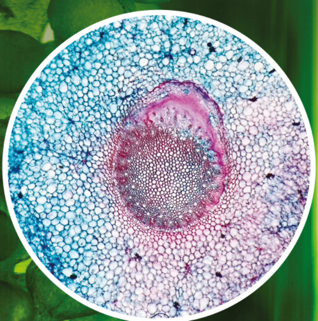
Recent Advancement in Microbial Biotechnology

Agricultural and Industrial Approach



Edited by

Surajit De Mandal

Ajit Kumar Passari

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Chapter 2

Phosphate-solubilizing bacteria: Recent trends and applications in agriculture

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Chapter outline

1 Introduction

Organized agriculture involving the use of plants and animals was developed several years ago. With the advancement in time, agricultural practices saw improved methods such as irrigation, organic farming, use of chemical fertilizers, resistant crops, etc. However, the exponential increase in population demanded an increase in agricultural produce from the available land. To suffice the food demands from existing agricultural land, fertilizers are used in an unwarranted manner, in turn, leading to declining soil health and fertility (Tilak et al., 2005).

As the world's human population unceasingly increases, furnishing food to this growing population will be one of the utmost challenges. To face this challenge, we need to focus on the soil biotic system and the agro-ecosystem as a whole. We need to better understand the complex mechanisms and interactions

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that control agricultural land stability. At present, there is a limitation on the timely distribution of food produced in sufficient amounts, due to the high-input of the green revolution in agriculture. However, a rise in population at high frequency has threatened global food security. To withstand the pressure of the increasing population, food production has to be increased significantly, which will require another green revolution (Leisinger, 1999; Vasil, 1998).

Fertilizers add nutrients to soil increasing soil fertility and plant growth. However, the food value of plants is reduced due to the use of chemical fertilizers. Using exorbitant amounts of chemical fertilizers not only affects the quality of food but also gives rise to many diseases such as stomach cancer, goiter, and several vector-borne diseases. It also leads to groundwater contamination (Savci, 2012). After harvesting the crops, the nutrient reservoirs in the soil reduces. To remedy this deficiency of nutrients, more chemical fertilizers are applied, and this cycle continues, further worsening the soil condition. Reduction in the usage of chemical fertilizers and the improvement of soil health are the problems requiring immediate handling. Biological control is considered as an alternative way of reducing the use of chemicals in agriculture.

Phosphorus (P), an important nutrient in terms of plant requirements and uptake, is found in two forms in the soil: organic and inorganic. Being available abundantly in insoluble forms, it is, however, inaccessible to the plants. Hence, to suffice the nutritional requirements of the crops, P is supplemented through chemical fertilizers containing nitrogen, phosphorus, and potassium (NPK). A substitute for the use of chemical fertilizers is the use of biofertilizers, which include organisms that can convert inorganic phosphorus present in the soil to soluble forms that plants can assimilate. These are the phosphate-solubilizing microorganisms (PSMs).

2 Phosphorus in soil

Phosphate is an important element for plant growth, next to nitrogen and potassium. Plants require P for macromolecular biosynthesis, signal transduction, and respiration, photosynthesis, etc. (Khan, Zaidi, Ahemed, & Wani, 2010). Plants are unable to use phosphate directly as most, i.e., 95%–99% of phosphate in the soil is in an unavailable form, i.e., insoluble or precipitated form (Pandey & Maheshwari, 2007). This unavailable form of phosphate is converted to available form by phosphate-solubilizing bacteria.

According to Goldstein, Rogers, and Mead (1993), chemical phosphatic fertilizer production being a highly energy-intensive process for meeting the needs of the world, energy worth the US $4 billion yearly is required. Fertilizers added to the soil get precipitated as metal complexes (Stevenson, 2005), further making it unavailable for plant uptake. This accumulated phosphate is sufficient to sustain maximum agricultural phosphorus requirements for another 10 decades (Goldstein et al., 1993).

Phosphorus is found in organic forms in soil surface layers, i.e., the topsoil. The most abundant component of this organic form is phytate (Richardson, 1994). While in the bulk soil, phosphorus being less abundant, its uptake by plants is limited. The most soluble minerals, such as potassium, travels through the soil via bulk flow and diffusion, but P moves mainly by diffusion. According to Daniel, Schachtman, and Ayling (1998), because of the low diffusion rate of P, increased P uptake rates of plants result in a P depletion zone around the roots. Plants obtain their P from the soil solution as H_2PO_4 and HPO_4^{-2}. The uptake of HPO_4^{-2} by the plant is slower than the uptake of H_2PO_4 (Fig. 1).

3 Phosphate solubilization by plant growth-promoting microorganisms in plant rhizosphere

According to Kloepper and Schroth (1981), plant growth-promoting rhizobacteria (PGPR) by the production of substances required for plant growth, influence the rhizosphere flora. There are two modes for promoting plant growth, namely, direct and indirect. In the direct mechanism, the PGPR aids in the supply of nutrients by making available nitrogen, phosphorus, potassium, and essential minerals to the plants. While in the indirect mode, PGPR protects from pathogens by preventing their colonization, by acting as biocontrol agents. Microbes present in the soil are mainly encountered in nutrient-rich regions such as the topsoil layer and the rhizosphere, i.e., around the plant root. Some microbial strains can induce plant growth, augment soils, remove pollutants, and protect plants against pathogens (Tripathi, Nagarajan, & Verma, 2002). The PGPR are found in rhizosphere soil, but their count is not high enough to gain dominance over other microflora present in the rhizosphere. Therefore, the plant rhizosphere needs to be supplemented with high concentrations of

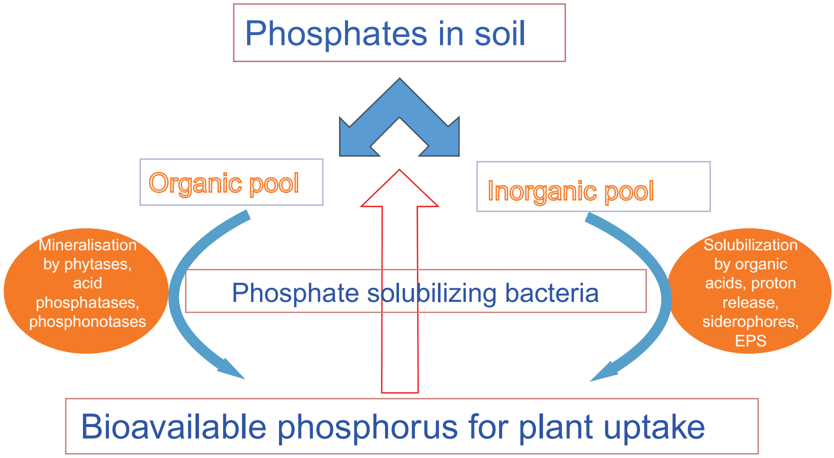

FIG. 1 Mechanisms for solubilization of phosphates in soil.

PGPR. Inoculation of PGPR in the soil is essential because it leads to increased nutrient availability as well as improves the physicochemical and biological properties of soil.

PGPR are categorized as extracellular PGPR (ePGPR) and intracellular PGPR (iPGPR) (Viveros, Jorquera, Crowley, Gajardo, & Mora, 2010). The ePGPR are found on the rhizoplane, in the rhizosphere, and in the intercellular spaces of root cortex cells. The iPGPR resides in nodule-like structures present in the root cells. Numerous bacterial species belonging to the genera *Agrobacterium, Arthrobacter, Azotobacter, Azospirillum, Bacillus, Burkholderia, Caulobacter, Chromobacterium, Erwinia, Flavobacterium, Micrococcus, Pseudomonas,* and *Serratia* are included in ePGPR category (Ahemad & Kibret, 2014).

The microbial flora that colonizes the rhizosphere is also actively engaged in phosphate solubilization and mobilization in soil. Soil microorganisms play a vital role in providing phosphate to plants by solubilizing inorganic P and mineralizing organic P present in the soil (Adhya et al., 2015). Richardson, Hadobas, and Hayes (2001) have documented the beneficial effects of P-solubilizing bacteria on agronomic crops. According to Villegas and Fortin (2002), some bacterial species in soil having good P-solubilizing activities belong to the genus *Mesorhizobium*, *Rhizobium, Klebsiella, Acinetobacter, Enterobacter*, *Erwinia, Achrobacter, Micrococcus, Pseudomonas,* and *Bacillus.* Along with the bacterial strains, fungi such as *Penicillium* and *Aspergillus* are also efficient P-solubilizers (Whitelaw, 2000).

