. 2011a, b; Pei-Xiang et al. 2012; Sharma et al. 2013) and from salinity and heavy metal-stressed environments (Etesami 2018a; Etesami and Beattie 2018; Etesami and Maheshwari 2018; Zhu et al. 2011; Layek et al. 2018). Soil PSMs include bacterial genera viz. Micrococcus, Bacillus, Flavobacterium, Enterobacter, Klebsiella, Azotobacter, Vibrio, Chryseobacterium, Xanthobacter, Erwinia, Burkholderia. Acinetobacter. Pantoea. Arthrobacter. Achromobacter. Agrobacterium, Pseudomonas, fungi of Aspergillus, Trichoderma, Rhizoctonia solani, Glomus manihotis, Fusarium, Helminthosporium, Alternaria, and Penicillium and some Actinomyces such as Streptomyces and Micromonospora, as well as some cyanobacteria (i.e., Anabaena sp., Calothrix braunii, Nostoc sp., and Scytonema sp.) (Behera et al. 2014; Sharma et al. 2013). It has also been reported that some rhizobial strains can also dissolve organic and inorganic phosphates. Of the bacteria mentioned above, the bacteria with multiple plant growth-promoting (PGP) traits such as *Pseudomonas*, *Bacillus*, *Burkholderia*, *Streptomyces*, and Pantoea have been reported among the most efficient PSB as well as important bioinoculants (Islam and Hossain 2012; Rodríguez and Fraga 1999). Bacteria are more effective at solubilizing phosphorus than fungi (Alam et al. 2002; Sharma et al. 2013; Ram and Meena 2014) and play a remarkable role in mediating the transformation of complex form of essential micro- and macronutrient elements into more available form for swift acquisition by the plants (Sharma et al. 2013). PSB comprise 1-50% of the soil microbial population, while phosphorus-solubilizing fungi (PSF) comprise only 0.1-0.5% (Chen et al. 2006; Kucey 1983). In general, P solubilization by microorganisms depends on many factors including nutritional, physiological, and growth condition of the culture (Behera et al. 2014).

8.6 Mechanisms of PSB in Increasing P Availability

PSB directly and indirectly contribute to increasing the available P to the plant. In the direct method, the presence of microorganisms is necessary, for example, when the microorganisms increase the P available to the plant by releasing organic and inorganic acids. In an indirect way, the presence of these microorganisms during the increase of plant phosphorus is not necessary. In this case, microorganisms secrete enzymes capable of mineralizing organic P. According to previous findings, there have been some potential mechanisms by which PSB could increase the availability of P (P release from insoluble phosphates) and thereby promote plant growth (Sharma et al. 2013). One of the first mechanisms suggested in the literature is the production of low-molecular-weight organic acids (Goldstein 1986; Kim et al. 1997a). By chelating the cations bound to phosphate through their hydroxyl and carboxyl groups, the released organic acids convert insoluble P forms into soluble forms (Kpomblekou-a and Tabatabai 1994). Different organic acids (in terms of both amount and type) such as oxalic acid, malic acid, succinic acid, propionic acid, 2-ketogluconic acid, 2-hydroxyglutaric acid, formic acid, citric acid, and lactic acid (Chen et al. 2006; Rodríguez and Fraga 1999) have been produced by PSB (i.e., Acinetobacter sp., Sinorhizobium meliloti, Bacillus spp., B. megaterium, Burkholderia sp., Enterobacter sp., E. agglomerans, Microbacterium sp., Pseudomonas sp., P. fluorescens, P. trivialis, P. poea, Serratia sp., Ralstonia sp., Pantoea sp., and Klebsiella sp.), but gluconic acid has been reported to be as the

principal organic acid produced by these bacteria (Bianco and Defez 2010; Castagno et al. 2011; Islam and Hossain 2012; Ogut et al. 2010; Panhwar et al. 2011a, b; Perez-Lopez et al. 2007; Sharma et al. 2013; Vyas and Gulati 2009).