The use of PGPR as inoculants helps to increase growth, yield, and uptake of nutrients by crop plants. The field and pot trials with PGPR have been reported to show increased yields as well as increased P uptake from marginal to a significant level (10%–27%) (Altomare, Norvell, Bjorkman, & Harman, 1999). Inoculation of *Pseudomonas striata* and *Bacillus polymyxa* in soil resulted in an increase in nodulation, nitrogenase activity, dry matter yield, P uptake, and grain yield of chickpea plants as compared to uninoculated controls. An increase in grain yield of maize and wheat crops, with increased P uptake, was observed under field conditions as reported by Himani and Reddy (2011).

4 Phosphate-solubilizing bacteria as biofertilizers

The application of phosphatic fertilizers can result in phosphate availability to the crops and subsequent increase in crop yields. However, the cost of chemical fertilizer being high and its aftereffects on the soil health makes chemical fertilizers undesirable and unaffordable. However, with the increasing population and increasing food demand, balancing the demand, cost-effectiveness, and environmental safety is a challenging task. Agronomists are therefore looking for an alternative source for the chemical fertilizers that will give higher yields, be environmentally safe, and cost-effective also. The application of PGPR in agricultural practices is an effective alternative. The application of PSM in-field practices has a number of advantages such as increased nutrient availability, improvement in fertility of the soil, better plant growth and higher crop yield, protection against pathogens, environmental pollution-free, soil health, and conditioning, cost-effective technology (Saber, Nahla, & Chedly, 2005).

The naturally occurring population of P-solubilizing bacteria and fungi is present in almost all rhizospheres. Most of the P-containing inorganic compounds, for example, di- and tri-calcium phosphate, hydroxyapatite, etc., are insoluble and are solubilized by bacterial species present in the soil. Among the reported microbial strains having solubilizing ability include mycorrhizal fungi, *Aspergillus, Penicillium* (Khan & Bhatnagar, 1977), while among bacterial genera include *Agrobacterium, Bacillus, Rhizobium, Burkholderia, Achromobacter, Micrococcus, Pseudomonas, Aereobacter, Flavobacterium,* etc. (Igual, Valverde, Cervantes, & Velázquez, 2001; Kucey, Janzen, & Leggett, 1989; Subbarao, 1988; Whitelaw, 2000). Among the soil phosphate solubilizers, bacteria constitute 10%–50% and P-solubilizing fungi are a meagre 0.1%–0.5% (Chen, Rekha, Arunshen, Lai, & Young, 2006).

Most of the studies on P-solubilizers reported the isolation of phosphate solubilizers from the soil, their preliminary characterization, and evaluating the solubilizing efficiency of microorganisms under laboratory conditions and pot assays. Studies on P-solubilizing activity were carried out mostly using agar media assays showing zones of clearing indicating the solubilization, such as on Pikovaskaya's agar media and colorimetric assays for quantifying the solubilized phosphates. Some researchers, however, reported a lack of consistency and correlation between plate assays and phosphate estimations in liquid cultures (Sharma, Sayyed, Trivedi, & Gobi, 2013). Due to the low number of naturally occurring P-solubilizers in the soils, the P concentrations released in the soil by the activity of these solubilizers are not sufficient to support plant growth. Hence, a vital necessity has arisen for research involving isolation and efficiency checking of PSMs. Best field applicants can be used for P-solubilizing activity in the soil to take advantage of this property for plant yield enhancement (Bhattacharyya & Jha, 2012).

5 Mechanisms of phosphate solubilization

Soil microorganisms are capable of solubilizing available P sources to forms assimilated by the plants (Toro, 2007; Wani, Khan, & Zaidi, 2007). Bacteria capable of P-solubilization belong to the genera *Bacillus, Burkholderia, Rhizobium, Pseudomonas, Achromobacter, Agrobacterium, Micrococcus, Enterobacter, Flavobacterium,* and *Erwinia*. Some bacterial species are also able to carry out both the processes, i.e., mineralize organic P and solubilize inorganic P (Hilda & Fraga, 2000; Khiari & Parent, 2005). The number of P-solubilization mechanisms found in microorganisms is quite large. It has also been reported that many saprophytic bacteria and fungi perform phosphorus-solubilizing activity through chelation-mediated mechanisms (Whitelaw, 2000).

5.1 Inorganic P solubilization

Studies on the solubilization of phosphoric compounds such as dicalcium phosphate, tricalcium phosphate, rock phosphate, etc., containing an insoluble form of P, by bacteria have been described (Goldstein, 1986). PSMs produce substances such as organic acids, which are responsible for the solubilizing ability. Acidification of the medium leads to the release of organic acids by the P-solubilizing bacteria (Goldstein, 1995; Halvorson, Keynan, & Kornberg, 1990; Kim, Jordan, & Donald, 1998; Kim, Jordan, & Krishnan, 1997; Maliha, Samina, Najma, Sadia, & Farooq, 2004). Phosphate-bound cations are chelated by the action of organic acids, especially hydroxylic and carboxylic groups, converting the phosphate to soluble form (Kpomblekou & Tabatabai, 1994; Sagoe, Ando, Kouno, & Nagaoka, 1998). Cations associated with bound phosphate are Al, Fe, Ca, etc., and the release of these cations due to the lower pH of soil observed (Kpomblekou & Tabatabai, 1994; Stevenson, 2005). According to Zaidi, Khan, Ahemad, and Oves (2009), the solubilization takes place by direct oxidation pathway on the outer surface of the cytoplasmic membrane. The quality of the acids produced determines the degree of solubilization; the quantity is less important (Scervino et al., 2010).

Apart from the release of organic acid, which causes the release of bound phosphate, various microbial mechanisms, including proton extrusion, have been reported to be involved in the solubilization processes (Dutton & Evans, 1996; Nahas, 1996; Surange, Wollum, Kumar, & Nautiyal, 1995). Goldstein (1995) and Deubel and Merbach (2000) have reported the production of gluconic and keto-gluconic acids, which are low-molecular-weight acids, that acidify rhizosphere soil leading to the release of P. Lowering of rhizosphere pH is due to the biological production of proton/bicarbonate release that is responsible for the anionic-cationic balance and gaseous (O_2/CO_2) exchanges. It is observed that the P-solubilization by bacteria has a direct correlation with the pH of the medium. According to Hinsinger (2001), root exudates released in the soil also are responsible for altering the P levels.

The phosphate-solubilizing microflora produces organic acids in the process of solubilization of bound inorganic phosphate. The following changes occur as the result of the organic acid production (Halder, Mishra, Bhattacharyya, & Chakrabartty, 1990; Nahas, 1996) acting alone or in the presence of other solubilizing compounds. Reduction of soil pH, i.e., acidic pH, cation chelation, blockage of adsorption sites for binding of soil particles, the formation of metal complexes such as calcium phosphate that are soluble, and thereby releasing the P.

5.2 Organic phosphate mineralization by PSM

Organic phosphorus present in the soil constitutes 40%–90% of the total phosphorus found in the soil. Organic acids and phosphatase production are the basic mechanisms in mineral phosphate solubilization and organic phosphorous mineralization in soil (Hilda & Fraga, 2000). Almost 50% of microflora found in rhizosphere soil harbor the potential to mineralize phosphates. This potential is because of the production of phosphatases (Cosgrove, 1967; Goldstein, 1994; Tarafdar, Rao, & Bala, 1988). The enzyme phosphatase or phosphohydrolases can mineralize insoluble phosphates. The phosphatases hydrolyze phosphodiester bonds present in phosphate complexes. The acid phosphatases have an optimal activity in the pH range between acidic to neutral, while the alkaline phosphatases have an optimal activity in the alkaline pH range. Phosphatases show substrate specificity and may be further classified as specific or nonspecific types. As reported by Rossolini et al. (1998), nonspecific phosphatases are produced in elevated amounts by some strains of bacteria.

Organic phosphate is the substrate for alkaline and acid phosphatases that convert it to inorganic insoluble phosphate (Beech, Paiva, Caus, & Coutinho, 2001). Rhizosphere microflora produces organic anions, siderophores, and acid phosphatases in the soil surrounding plant roots, as reported by Yadaf and Tarafdar (2001), while mineralization of organic phosphorus present in the soil is brought about by alkaline phosphatase enzymes as noted by Tarafdar and Claasen (1988). Kim et al. (1998) reported the process of phosphorus discharge from hydroxyapatite by *Enterobacter agglomerans*. While *Bacillus, Streptomyces, Pseudomonas,* etc., when used together as mixed cultures, are found to give the better activity of organic P-mineralization (Molla, Chowdhury, Islam, & Hoque, 1984). Strains from genera *Arthrobacter, Bacillus, Enterobacter, Flavobacterium, Pseudomonas, Rhizobium, Rhodococcus, Serratia,* etc., are included as the most efficient P-solubilizers among bacteria (Bhattacharyya & Jha, 2012). PGPR uses different approaches to make use of the unavailable form of phosphorous. Mechanism of phosphate solubilization employed by PGPR includes the production of compounds like organic acids, which will aid in the dissolution of inorganic P, production of enzymes like phytases and degradation of complexes holding the P (Sharma et al., 2013).

6 Effect of phosphate solubilizers on plant growth and crop yield

Most of the studies demonstrating the increased uptake of P and grain yield following inoculation of seedlings with PSM were worked on showing the actual effects of bioinoculants on plant growth (Gerretsen, 1948). An increase in the uptake of PO_4 from both soil and fertilizer sources was reported by Sundara Rao, Bajpai, Sharma, and Subbaiah (1963) in the case of seeds inoculated with *Bacillus megaterium*. The benefits of using PSMs in the soil, along with the application of insoluble forms of P sources such as rock phosphate, tricalcium phosphate, and bone meal was initially reported by some workers (Ahmed & Jha, 1977; Loheuarete & Berthelin, 1988). Ahmed and Jha (1977), who reported hydroxylapatite and rock PSMs. They further reported that an increase in P uptake and yield being observed due to the inoculation of soil with *Bacillus megaterium* and *Bacillus circulans*. Increased P uptake resulting in increased plant growth, has been reported in calcareous soil inoculated with PSMs (Khalafallah, Saber, Abel-El, & Maksound, 1982). The inoculation of rice seedlings with mixed cultures of *Azotobacter chroococcum*, *Pseudomonas striata*, and *Aspergillus awamori* resulted in increased N, P uptake, and also subsequent increase in the yield of grain and straw, as observed by Kundu and Gaur (1984).

In a greenhouse experiment, increased P uptake was observed along with increased plant height in finger millet. The soil was inoculated with *Bacillus circulans* and 32P-labeled superphosphate and tricalcium phosphate (Raj, Bagyaraj, & Manjunath, 1981). It is difficult to prove the effects of phosphate solubilization on greenhouse soil or field soil compared to studies carried out in the laboratory conditions. However, plant growth responses to PSM addition have been reported in many studies (Kucey et al., 1989).

Studies on the effect of P-solubilizing *Penicillium* sp., on the P composition of soil as well as the growth and yield in maize, were described by Praveen, Kuligod, Hebsur, Patil, and Kulkarni (2012). According to this report, a 20%–23% increase in yield, over the control, was seen in maize crop after dual inoculation of P-solubilizers. The successful application of PSMs for different crops is summarized in Table 1.

TABLE 1 Phosphate-solubilizing microorganisms used as growth promotors for different agricultural crops/plants.

Phosphate-solubilizing microorganism	Crop/plant	Reference
Azospirillum sp.	Maize, sorghum, wheat	Kapulnik, Gafny, and Okon, 1985, Baldani, Baldani, and Döbereiner (1987), and Sarig, Okon, and Blum (1990)
Aspergillus niger	Wheat	Xiao, Zhang, Fang, and Chi (2013)
Aspergillus awamori S29	Mung bean	Jain, Saxena, and Sharma (2012)
Azotobacter chroococcum	Wheat	Islam et al. (2007)
Azotobacter chroococcum and *Bacillus subtilis*	Wheat	Kumar, Bauddh, Barman, and Singh (2014)
Azotobacter; Bacillus	Wheat	Kloepper, Lifshitz, and Zablotowicz (1989)

TABLE 1 Phosphate-solubilizing microorganisms used as growth promotors for different agricultural crops/plants—cont'd

Phosphate-solubilizing microorganism	Crop/plant	Reference
Azotobacter chroococcum, Saccharomyces cerevisiae, and *Bacillus megaterium*	*Moringa oleifera*	Zayed (2012)
Aspergillus niger, Penicillium aculeatum	Chinese cabbage	Wang et al. (2015)
Bacillus circulans and *Cladosporium herbarum*	Wheat	Islam et al. (2007) and Singh and Kapoor (1999)
Bacillus megaterium and *Azotobacter chroococcum*	Wheat	Rodríguez and Fraga (1999)
Bacillus sp. and *Pseudomonas* sp.	Sesame	Jahan, Mahallati, Amiri, and Ehyayi (2013)
Bacillus megaterium and *Azotobacter chroococcum*	Wheat	Brown (1974)
Bacillus thuringiensis	Rice	David, Raj, Linda, and Rhema (2014)
Bacillus spp.	Peanut, potato, sorghum, wheat	Broadbent, Baker, Franks, and Holland (1977), Burr, Schroth, and Suslow (1978), and Capper and Campbell (1986)
Bradyrhizobium + Glomus fasciculatum + Bacillus subtilis	Green gram	Zaidi and Khan (2006)
Burkholderia cepacia	Maize	Zhao et al. (2014)
Burkholderia gladioli	Oil palm	Istina, Widiastuti, Joy, and Antralina (2015)
Burkholderia gladioli	Sweet leaf	Mamta et al. (2010)
Mesorhizobium mediterraneum	Chickpea and barley	Peix et al. (2001)
Mycorrhiza + *Pseudomonas putida*	Barley	Mehrvarz, Chaichi, and Alikhani (2008)

Continued

TABLE 1 Phosphate-solubilizing microorganisms used as growth promotors for different agricultural crops/plants—cont'd

Phosphate-solubilizing microorganism	Crop/plant	Reference
Pseudomonas sp.	Soybean crop	Son, Diep, and Giang (2006)
Pseudomonas putida and *Pseudomonas fluorescens*	Canola, lettuce, and tomato	Hall, Pierson, Ghosh, and Glick (1996) and Glick, Changping, Sibdas, and Dumbroff (1997)
Pseudomonas putida and *Pseudomonas fluorescens*	Potato, radishes, rice, sugar beet, tomato, lettuce, apple, citrus, beans, ornamental plants, and wheat	Suslov (1982), Lemanceau (1992), Kloepper (1994), and Kloepper, Lifshitz, and Schroth (1988)
Pseudomonas	*Zea mays* L	Walpola and Yoon (2012) and Bano and Fatima (2009)
Pseudomonas	Soybean	Walpola and Yoon (2012) and Son et al. (2006)
Pseudomonas putida	Moss	Tani, Akita, Murase, and Kimbara (2011)
Pseudomonas chlororaphis and *Pseudomonas putida*	Soybean	Islam et al. (2007) and Singh and Kapoor (1999)
Pseudomonas fluorescent	Peanut	Dey, Pal, Bhatt, and Chauhan (2004)
Pseudomonas striata and *Glomus fasciculatum*	Soybean, wheat	Mahanta et al. (2014)
Paenibacillus favisporus TG1R2	Soybeans	Fernández Bidondo et al. (2011)
Pantoea agglomerans (PSB-1) and *Burkholderia anthina* (PSB-2)	Mung bean	Walpola and Yoon (2013)
Rhizobium tropici CIAT899	Beans	Tajini, Trabelsi, and Drevon (2012)
Serratia sp.	Wheat	Swarnalakshmi et al. (2013)

7 PSB application methods in agriculture

The commonly used method for the application of P-solubilizing microbial inoculants is seed surface application. Traditionally, this method is used before the sowing of seeds and is one of the easiest methods to follow. Application of PSMs in a proper systematic way such that each seed is coated with the microorganism is very important. A sticker solution helps to adhere the bacteria to the seeds and may be added during the application process. Gum arabic is an example of a sticker that is used for adherence to the phosphate-solubilizers on the seed (Khan, Zaidi, & Wani, 2007). PSM may be added to the soil instead of applying to the seeds. This mode of application is used when the seeds are pretreated with pesticides, which may interfere with the PSMs if applied together.