In some studies, there is a direct relationship between the amount of produced organic acid and the amount of solubilized P, but in some studies, such a relationship has not been observed (Vyas and Gulati 2009). Some researchers reported the solubilization of insoluble phosphates by PSB without producing organic acids (Chen et al. 2006; Illmer and Schinner 1992). These findings suggests that organic acids cannot be the only mechanism for solubilizing phosphorus by bacteria, but mechanisms such as the production of inorganic acids and the release of proton (H⁺) as a result of absorption of cations such as NH_4^+ are also involved in this work (Illmer and Schinner 1992).

An important part of soil P is as organic P, which is in fact not available to the plant. Therefore, these organic P compounds need to be converted into mineral form by enzymes. Secretion of hydrolytic enzymes (e.g., phosphatases and phytases) is another mechanism of PSB such as *Bacillus megaterium* and *S. meliloti* to increase P availability to the plant (Bianco and Defez 2010; Dey et al. 2004; Rodríguez et al. 2006; Sharma et al. 2013; Verma et al. 2015a). Since P mobility in soils is low, it is necessary that the roots move themselves to the sites where P is accumulated. The rooting system is the main channel for water absorption and mineral elements in all plants. One of the known mechanism by which IAA-producing PSB affect P uptake is by increasing development and growth of plant roots, causing root systems with larger surface area and enhanced number of root hairs, which are then able to access more P (Etesami and Beattie 2017; Etesami and Maheshwari 2018).

Application of PSB such as *Bacillus* spp., *Acinetobacter* sp., *B. megaterium*, *Pseudomonas* sp., *P. trivialis*, and *P. poea* alone or in combination with low rate of P fertilizers or with varying doses of P fertilizers has been shown to remarkably augment P availability in soils as well as high P uptake by major crops (Duarah et al. 2011; Gyaneshwar et al. 2002; Ogut et al. 2010; Oliveira et al. 2009; Panhwar et al. 2011a, b; Sapsirisopa et al. 2009; Sharma et al. 2007; Toro et al. 1997; Vyas and Gulati 2009; Yildirim et al. 2011; Meena et al. 2017a), augment the efficiency of P fertilizer, and diminish about 25–50% of the required P to crop plants (Adesemoye et al. 2010; Attia et al. 2009; Duarah et al. 2011; Güneş et al. 2009; Gyaneshwar et al. 2002; Kennedy et al. 2004; Kumar et al. 2010; Yildirim et al. 2011).

Since most of the PSB are heterotrophic and dependent on carbon and energy sources (Nahas 2007), to ensure their growth, organic acid production, and hence solubilization of insoluble phosphate compounds, metabolizable carbon compounds must be applied as an energy source to the PSB (Vassilev and Vassileva 2003; Meena et al. 2015b), especially in soils of arid and semiarid regions. Previous studies have also shown that use of PSB along with organic amendments could be a promising management strategy to increase PUE of insoluble P resources (i.e., RP) for crop production (Abbasi et al. 2013; Adnan et al. 2017; Fallah Nosratabad et al. 2017; Dadhich et al. 2015). Some examples of PSB that have been able to increase P availability from P sources with low P solubility in the presence or absence of an organic amendment are shown in Table 8.1.