The PSM may be applied alone or maybe co-inoculated together with other bioinoculants. Application of PSM to the soil will increase the PSM count per unit area, thus making soluble phosphates available to the plants. However, there are a number of disadvantages of the application process, such as the availability of enough bioinoculant quantity for total seed surface, contact with chemicals, bacterial movement away from plant roots, or seeds after planting.

8 Recent developments

The application of phosphate solubilizers has yielded good results in a number of crops. Wheat crop showed an increase in grain yield by 17%–18% (Suleman et al., 2018), while a 10%–20% increase in yield was reported for maize, sorghum, and wheat, using a combination of bio-inoculants (Rodríguez & Fraga, 1999). An improved sugarcane yield has been recorded by Sundara, Natarajan, and Hari (2002). The field applications of a number of P-solubilizers such as *Azotobacter* sp., *Bacillus megaterium*, *Bacillus circulans*, *Bacillus subtilis*, and *Pseudomonas striata*, have been carried out with satisfactory results (Bano & Fatima, 2009; Pandey, Trivedi, Kumar, & Palni, 2006; Rodríguez & Fraga, 1999; Satyaprakash, Nikitha, Reddi, Sadhana, & Vani, 2017; Vikram & Hamzehzarghani, 2008). *Penicillium bilaii*, a P-solubilizer, is commercially available as JumpStart (Satyaprakash et al., 2017). N- and P-deficient agrosystems can be treated P-solubilizers in combination with nitrogen-fixing bacteria as an integrated treatment system (Bargaz, Lyamlouli, Chtouki, Zeroual, & Dhiba, 2018). Similar studies by Afzal and Bano (2008) and Yousefi, Khavazi, Moezi, Rejali, and Nadian (2011) showed increased yields in the wheat crop when PSM was used in combination with nitrogen fixers and arbuscular mycorrhizal (AM) fungi. Some studies have also been focused on the application of P-solubilizers for soil reclamation, mostly for the degraded minefields (Chen & Liu, 2019; Liang, Liu, Jia, et al., 2020), which could be used for agricultural practices.

A lot of research on the genetic and molecular aspects of phosphate solubilization has been carried out in recent years. These studies were focused on understanding the mechanisms of the solubilization process. Sashidhar and Podile (2010) have reported studies on proton transport and involvement of the enzyme glucose dehydrogenase in the solubilization process by direct oxidation pathway. Liang et al. (2020) have used the metagenomic approach for studying the effects of P-solubilizer application and the changes occurring in the course of the process during the reclamation of mining soils. During the study, the predominance of genes involved in phosphate solubilization and mineralization, such as gcd gene, was observed. In another study carried out by Zeng, Wu, Wang, and Ding (2017), the molecular mechanisms of P-solubilization, gene expression, and effects of P-solubilization on the growth of *Burkholderia multivorans* WS-FJ9, were investigated and reported. Similar studies were carried out by using molecular tools to understand the ecology, presence, abundance, survival, and interactions of P-solubilizers in different environments that have been carried out (Jorquera, Crowley, Marschner, et al., 2011; Oliveira et al., 2009; Richardson & Simpson, 2011).

Several phosphatase-encoding genes involved in the solubilization of P, both inorganic and organic, were cloned and studied for their efficiency (Rodríguez, Fraga, Gonzalez, & Bashan, 2006). Goldstein and Liu (1987) first reported the cloning of P-solubilization genes in Gram-negative bacteria *Erwinia herbicola*. Fraga, Rodriguez, and Gonzalez (2001) reported the genetic manipulation of a bioinoculant *Burkholderia cepacia* IS-16. The napA phosphatase gene from *Morganella morganii* was inserted in this bioinoculant strain, using the vector pRK293. Thus, the rhizobacteria occurring in nature can be made more efficient by inserting genes for P-solubilization in their genome.

The PSMs can be genetically manipulated and expressed in rhizobacterial strains, thus increasing their efficiency to solubilize P and making them more effective agricultural inoculants. Cloning and expression of genes for phosphate solubilization in rhizobacterial strains, such as using appropriate promoters, has been used as a successful technology. By applying the techniques of gene manipulation, P-solubilizers can further improve their plant growth-promoting ability.

Rossolini et al. (1998) reported the isolation of genes responsible for encoding acid phosphatases from different bacterial species. Thaller and group have worked on the sequence analysis of phosphatase genes, which were cloned and classified into three families, namely, class A, class B, and class C phosphatases (Thaller, Berlutti, Schippa, Lombardi, & Rossolini, 1994; Thaller, Giovanna, Serena, & Rossolini, 1995; Thaller, Schippa, Bonci, Cresti, & Rossolini, 1997). Several genes have been isolated from *Escherichia coli*, responsible for encoding enzymes involved in phosphate solubilization, such as *ush*A, which encodes for 5′-nucleotidase (Burns & Beacham, 1986), *agp,* which encodes enzyme, acid glucose-1-phosphatase (Pradel & Boquet, 1990) and *cpd*B, encoding the 2′-3′ cyclic phosphodiesterase (Beacham & Garrett, 1980).

Several authors have well documented some recent relevant research on P-solubilization (Buch, Archana, & Naresh Kumar, 2008; Ghosh, Barman, Mukherjee, & Mandal, 2016; Jha, Dafale, & Purohit, 2019; Li, Wu, Ye, & Yang, 2018; Liu et al., 2020; Park, Lee, Jung, et al., 2010; Yang et al., 2016; Zeng, Wu, & Wen, 2016). With the genetic manipulation of rhizosphere bacteria and the development of technologies for the application of these bacteria in the field, sustainable agricultural practices promise a rise in productivity.

9 Conclusions

The use of biological agents is the only alternative to avoid use of chemical fertilizers and their harmful effects. Biofertilizers can completely replace the chemical fertilizers leading to sustainable agricultural practices. Crop production can be boosted using biofertilizers, including the P-solubilizers, thus contributing to sustainable agriculture. The effectiveness of PSM in the plant rhizosphere will depend on its ability to colonize, compete, survive, and proliferate, in the presence of other microflora. The application and successful colonization of PSM in the soil are essential for plant growth and, ultimately, for sustainable agriculture. Application of PSMs to soils deficient in plant-available phosphate can mobilize the bound phosphates for plant uptake. They should be efficient enough and should survive and thrive in the rhizosphere, postapplication. Field trials should be undertaken adequately for maximum exploitation of the effective strains. The genetic manipulation of the PSM with phosphate-solubilizing genes can help in developing the desirable bioinoculants.

References

Adhya, T. K., Kumar, N., Reddy, G., Podile, R. A., Bee, H., & Samantaray, B. (2015). Microbial mobilization of soil phosphorus and sustainable P management in agricultural soils. Special section: Sustainable phosphorus management. *Current Science*, *108*, 1280–1287.

Afzal, A., & Bano, A. (2008). *Rhizobium* and phosphate solubilizing bacteria improve the yield and phosphorus uptake in wheat (*Triticum aestivum* L.). *International Journal of Agriculture and Biology*, *10*, 85–88.

Ahemad, M., & Kibret, M. (2014). Mechanisms and applications of plant growth promoting rhizobacteria: Current perspective. *Journal of King Saud University Science*, *26*, 1–20.

Ahmed, N., & Jha, K. K. (1977). Effect of inoculation with phosphate solubilizing organisms on the yield and P uptake of gram. *Journal of the Indian Society of Soil Science*, *25*, 391–393.

Altomare, C., Norvell, W. A., Bjorkman, T., & Harman, G. E. (1999). Solubilization of phosphorous and micronutrients by plant growth promoting biocontrol fungus, *Trichoderma harzianum*. *Applied and Environmental Microbiology*, *65*, 26–29.

Baldani, V. L. D., Baldani, J. I., & Döbereiner, J. (1987). Inoculation on field-grown wheat (*Triticum aestivum*) with *Azospirillum* spp. in Brazil. *Biology and Fertility of Soils*, *4*, 37–40.

Bano, A., & Fatima, M. (2009). Salt tolerance in *Zea mays* (L) following inoculation with *Rhizobium* and *Pseudomonas*. *Biology and Fertility of Soils*, *45*, 405–413.

Bargaz, A., Lyamlouli, K., Chtouki, M., Zeroual, Y., & Dhiba, D. (2018). Soil microbial resources for improving fertilizers efficiency in an integrated plant nutrient management system. *Frontiers in Microbiology*, *9*, 1606.

Beacham, I. R., & Garrett, S. (1980). Isolation of *Escherichia coli* mutants (cpdB) deficient in periplasmic 2-cyclic phosphodiesterase and genetic mapping of the cpdB locus. *Journal of General Microbiology*, *119*, 31–34.

Beech, I. B., Paiva, M., Caus, M., & Coutinho, C. (2001). Enzymatic activity and within biofilms of sulphate-reducing bacteria. In P. G. Gilbert, D. Allison, M. Brading, J. Verran, & J. Walker (Eds.), *Biofilm community interactions: Chance or necessity?* (pp. 231–239). Cardiff: BioLine.

Bhattacharyya, P. N., & Jha, D. K. (2012). Plant growth-promoting rhizobacteria (PGPR): Emergence in agriculture. *World Journal of Microbiology and Biotechnology*, *28*, 1327–1350.

Broadbent, P., Baker, K. F., Franks, N., & Holland, J. (1977). Effect of *Bacillus* spp. on increased growth of seedlings in steamed and in non-treated soil. *Phytopathology*, *67*, 1027–1034.

Brown, M. E. (1974). Seed and root bacterization. *Annual Review of Phytopathology*, *12*, 181–197.

Buch, A., Archana, G., & Naresh Kumar, G. (2008). Metabolic channeling of glucose towards gluconate in phosphate-solubilizing *Pseudomonas aeruginosa* P4 under phosphorus deficiency. *Research in Microbiology*, *59*, 635–642.

Burns, D. M., & Beacham, I. R. (1986). Nucleotide sequence and transcriptional analysis of the *Escherichia coli* ushA gene, encoding periplasmic UDP-sugar hydrolase (5′-nucleotidase): Regulation of the ushA gene, and the signal sequence of its encoded protein product. *Nucleic Acids Research*, *14*, 4325–4342.

Burr, T. J., Schroth, M. N., & Suslow, T. (1978). Increased potato yields by treatment of seed pieces with specific strains of *Pseudomonas fluorescens* and *Pseudomonas putida*. *Phytopathology*, *68*, 1377–1383.

Capper, A. L., & Campbell, R. (1986). The effect of artificially inoculated antagonistic bacteria on the prevalence of take-all disease of wheat in field experiment. *The Journal of Applied Bacteriology*, *60*, 155–160.

Chen, Q., & Liu, S. (2019). Identification and characterization of the phosphate-solubilizing bacterium *Pantoea* sp. S32 in reclamation soil in Shanxi, China. *Frontiers in Microbiology*, *10*, 2171.

Chen, Y. P., Rekha, P. D., Arunshen, A. B., Lai, W. A., & Young, C. C. (2006). Phosphate solubilizing bacteria from subtropical soil and their tricalcium phosphate solubilizing abilities. *Applied Soil Ecology*, *34*, 33–41.

Cosgrove, D. J. (1967). Metabolism of organic phosphates in soil. In A. D. Mclaren, & G. H. Peterson (Eds.), *Vol. I. Soil biochemistry* (pp. 216–228). New York: Marcel & Dekker.

Daniel, P., Schachtman, R. J. R., & Ayling, S. M. (1998). Phosphorus uptake by plants: From soil to cell. *Plant Physiology*, *116*, 447–453.

David, P., Raj, R. S., Linda, R., & Rhema, S. B. (2014). Molecular characterization of phosphate solubilizing bacteria (PSB) and plant growth promoting rhizobacteria (PGPR) from pristine soils. *International Journal of Innovative Science Engineering and Technology*, *1*, 317–324.

Deubel, A. G., & Merbach, W. (2000). Transformation of organic rhizodeposits by rhizoplane bacteria and its influence on the availability of tertiary calcium phosphate. *Journal of Plant Nutrition and Soil Science*, *163*, 387–392.

Dey, R., Pal, K. K., Bhatt, D. M., & Chauhan, S. M. (2004). Growth promotion and yield enhancement of peanut (*Arachis hypogaea* L.) by application of plant growth-promoting rhizobacteria. *Microbiological Research*, *159*, 371–394.

Dutton, V. M., & Evans, C. S. (1996). Oxalate production by fungi: Its role in pathogenicity and ecology in the soil environment. *Canadian Journal of Microbiology*, *42*, 881–895.

Fernández Bidondo, L., Silvani, V., Colombo, R., Pérgola, M., Bompadre, J., & Godeas, A. (2011). Pre-symbiotic and symbiotic interactions between *Glomus intraradices* and two *Paenibacillus* species isolated from AM propagules. *In vitro* and *in vivo* assays with soybean (AG043RG) as plant host. *Soil Biology and Biochemistry*, *43*, 1866–1872.

Fraga, R., Rodriguez, H., & Gonzalez, T. (2001). Transfer of the gene encoding the NapA acid phosphatase from *Morganella morganii* to *Burkholderia cepacia* strain. *Acta Biotechnologica*, *21*, 359–369.

Gerretsen, F. C. (1948). The influence of microorganisms on the phosphate intake by the plant. *Plant and Soil*, *1*, 51–81.

Ghosh, R., Barman, S., Mukherjee, R., & Mandal, N. C. (2016). Role of phosphate solubilizing *Burkholderia* spp. for successful colonization and growth promotion of *Lycopodium cernuum* L. (Lycopodiaceae) in lateritic belt of Birbhum district of West Bengal, India. *Microbiological Research*, *183*, 80–91.

Glick, B. R., Changping, L., Sibdas, G., & Dumbroff, E. B. (1997). Early development of canola seedlings in the presence of the plant growth-promoting rhizobacterium *Pseudomonas putida* GR12-2. *Soil Biology and Biochemistry*, *29*, 1233–1239.

Goldstein, A. H. (1986). Bacterial solubilization of mineral phosphates: Historical perspectives and future prospects. *American Journal of Alternative Agriculture*, *1*, 57–65.

Goldstein, A. H. (1994). Involvement of the quinoprotein glucose dehydrgenase in solubilization of exogenous phosphates by gram-negative bacteria. In A. Torriani-Gorini, E. Yagil, & S. Silver (Eds.), *Phosphate in microorganisms: Cellular and molecular biology*. Washington, DC: ASM Press.

Goldstein, A. H. (1995). Recent progress in understanding the molecular genetics and biochemistry of calcium phosphate solubilization by Gram negative bacteria. *Biological Agriculture and Horticulture*, *12*, 185–193.

Goldstein, A. H., & Liu, S. T. (1987). Molecular cloning and regulation of a mineral phosphate solubilizing gene from *Erwinia herbicola*. *Biotech*, *5*, 72–74.

Goldstein, A. H., Rogers, R. D., & Mead, G. (1993). Mining by microbe. *Biotechnology*, *11*, 1250–1254.

Halder, A. K., Mishra, A. K., Bhattacharyya, P., & Chakrabartty, P. K. (1990). Solubilization of rock phosphate by *Rhizobium* and *Bradyrhizobium*. *The Journal of General and Applied Microbiology*, *36*, 81–92.

Hall, J. A., Pierson, D., Ghosh, S., & Glick, B. R. (1996). Root elongation in various agronomic crops by the plant growth promoting rhizobacterium *Pseudomonas putida* GR12-2. *Israel Journal of Plant Science*, *44*, 37–42.

Halvorson, H. O., Keynan, A., & Kornberg, H. L. (1990). Utilization of calcium phosphates for microbial growth at alkaline pH. *Soil Biology and Biochemistry*, *22*, 887–890.

Hilda, R. R., & Fraga, R. (2000). Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances*, *17*, 319–359.

Himani, S., & Reddy, M. S. (2011). Effect of inoculation with phosphate solubilizing fungus on growth and nutrient uptake of wheat and maize plants fertilized with rock phosphate in alkaline soils. *European Journal of Soil Biology*, *47*, 30–34.