PSB	P sources	Effect	References
Pseudomonas, Pantoea, Mycobacterium, Bacillus, Rhizobia, Burkholderia, Arthrobacter, and Enterobacter	Rock phosphate (RP), single super phosphate (SSP), farmyard manure (FYM), and poultry manure (PM)	PSB could increase Olsen-extractable P in all P sources compared to the control, but this increase was higher in organic sources (PM and FYM) than mineral P sources (SSP and RP)	Adnan et al. (2017)
Bacillus, Rhodococcus, Arthrobacter, Serratia, Chryseobacterium, Delftia, Gordonia, and Phyllobacterium	Tricalcium phosphate (TCP)	These PSB could solubilize considerable amount of TCP in the medium by secreting organic acids	Chen et al. (2006)
Agrobacterium tumefaciens	Poultry manure (PM) and rock phosphate (RP)	The combined use of phosphate-solubilizing bacterium and PM with RP increased Olsen-extractable P (25 mg P kg ⁻¹) that was maintained at high levels without any loss	Abbasi et al. (2015)
Pantoea cypripedii and P. plecoglossicida	Rock phosphate (RP)	The combined use of PSB and RP increased the growth indices and total P uptake in maize and wheat crops compared to control	Kaur and Reddy (2015)
Bacillus spp.	Rock phosphate (RP)	PSB solubilized significantly high amounts of P (20.05– 24.08 mg kg ⁻¹) compared to control (19–23.10 mg kg ⁻¹) treatments.	Panhwar et al. (2011b)
Bacillus sp.	Rock phosphate (RP)	The application of PSB enhanced soluble P in the soil solution	Panhwar et al. (2013)
Bacillus sp.	Rock phosphate (RP) and compost	PSB along with compost indicated an increase of 12.9% and 4.3% in P contents in straw and grains of chickpea, respectively, compared to control	Ditta et al. (2018)
Pseudomonas, Azospirillum, and Agrobacterium	Poultry manure (PM), rock phosphate (RP), and compost	PSB along with PM and compost resulted in more increase in wheat plant yield, P uptake, and P utilization efficiency (PUE) compared to control	Abbasi et al. (2013)

Table 8.1 Role of PSB (phosphate-solubilizing bacteria) in increasing the solubility and availability of P from P sources with low P solubility in the presence or absence of an organic amendment

PSB	P sources	Effect	References
P. fluorescens	Tricalcium phosphate (TCP)	PSB reduced the transformation of Olsen-P to Ca ₁₀ -P, thus increasing P availability in soil solution	Shi et al. (2017)
B. megaterium	Rock phosphate (RP) and organic manure	PSB along with organic fertilizers were effective at solubilizing RP	Alzoubi and Gaibore (2012)

Table 8.1 (continued)

In addition to PSB, IAA, ACC deaminase, and siderophore-producing bacteria can also indirectly provide P for the plant (Etesami et al. 2015b, c; Etesami and Beattie 2017). The mechanisms by which these bacteria lead to an increase in P availability are shown in Fig. 8.2.

8.7 Mechanisms of Phosphate-Solubilizing-AMF in Increasing P Availability

Mycorrhiza is a symbiotic relationship between the roots of plants and fungi. AMF belong to phylum Glomeromycota, which form symbiotic associations. This mycorrhizal symbiosis is one of the oldest types of symbioses known between mycorrhizal fungi and a wide variety of plants. More than 80% of the plants on Earth are benefiting from this mycorrhizal symbiosis. In other words, AMF are widely distributed and can be found on all Earth ecosystems where plants can grow (Redecker et al. 2013; Datta et al. 2017b). Arbuscular mycorrhizal fungi can also colonize and establish symbiotic, reciprocally advantageous associations with the roots of most agricultural crop plants (Munyanziza et al. 1997) and augment the effective absorptive area of the roots by forming an extensive extraradical hyphal network, which boosts the efficiency of the absorption of micro- and macronutrients. By a high-affinity P-uptake mechanism and scavenging the available P through their hyphae, which are important in the absorption of P and P transfer from the AMF to plants and act as a bridge between the soil and plant roots (Bianciotto and Bonfante 2002; Harrison and van Buuren 1995; Liu et al. 2000), AMF influence P content and enhance P nutrition in plants as has been widely reported over the years (Barea et al. 2002; Giovannetti et al. 2006).

The root system is known as the main channel for water absorption and mineral elements in all plants. One of the scientific solutions proposed to increase the growth and efficiency of the root system of plants is the use of symbiotic microorganisms, such as mycorrhizal fungi, along with appropriate chemical and organic inputs in the vicinity of the root system of the plants. Mycorrhizal symbiosis is one of the most well-known and, at the same time, the most extensive and most important symbiosis on the planet Earth. The most important effect of the mycorrhizal symbiosis association is the increase in the absorption of mineral elements and especially P in host plants. This effect is more evident especially in areas where