Hinsinger, P. (2001). Bioavailability of soil inorganic P in the rhizosphere as affected by root induced chemical changes: A review. *Plant and Soil*, *237*, 173–195.

Igual, J. M., Valverde, A., Cervantes, E., & Velázquez, E. (2001). Phosphate-solubilizing bacteria as inoculants for agriculture: Use of updated molecular techniques in their study. *Agronomie*, *21*, 561–568.

Islam, T. M., Deora, A., Hashidoko, Y., Rahman, A., Ito, T., & Tahara, S. (2007). Isolation and identification of potential phosphate solubilizing bacteria from the rhizoplane of *Oryza sativa* L. cv. BR29 of Bangladesh. *Verlag der Zeitschrift für Naturforschung*, *62c*, 103–110.

Istina, I. N., Widiastuti, H., Joy, B., & Antralina, M. (2015). Phosphate solubilizing microbe from Saprists peat soil and their potency to enhance oil palm growth and P uptake. *Procedia Food Science*, *3*, 426–435.

Jahan, M., Mahallati, M. N., Amiri, M. B., & Ehyayi, H. R. (2013). Radiation absorption and use efficiency of sesame as affected by biofertilizers inoculation in a low input cropping system. *Industrial Crops and Products*, *43*, 606–611.

Jain, R., Saxena, J., & Sharma, V. (2012). Effect of phosphate-solubilizing fungi *Aspergillus awamori* S29 on mungbean (*Vigna radiata* cv. RMG 492) growth. *Folia Microbiologica*, *57*, 533–541.

Jha, V., Dafale, N. A., & Purohit, H. J. (2019). Regulatory rewiring through global gene regulations by PhoB and alarmone (p) ppGpp under various stress conditions. *Microbiological Research*, *227*, 126309.

Jorquera, M. A., Crowley, D. E., Marschner, P., et al. (2011). Identification of β-propeller phytase-encoding genes in culturable *Paenibacillus* and *Bacillus* spp. from the rhizosphere of pasture plants on volcanic soils. *FEMS Microbiology Ecology*, *75*, 163–172.

Kapulnik, J., Gafny, R., & Okon, Y. (1985). Effect of *Azopirillum* spp. inoculation on root development and NO-3 uptake in wheat (*Titicum aestivum* cv. Miriam) in hydroponic systems. *Canadian Journal of Botany*, *63*, 627–631.

Khalafallah, M. A., Saber, M. S. M., Abel-El, & Maksound, H. K. (1982). Influence of phosphate dissolving bacteria on the efficiency of superphosphate in calcareous soil cultivated with Viciafaba Z. pflangernachr. Bodenkel. *Journal of Plant Nutrition and Soil Science*, *145*, 455–459.

Khan, J. A., & Bhatnagar, R. M. (1977). Studies on solubilization of insoluble phosphates by microorganisms: Part I. Solubilization of Indian phosphate rocks by Aspergillus niger and Penicillium spp. *Fertilizer Technology*, *14*, 329–333.

Khan, M. S., Zaidi, A. M., Ahemed, M. O., & Wani, P. A. (2010). Plant growth promotion by phosphate solubilizing fungi—Current perspective. *Archives of Agronomy and Soil Science*, *56*, 73–98.

Khan, M. S., Zaidi, A., & Wani, P. A. (2007). Role of phosphate-solubilizing microorganisms in sustainable agriculture—A review. In *Vol. 27. Agronomy for sustainable development* (pp. 29–43). Springer Verlag/EDP Sciences/INRA.

Khiari, L., & Parent, L. E. (2005). Phosphorus transformations in acid light-textured soils treated with dry swine manure. *Canadian Journal of Soil Science*, *85*, 75–87.

Kim, K. Y., Jordan, D., & Donald, G. A. M. (1998). Effect of phosphate-solubilizing bacteria and vascular-arbuscular mycorrhizae on tomato growth and soil microbial activity. *Biology and Fertility of Soils*, *26*, 79–87.

Kim, K. Y., Jordan, D., & Krishnan, H. B. (1997). *Rahnella aqualitis*, a bacterium isolated from soybean rhizosphere, can solubilize hydroxyapatite. *FEMS Microbiology Letters*, *153*, 273–277.

Kloepper, J. W. (1994). Plant growth promoting bacteria (other systems). In J. Okon (Ed.), *Azospirillum/plant association* (pp. 137–154). Boca Raton, FL: CRC Press.

Kloepper, J. W., Lifshitz, K., & Schroth, M. N. (1988). *Pseudomonas* inoculants to benefit plant production. In *ISI atlas of science: Animal and plant sciences* (pp. 60–64). Philadelphia: Institute for Public Information.

Kloepper, J. W., Lifshitz, K., & Zablotowicz, R. M. (1989). Free-living bacterial inocula for enhancing crop productivity. *Trends in Biotechnology*, *7*, 39–43.

Kloepper, J. W., & Schroth, M. N. (1981). Relationship of *in vitro* antibiosis of plant growth promoting rhizobacteria to plant growth and the displacement of root microflora. *Phytopathology*, *71*, 1020–1024.

Kpomblekou, K., & Tabatabai, M. A. (1994). Effect of organic acids on release of phosphorus from phosphate rocks. *Soil Science*, *158*, 442–453.

Kucey, R. M. N., Janzen, H. H., & Leggett, M. E. (1989). Microbially mediated increased in plant available phosphorus. *Advances in Agronomy*, *42*, 198–228.

Kumar, S., Bauddh, K., Barman, S. C., & Singh, R. P. (2014). Amendments of microbial bio fertilizers and organic substances reduces requirement of urea and DAP with enhanced nutrient availability and productivity of wheat (*Triticum aestivum* L.). *Ecological Engineering*, *71*, 432–437.

Kundu, B. S., & Gaur, A. C. (1984). Rice response to inoculation with N fixing and P solubilizing microorganisms. *Plant and Soil*, *79*, 227–234.

Leisinger, K. M. (1999). Biotechnology and food security. *Current Science (India)*, *76*, 488–500.

Lemanceau, P. (1992). Effects benefiques de rhizobacteries sur les plantes: exemple des *Pseudomonas* spp. fluorescent. *Agronomie*, *12*, 413–437.

Li, G. X., Wu, X. Q., Ye, J. R., & Yang, H. C. (2018). Characteristics of organic acid secretion associated with the interaction between *Burkholderia multivorans* WS-FJ9 and poplar root system. *BioMed Research International*, *2018*, 9619724.

Liang, J., Liu, J., Jia, P., et al. (2020). Novel phosphate-solubilizing bacteria enhance soil phosphorus cycling following ecological restoration of land degraded by mining. *The ISME Journal*, *14*, 1600–1613.

Liu, Y. Q., Wang, Y. H., Kong, W. L., Liu, W. H., Xie, X. L., & Wu, X. Q. (2020). Identification, cloning and expression patterns of the genes related to phosphate solubilization in *Burkholderia multivorans* WS-FJ9 under different soluble phosphate levels. *AMB Express*, *10*, 108.

Loheuarete, F., & Berthelin, J. (1988). Effect of phosphate solubilizing bacteria on maize growth and root exudates over four levels of labile phosphorus. *Plant and Soil*, *105*, 11–17.

Mahanta, D., Rai, R. K., Mishra, S. D., Raja, A., Purakayastha, T. J., & Varghese, E. (2014). Influence of phosphorus and biofertilizers on soybean and wheat root growth and properties. *Field Crops Research*, *166*, 1–9.

Maliha, R., Samina, K., Najma, A., Sadia, A., & Farooq, L. (2004). Organic acids production and phosphate solubilization by phosphate solubilizing microorganisms under *in vitro* conditions. *Pakistan Journal of Biological Sciences*, *7*, 187–196.

Mamta, R. P., Pathania, V., Gulati, A., Singh, B., Bhanwra, R. K., & Tewari, R. (2010). Stimulatory effect of phosphate-solubilizing bacteria on plant growth, stevioside and rebaudioside—A contents of *Stevia rebaudiana* Bertoni. *Applied Soil Ecology*, *46*, 222–229.