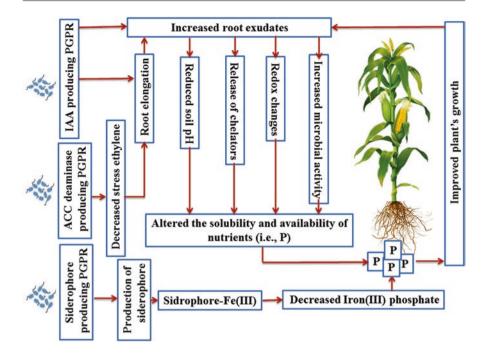


Fig. 8.2 Schematic representation of mechanisms by which IAA, ACC deaminase, and siderophore-producing PGPR may affect P availability in the rhizosphere. 1-aminocyclopropane-1-carboxylate deaminase producing PGPR hydrolyzes the ethylene precursor 1-aminocyclopropane-1-carboxylate (ACC) to ammonia and α -ketobutyrate (α -KB) and thus prevents the production of stress ethylene. The result of decreased ethylene production is the increase in root length and subsequently increased root exudates. One of the most common roles of IAA in the plant is the increase in root length and root exudates. One of the growth of plants and PGPR in rhizosphere. Root exudates also contain different chemical molecules such as chelating agents that mobilize the availability of P in P-deficient soils. Siderophore prevents iron phosphate (FePO₄) precipitation through chelating iron (Fe³⁺), and in the absence of free iron, P can be absorbed by the plant. Phosphorus uptake by the plant increases plant growth, and increase in the number of PGPR and increased P availability in the rhizosphere, and this process continues in a cycle

plant-available P in soils is low or due to drought, the diffusion coefficient of P has been significantly reduced. The absorption of nutrients, e.g., P, which is carried out through diffusion process and moving toward the root, depends on rate of their diffusion in the soil and on the distances that must be traversed to reach the absorbing surfaces the root. It is known that the mycorrhizal roots have higher density than non-mycorrhizal roots. The presence of extraradical hyphal network, which penetrates up to 24 cm away from the root surface, results in decreasing the distance that P must go through to reach the absorbing surfaces of the root, and thereby the rate of absorption of the element increases (Smith and Smith 2011; Meena et al. 2017b).

The rate of development of extraradical hyphae is, on average, 800 times the rate of development of the root system of the plant. Therefore, the P-depleted region around the hyphae of mycorrhizal fungi is more restricted than that of around root hairs, which is why more P is absorbed in the mycorrhizal symbiosis (Smith and Smith 2011; Meena et al. 2018a). On the other hand, the thickness of hyphae of mycorrhizal fungi is one-tenth of that of the root hairs, so these fungal hyphae penetrate into the pores of the soil where the roots cannot penetrate them and thereby absorb more P. In mycorrhizal plants, P is absorbed through fungal hyphal network and transmitted through the cytoplasmic channel of the fungal network to the plant, in which the transfer rate of P to the plant is much higher than its transfer rate in the soil (Smith and Smith 2011). Arbuscular mycorrhizal fungi increase the absorption area of the root zone by 10-100%, thereby improving the ability of plants to use more soil resources. The roots of mycorrhizal plants can explore more soil volume due to their extramatrical hyphae that make easy them for taking up and translocating more P than by plants non-inoculated with mycorrhizal fungi (Guo et al. 2010; Gogoi et al. 2018).

There is evidence of activity of acid phosphatase and alkaline phosphatase enzymes in mycorrhizal fungi, which indicates the ability of these fungi to use phosphorus existing in organic compounds (Antibus et al. 1992). On the other hand, these fungi, by secretion of organic acids such as oxalic acid/oxalates, which have a higher affinity to combine with Ca, Fe, and Al ions in comparison to P, release P from insoluble metal compounds and absorb the released P (Miyasaka and Habte 2001). The secreted oxalates are eventually degraded by actinomycetes and converted to CO_2 . The carbon dioxide released, by lowering pH in alkaline soils, releases more P from insoluble P compounds and makes it available to the plant (Miransari 2010; Smith and Read 2010; Meena et al. 2017c). It has been estimated that about 80% of the P taken up by a mycorrhizal plant is supplied by AM fungus (Marschner and Dell 1994). In general, it is believed that mycorrhizal fungi can be a good alternative to a part of the chemical fertilizers used, especially phosphate fertilizers, in different systems (Ghorchiani et al. 2018).

8.8 Synergistic Effects of PSB and Phosphate-Solubilizing-AMF in Increasing P Availability

One of the ways to boost the efficiency of microorganisms is co-inoculation of microorganisms (Etesami et al. 2015c; Nadeem et al. 2014) that through various mechanisms leads to stimulating plant growth (Bashan et al. 2004). There is an accruing and synergistic effect of PSB combined with AMF (Table 8.2). They (dual inoculation of PSB and phosphate-solubilizing-AMF) have disclosed better performance in terms of sustainable plant growth on nutrient-poor environments (Lee et al. 2015; Mohamed et al. 2014; Nadeem et al. 2014; Xun et al. 2015; Zarei et al. 2006; Verma et al. 2015b). Increased yields of crop plants (Mäder et al. 2011), augmented fruit quality (Bona et al. 2016; Ordookhani et al. 2010), improved nutrient use efficiency of chemicals fertilizers, enhanced phytoremediation

PSB	AM fungi	Experimental	Effect	References
	6	plant		
Pseudomonas fluorescens	Funneliformis mosseae	Maize (Zea mays L.)	Under the conditions of fertilization with phosphate rock, dual inoculation of maize plants with AM fungus and phosphate-solubilizing bacterium led to a significant increase in colonization of root, the grain yield of maize, plant vegetative and reproductive traits, and P and N content in plant tissue in comparison with non-inoculated controls and the plants inoculated with these microorganisms alone	Ghorchian et al. (2018)
Coccus sp., Streptococcus sp., and Bacillus sp.	unknown	Maize (Zea mays L.)	Compared to control and single inoculation, co-inoculation of maize with AM <i>fungus</i> and PSB significantly promoted mineralization of phosphate rock in soil and improved all growth parameters including shoot (56%), height (41%), root yield (52%), and N (80%) and P (91%) uptake by the maize plants	Wahid et al. (2016)
Bacillus polymyxa	Rhizophagus fasciculatus	Terminalia paniculata and T. tomentosa	The combined inoculation of phosphate-solubilizing bacterium and AM fungus brought marked increase in plant growth, dry matter, and P uptake when, compared to individual inoculants or non-inoculated plants. The increase in growth was attributed to the increase in P uptake in shoots of the seedlings	Jang et al. (2016)

Table 8.2 The synergistic effects of AMF (arbuscular mycorrhizal fungi) and PSB (phosphate-solubilizing bacteria) on the plants grown in soil with low available P

PSB	AM fungi	Experimental plant	Effect	References
B. subtilis	Claroideoglomus etunicatum, Funneliformis mosseae, and Rhizophagus intraradices	Acacia gerrardii	The combined inoculation of <i>A. gerrardii</i> with <i>B. subtilis</i> and AM fungi resulted in a significant increase in shoot and root dry weight, nodule number, and leghemoglobin content in comparison with non-inoculated controls and the plants inoculated with these microorganisms alone under salinity stress. Co-inoculation and single inoculation of <i>A. gerrardii</i> increased the N, P, K, Mg, and Ca contents and phosphatase activities in salt-stressed <i>A. gerrardii</i> tissues and diminished concentration of Na and Cl	Hashem et al. (2016)
Bacillus polymyxa	Glomus mosseae	Onion (<i>Allium cepa</i> L.)	Co-inoculation of onion with AM fungus and phosphate-solubilizing bacterium significantly augmented shoot fresh and dry weights, plant height, root fresh and dry weights, average bulb diameter, and total yield in comparison with non-inoculated controls and the plants inoculated with these microorganisms alone	Mohamed (2015)

Table 8.2 (continued)