Mehrvarz, S., Chaichi, M. R., & Alikhani, H. A. (2008). Effects of phosphate solubilizing microorganisms and phosphorus chemical fertilizer on yield and yield components of barely (*Hordeum vulgare* L.). *American-Eurasian Journal of Agricultural & Environmental Sciences*, *3*, 822–828.

Molla, M. A. Z., Chowdhury, A. A., Islam, A., & Hoque, S. (1984). Microbial mineralization of organic phosphate in soil. *Plant and Soil*, *78*, 393–399.

Nahas, E. (1996). Factors determining rock phosphate solubilization by microorganism isolated from soil. *World Journal of Microbiology and Biotechnology*, *12*, 18–23.

Oliveira, C. A., Sa, N. M. H., Gomes, E. A., Marriel, I. E., Scotti, M. R., Guimaraes, C. T., et al. (2009). Assessment of the mycorrhizal community in the rhizosphere of maize (*Zea mays* L.) genotypes contrasting for phosphorus efficiency in the acid savannas of Brazil using denaturing gradient gel electrophoresis (DGGE). *Applied Soil Ecology*, *41*, 249–258.

Pandey, P., & Maheshwari, D. (2007). Bioformulation of *Burkholderia* sp. MSSP with a multispecies consortium for growth promotion of *Cajanus cajan*. *Canadian Journal of Microbiology*, *53*, 213–222.

Pandey, A., Trivedi, P., Kumar, B., & Palni, L. M. S. (2006). Characterization of a phosphate solubilizing and antagonistic strain of *Pseudomonas putida* (B0) isolated from a sub-alpine location in the Indian central Himalaya. *Current Microbiology*, *53*, 102–107.

Park, K. H., Lee, O. M., Jung, H. I., et al. (2010). Rapid solubilization of insoluble phosphate by a novel environmental stress-tolerant *Burkholderia vietnamiensis* M6 isolated from ginseng rhizospheric soil. *Applied Microbiology and Biotechnology*, *86*, 947–955.

Peix, A., Rivas-Boyero, A. A., Mateos, P. F., Rodriguez-Barrueco, C., Martinez-Molina, E., & Velazquez, E. (2001). Growth promotion of chickpea and barley by a phosphate solubilizing strain of M*esorhizobium mediterraneum* under growth chamber conditions. *Soil Biology and Biochemistry*, *33*, 103–110.

Pradel, E., & Boquet, P. L. (1990). Nucleotide sequence and transcriptional analysis of the *Escherichia coli* agp gene encoding periplasmic acid glucose-1-phosphatase. *Journal of Bacteriology*, *172*, 802–807.

Praveen, M. P., Kuligod, V. B., Hebsur, N. S., Patil, C. R., & Kulkarni, G. N. (2012). Effect of phosphate solubilizing fungi and phosphorus levels on growth, yield and nutrient content in maize (*Zea mays* L.). *Karnataka Journal of Agricultural Sciences*, *25*, 58–62.

Raj, J., Bagyaraj, D. J., & Manjunath, A. (1981). Influence of soil inoculation with vesicular arbuscular mycorrhizal fungus and a phosphate dissolving bacterium on plant growth and ^{32}P uptake. *Soil Biology and Biochemistry*, *13*, 105–108.

Richardson, A. E. (1994). Soil microorganisms and phosphorus availability. In C. E. Pankhurst, B. M. Doube, V. V. S. R. Gupta, & P. R. Grace (Eds.), *Soil biota, management in sustainable farming systems* (pp. 50–62). Melbourne: CSIRO.

Richardson, A. E., Hadobas, P. A., & Hayes, J. E. (2001). Extracellular secretion of *Aspergillus phytase* from *Arabidopsis* roots enables plants to obtain phosphorus from phytate. *The Plant Journal*, *25*, 641–649.

Richardson, A. E., & Simpson, R. J. (2011). Soil microorganisms mediating phosphorus availability update on microbial phosphorus. *Plant Physiology*, *156*, 989–996.

Rodríguez, H., & Fraga, R. (1999). Phosphate solubilizing bacteria and their role in plant growth promotion. *Biotechnology Advances*, *17*, 319–339.

Rodríguez, H., Fraga, R., Gonzalez, T., & Bashan, Y. (2006). Genetics of phosphate solubilization and its potential applications for improving plant growth-promoting bacteria. *Plant and Soil*, *287*, 15–21.

Rossolini, G. M., Shippa, S., Riccio, M. L., Berlutti, F., Macaskie, L. E., & Thaller, M. C. (1998). Bacterial nonspecific acid phosphatases: Physiology, evolution, and use as tools in microbial biotechnology. *Cellular and Molecular Life Sciences*, *54*, 833–850.

Saber, K., Nahla, L. D., & Chedly, A. (2005). Effect of P on nodule formation and N fixation in bean. *Agronomy for Sustainable Development*, *25*, 389–393.

Sagoe, C. I., Ando, T., Kouno, K., & Nagaoka, T. (1998). Relative importance of protons and solution calcium concentration in phosphate rock dissolution by organic acids. *Soil Science & Plant Nutrition*, *44*, 617–625.

Sarig, S., Okon, Y., & Blum, A. (1990). Promotion of leaf area development and field in *Sorghum bicolor* inoculated with *Azospirillum brasilense*. *Symbiosis*, *9*, 235–245.

Sashidhar, B., & Podile, A. R. (2010). Mineral phosphate solubilization by rhizosphere bacteria and scope for manipulation of the direct oxidation pathway involving glucose dehydrogenase. *Journal of Applied Microbiology*, *109*, 1–12.

Satyaprakash, M., Nikitha, T., Reddi, E. U. B., Sadhana, B., & Vani, S. S. (2017). A review on phosphorous and phosphate solubilising bacteria and their role in plant nutrition. *International Journal of Current Microbiology and Applied Sciences*, *6*, 2133–2144.

Savci, S. (2012). An agricultural pollutant: Chemical fertilizer. *International Journal of Environmental Science and Development*, *3*, 77–80.

Scervino, J. M., Mesa, M. P., Monica, I. D., Recchi, M., Moreno, N. S., & Godeas, A. (2010). Soil fungal isolates produce different organic acid patterns involved in phosphate salts solubilization. *Biology and Fertility of Soils*, *46*, 755–763.

Sharma, S. B., Sayyed, R. Z., Trivedi, M. H., & Gobi, T. A. (2013). Phosphate solubilizing microbes: Sustainable approach for managing phosphorus deficiency in agricultural soils. *Springer Plus*, *2*, 587.

Singh, S., & Kapoor, K. K. (1999). Inoculation with phosphate solubilizing microorganisms and a vesicular arbuscular mycorrhizal fungus improves dry matter yield and nutrient uptake by wheat grown in a sandy soil. *Biology and Fertility of Soils*, *28*, 139–144.

Son, T. T. N., Diep, C. N., & Giang, T. T. M. (2006). Effect of bradyrhizobia and phosphate solubilizing bacteria application on soybean in rotational system in the Mekong delta. *Omonrice*, *14*, 48–57.

Stevenson, E. J. (2005). *Cycles of soil: Carbon, nitrogen, phosphorus, sulfur, micronutrients*. New York: John Wiley and Sons.

Subbarao, N. S. (1988). Phosphate solubilizing microorganism. In *Biofertilizer in agriculture and forestry* (pp. 133–142). Hissar, India: Regional Biofert. Dev. Centre.

Suleman, M., Yasmin, S., Rasul, M., Yahya, M., Atta, B. M., & Mirza, M. S. (2018). Phosphate solubilizing bacteria with glucose dehydrogenase gene for phosphorus uptake and beneficial effects on wheat. *PLoS One*, *13*, e0204408.

Sundara, B., Natarajan, V., & Hari, K. (2002). Influence of phosphorus solubilizing bacteria on the changes in soil available phosphorus and sugarcane and sugar yields. *Field Crops Research*, *7*, 43–49.

Sundara Rao, W. V. B., Bajpai, P. D., Sharma, J. P., & Subbaiah, B. V. (1963). Solubilization of phosphates by phosphate solubilizing organisms using 32 P as tracer and influence of seed bacteriazation on the uptake by the crop. Indian Soc. *Soil Science*, *11*, 209–218.