PSB	AM fungi	Experimental plant	Effect	References
Burkholderia cepacia	G. etunicatum	Wheat	Co-inoculation of wheat with <i>B. cepacia</i> and <i>G.</i> <i>etunicatum</i> increased all growth and yield parameters in comparison with non-inoculated controls and the wheat inoculated with these microorganisms alone. Co-inoculation also increased crop yield and N concentration more than 50% and 90%, respectively	Saxena and Jha (2014)
Pseudomonas fluorescens	<i>G. mosseae</i> and <i>G. intraradices</i>	Wheat	Combined application of <i>P. fluorescens, G. mosseae</i> , and <i>G. intraradices</i> augmented shoot dry matter yield, seed grain spike number, and grain yield by 52%, 19%, and 26%, respectively, in comparison with non-inoculated controls and the plants inoculated with these microorganisms alone	Yousefi et al. (2011)
<i>Mortierella</i> sp.	<i>G.s aggregatum</i> and <i>G. mosseae</i>	Kostelelzkya virginica	Compared to single inoculation, co-inoculation of <i>G.s aggregatum</i> , <i>G.</i> <i>mosseae</i> , and <i>Mortierella</i> sp. augmented the AMF colonization (%) and <i>bacterial</i> populations under salinity stress (i.e., 100, 200, and 300 mM NaCl). Co- inoculation of salinity-stressed <i>K.</i> <i>virginica with bacterium</i> and AMF had significant effects on electrical conductivities of rhizosphere and bulk soils, pH values, and shoot and root dry weights and concentration of available P.	Zhang et al. (2011)

Table 8.2 (continued)

		Experimental		
PSB	AM fungi	plant	Effect	References
Pseudomonas striata	G. intraradices and G. mosseae	Maize (Zea-mays L.)	Both single inoculation and co-inoculation of maize with <i>P. striata</i> , <i>G.</i> <i>intraradices</i> , and <i>G.</i> <i>mosseae significantly</i> increased crop productivity, grain protein content, mycorrhizal root colonization, and inorganic P, thus showing a synergistic interaction between AMF and phosphate-solubilizing bacterium. Single inoculation of maize with AMF or co- inoculation of maize with AMF + P. striata + 75% P_2O_5 remained at par with single application of 100% P_2O_5 dose with regard to productivity, soil fertility status, and nutrient uptake (particularly P)	Suri et al. (2011)
Enterobacter sp. and B. subtilis	G. intraradices	Onion (<i>Allium cepa</i> L.)	Co-inoculation of onion with AM fungus and phosphate-solubilizing bacterium significantly augmented onion biomass and accumulation of N and P in onion tissues	Toro et al. (1997)

Table 8.2 (continued)

(Xun et al. 2015), and reduced application of chemical fertilizers (Adesemoye et al. 2009) are some of the most combined applications of PGPR/PSB and AMF/ phosphate-solubilizing-AMF used so far. Among co-inoculation, the interactions between AM fungi and PSB have been the subject of great interest. There is much speculation that PSB and AMF work together to provide the benefits to plant (Ordoñez et al. 2016). It has been well-proven that AMF and PSB acted synergistically and increased the growth of different plants as compared to that of the plants inoculated with each of them alone (Bona et al. 2017; Bouhraoua et al. 2015; Gamalero et al. 2004; Jangandi et al. 2016; Kalavathi et al. 2000; Kim et al. 1997a, b, 2010; Kothamasi et al. 2006; Mäder et al. 2011; Marulanda et al. 2009; Nadagouda and Lakshman 2010; Ordoñez et al. 2013; Saxena et al. 2013; 2015; Souchie et al. 2006; Toro et al. 1997; Wahid et al. 2016; Zhang et al. 2014; Zhang et al. 2016; Meena