Surange, S., Wollum, A. G., Kumar, N., & Nautiyal, C. S. (1995). Characterization of *Rhizobium* from root nodules of leguminous trees growing in alkaline soils. *Canadian Journal of Microbiology*, *43*, 891–894.

Suslov, T. V. (1982). Role of root-colonizing bacteria in plant growth. In M. S. Mount, & G. H. Lacy (Eds.), *Phytopathogenic prokariotes* (pp. 187–223). London: Academic Press.

Swarnalakshmi, K., Prasanna, R., Kumar, A., Pattnaik, S., Chakravarty, K., Shivay, Y. S., et al. (2013). Evaluating the influence of novel cyanobacterial biofilm biofertilizers on soil fertility and plant nutrition in wheat. *European Journal of Soil Biology*, *55*, 107–116.

Tajini, F., Trabelsi, M., & Drevon, J. J. (2012). Combined inoculation with *Glomus intraradices* and *Rhizobium tropici* CIAT899 increases phosphorus use efficiency for symbiotic nitrogen fixation in common bean (*Phaseolus vulgaris* L.). *Saudi Journal of Biological Sciences*, *19*, 157–163.

Tani, A., Akita, M., Murase, H., & Kimbara, K. (2011). Culturable bacteria in hydroponic cultures of moss *Racomitrium japonicum* and their potential as biofertilizers for moss production. *Journal of Bioscience and Bioengineering*, *112*, 32–39.

Tarafdar, J. C., & Claasen, N. (1988). Organic phosphorus compounds as a phosphorus source for higher plants through the activity of phosphatases produced by plant roots and microorganisms. *Biology and Fertility of Soils*, *5*, 308–312.

Tarafdar, J. C., Rao, A. V., & Bala, K. (1988). Production of phosphatases by fungi isolated from desert soils. *Folia Microbiologica*, *33*, 453–457.

Thaller, M. C., Berlutti, F., Schippa, S., Lombardi, G., & Rossolini, G. M. (1994). Characterization and sequence of PhoC, the principal phosphate-irrepressible acid phosphatase of *Morganella morganii*. *Microbiology*, *140*, 1341–1350.

Thaller, M. C., Giovanna, L., Serena, S., & Rossolini, G. M. (1995). Cloning and characterization of the NapA acid phosphatase phosphotransferase of *Morganella morganii*: Identification of a new family of bacterial acid phosphatase-encoding genes. *Microbiology*, *141*, 147–154.

Thaller, M. C., Schippa, S., Bonci, A., Cresti, S., & Rossolini, G. M. (1997). Identification of the gene (aphA) encoding the class B acid phosphatase/phosphotransferase of *Escherichia coli* MG 1655 and characterization of its product. *FEMS Microbiology Letters*, *146*, 191–198.

Tilak, K. V. B. R., Ranganayaki, N. L., Pal, K. K., De, R., Saxena, A. K., Nautiyal, C. S., et al. (2005). Diversity of plant growth and soil health supporting bacteria. *Current Science*, *89*, 136.

Toro, M. (2007). Phosphate solubilizing microorganisms in the rhizosphere of native plants from tropical savannas: An adaptive strategy to acid soils? In C. Velazquez, & E. Rodriguez-Barrueco (Eds.), *Developments in plant and soil sciences* (pp. 249–252). Dordrecht: Springer.

Tripathi, A. K., Nagarajan, T., & Verma, S. C. (2002). Inhibition of biosynthesis and activity of nitrogenase in *Azospirillum brasilense* Sp7 under salinity stress. *Current Microbiology*, *44*, 363–367.

Vasil, I. K. (1998). Biotechnology and food security for 21st century: A real world perspective. *Nature Biotechnology*, *16*, 399–400.

Vikram, A., & Hamzehzarghani, H. (2008). Effect of phosphate solubilizing bacteria on nodulation and growth parameters of green gram (*Vigna radiata* L. Wilczek). *Research Journal of Microbiology*, *3*, 62–72.

Villegas, J., & Fortin, J. A. (2002). Phosphorus solubilization and pH changes as a result of the interactions between soil bacteria and arbuscular mycorrhizal fungi on a medium containing NO_3 as nitrogen source. *Canadian Journal of Botany*, *80*, 571–576.

Viveros, O. M., Jorquera, M. A., Crowley, D. E., Gajardo, G., & Mora, M. L. (2010). Mechanisms and practical considerations involved in plant growth promotion by rhizobacteria. *Journal of Soil Science and Plant Nutrition*, *10*, 293–319.

Walpola, B. C., & Yoon, M. (2012). Prospectus of phosphate solubilizing microorganisms and phosphorus availability in agricultural soils: A review. *African Journal of Microbiology Research*, *6*, 6600–6605.

Walpola, B. C., & Yoon, M. (2013). Phosphate solubilizing bacteria: Assessment of their effect on growth promotion and phosphorous uptake of mung bean (*Vigna radiate* [L.] R. Wilczek). *Chilean Journal of Agricultural Research*, *73*, 275.

Wang, H., Liu, S., Zhal, L., Zhang, J., Ren, T., Fan, B., et al. (2015). Preparation and utilization of phosphate biofertilizers using agricultural waste. *Journal of Integrative Agriculture*, *14*, 158–167.

Wani, P. A., Khan, M. S., & Zaidi, A. (2007). Synergistic effects of the inoculation with nitrogen fixing and phosphate-solubilizing rhizobacteria on the performance of field grown chickpea. *Journal of Plant Nutrition and Soil Science*, *170*, 283–287.

Whitelaw, M. A. (2000). Growth promotion of plants inoculated with phosphate solubilizing fungi. *Advances in Agronomy*, *69*, 99–151.

Xiao, C., Zhang, H., Fang, Y., & Chi, R. (2013). Evaluation for rock phosphate solubilization in fermentation and soil–plant system using a stress-tolerant phosphate-solubilizing *Aspergillus niger* WHAK1. *Applied Microbiology and Biotechnology*, *169*, 123–133.

Yadaf, R. S., & Tarafdar, J. C. (2001). Influence of organic and inorganic phosphorus supply on the maximum secretion of acid phosphatase by plants. *Biology and Fertility of Soils*, *34*, 140–143.

Yang, M., Wang, C., Wu, Z., Yu, T., Sun, H., & Liu, J. (2016). Phosphate dissolving capacity, glucose dehydrogenase gene expression and activity of two phosphate solubilizing bacteria. *Wei Sheng Wu Xue Bao*, *56*, 651–663.

Yousefi, A., Khavazi, K., Moezi, A., Rejali, F., & Nadian, H. (2011). Phosphate solubilizing bacteria and arbuscular mycorrhizal fungi impacts on inorganic phosphorus fractions and wheat growth. *World Applied Sciences Journal*, *15*, 1310–1318.

Zaidi, A., & Khan, M. S. (2006). Co-inoculation effects of phosphate solubilizing microorganisms and *Glomus fasciculatumon* on green gram—*Bradyrhizobium* symbiosis. *Turkish Journal of Agriculture and Forestry*, *30*, 223–230.

Zaidi, A., Khan, M. S., Ahemad, M., & Oves, M. (2009). Plant growth promotion by phosphate solubilizing bacteria. *Acta Microbiologica et Immunologica Hungarica*, *56*, 263–284.

Zayed, M. S. (2012). Improvement of growth and nutritional quality of *Moringa oleifera* using different biofertilizers. *Annals of Agricultural Science*, *57*, 53–62.

Zeng, Q., Wu, X., Wang, J., & Ding, X. (2017). Phosphate solubilization and gene expression of phosphate-solubilizing bacterium *Burkholderia multivorans* WS-FJ9 under different levels of soluble phosphate. *Journal of Microbiology and Biotechnology*, *27*, 844–855.

Zeng, Q., Wu, X., & Wen, X. (2016). Effects of soluble phosphate on phosphate-solubilizing characteristics and expression of gcd gene in *Pseudomonas frederiksbergensis* JW-SD2. *Current Microbiology*, *72*, 198–206.

Zhao, K., Penttinen, P., Zhang, X., Ao, X., Liu, M., Yu, X., et al. (2014). Maize rhizosphere in Sichuan, China, hosts plant growth promoting *Burkholderia cepacia* with phosphate solubilizing and antifungal abilities. *Microbiological Research*, *169*, 76–82.