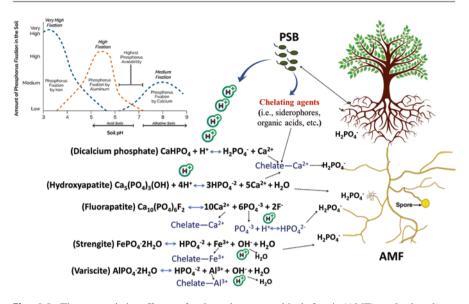


Fig. 8.3 The synergistic effects of arbuscular mycorrhizal fungi (AMF) and phosphatesolubilizing bacteria (PSB) in increasing availability of P to plant. Phosphate-solubilizing microorganisms enhance the capacity of plants to acquire P from soil through alteration of sorption equilibria that may result in increased net transfer of orthophosphate ions $(H_2PO_4^- \text{ and } HPO_4^{2-})$ into soil solution. Organic anions and protons are particularly effective at solubilizing precipitated forms of P (e.g., Ca phosphates under alkaline conditions and Fe and Al phosphates under acidic conditions), chelating metal ions that are commonly associated with complexed forms of soil P. According to Le Chatelier's principle, by increasing the concentration of any substance, the balance moves to the consumption of that material, and, by lowering the concentration of each substance, the balance proceeds to produce that material. Chelating agents, such as siderophore and organic anions, by reaction with Fe³⁺, Al³⁺, and Ca²⁺, remove these ions from the reaction, causing the balance to be moved to the right and thereby producing more $H_2PO_4^-$ and HPO_4^{2-} . The addition of H⁺ ion also causes the balance to be adjusted to the right in order to reduce the H⁺ ion, thereby producing more $H_2PO_4^-$ and HPO_4^{2-} . Arbuscular mycorrhizal fungi can take up and transfer orthophosphate ions to plant roots by their effective mycorrhizal mycelium, reaching microhabitats where orthophosphate is made available by P-mobilizing bacteria (PSB) and preventing quickly its immobilization by microbial biomass

et al. 2018c). In general, in this synergistic effect, AMF can only exploit soluble P sources. However, a large amount of P in the soil is in an unsolvable form, in which PSB can potentially make these insoluble forms available for uptake by AMF hyphae and plants. PSB probably augment the availability of P, which subsequently can be efficiently absorbed by AMF hyphae (Fig. 8.3) (Nazir et al. 2010; Toro et al. 1997; Mitran et al. 2018).

8.9 Conclusions and Future Prospects

Nonnormative and nonscientific use of phosphorus fertilizers is nothing but waste of money on one side and, on the other hand, the degradation and pollution of basic resources, namely, soil and water. It is known that PSB and PS-mycorrhizal fungi, if used as seed inoculation, can provide between 25% and 50% of the P requirement of the plant in soils with high total P and low plant available P. Therefore, it is recommended that inoculants of these microorganisms along with 50% of the chemical P fertilizer recommended by the soil test be used. It is known that different species of PSB and PS-mycorrhizal fungi have different abilities to dissolve lowsoluble P compounds, and usually it has been observed that the use of inoculants including several PSM has a much better effect in increasing the availability of P than the use of only one type of these microorganisms. Since most of PSM are heterotrophic and, as a result, dependent on organic matter in terms of carbon source supply, adding organic matter to the soil when using PSM usually results in increasing their efficiency. As a very good feature of PSM, it is possible to use them simultaneously with mycorrhizal fungi and other PGPR such as IAA, siderophores, and ACC deaminase producers. In this way, in addition to supplying the host plant with P, other plant nutrients will also be supplied, and at the same time, the plant will better grow as a result of the production of growth-promoting hormones by IAA-producing bacteria. When the plant is exposed to environmental stresses, especially drought and salinity, and there is a limit to the use of chemical fertilizers due to their effect on increasing the osmotic pressure of the soil solution and reducing the plant's ability to absorb water, the use of AM fungi can be a very suitable option. By increasing the level of root absorption, AM fungi not only increase the ability of the host plant to absorb water and mineral elements, by modifying the physical structure of the soil, but also create a more favorable environment for the growth of the host plant roots and ultimately reduce consumption of chemical fertilizers, especially phosphorus fertilizers. The possibility of using PSM with rock phosphate, sulfur, organic matter, and Thiobacillus bacteria is another potential of microorganisms. In general, broader research is needed on the efficacy of these microorganisms, along with various sources of organic and inorganic materials in different soils and climates and in the presence of the indigenous microflora under field conditions.

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