Chapter 10
Functional Aspect of Phosphate-Solubilizing Bacteria: Importance in Crop Production

Mohammad Saghir Khan, Ees Ahmad, Almas Zaidi, and Mohammad Oves

10.1 Introduction

Phosphorus (P) is one of the major macronutrients essentially required by plants and plays a critical role in photosynthesis, energy transfer, signal transduction, macromolecular biosynthesis, and respiration (Fernandez et al. 2007; Ahemad et al. 2009). After uptake by plants, P also stimulates root development and facilitates flower formation and quality and quantity of fruits and seed formation (Ahemad et al. 2009). Additionally, sufficient P concentration may increase the resistance ability of plants to diseases and adverse conditions. On the other hand, majority of the soils around the world are deficient in P, and hence, only 1–5 % of total soil P is available to plants (Molla and Chaudhury 1984). As a result of the acute deficiency, P is, therefore, applied in agronomic operations from external sources in order to fulfill the phosphatic demands of plants. The use of consistent and sometimes excessively higher rates of chemicals including phosphatic fertilizers in current high-input agricultural practices has, however, resulted in the damaging effects on composition and functions of rhizosphere microbes. Subsequently, the fertility of soil is disturbed. These factors together lead to losses in crop production. The reduction in overall growth of plants following excessive application of P occurs primarily due to poor P uptake ability of plants and rapid fixation/sorption ability of P with soil constituents as calcium, aluminum, and iron phosphate (Lindsay et al. 1989; Vassilev and Vassileva 2003; Tao et al. 2008). In order to reduce chemical addition to soils and spiraling cost, and undeniable deleterious environmental impacts of P fertilizers, there is an urgent need to find a suitable/feasible alternative to chemical fertilizers. In this regard, microbial communities capable of transforming insoluble/bound P into soluble and available forms, collectively called

M.S. Khan (✉) • E. Ahmad • A. Zaidi • M. Oves
Department of Agricultural Microbiology, Faculty of Agricultural Sciences, Aligarh Muslim University, Aligarh 202002, Uttar Pradesh, India
e-mail: khanms17@rediffmail.com

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as phosphate-solubilizing microorganisms (PSM), may be applied to overcome such barriers. Considering these, many researchers around the world have isolated PS bacteria from different soils (Perveen et al. 2002; Pérez et al. 2007; Chen et al. 2008; Khan et al. 2009a; Ahemad and Khan 2010; Hui et al. 2011; Xiang et al. 2011) and tested their ability as inoculants to see whether they have any impact on plant growth or not (Zaidi 1999; Zaidi et al. 2003, 2009a; Chen et al. 2006; Kumari et al. 2009; Khan et al. 2010). Interestingly, among microbiological option, many of PS bacteria belonging largely to the genera pseudomonads (Behbahani 2010; Ahemad and Khan 2011a), bacilli (Wani et al. 2007a; Behbahani 2010; Sanjotha et al. 2011; Yadav et al. 2011), rhizobia (Abd-Alla 1994; Alikhani et al. 2006; Abril et al. 2007; Chandra et al. 2007; Marra et al. 2011), and *Azotobacter* (Ivanova et al. 2006; Yi et al. 2008) when used as phosphatic inoculants have been found effective and more practical in sustainable agricultural practices for enhancing crop production by providing available forms of P to different plants (Bojinova et al. 2008; Adesemoye and Kloepper 2009; Oliveira et al. 2009; Yu et al. 2011) in different agro-ecological niches (Zaidi et al. 2003; Khan et al. 2007). In addition to P, the PSM including bacteria (Zaidi et al. 2009b; Zhu et al. 2011) and fungi (El-Azouni 2008; Khan et al. 2010) increase the growth of plants by other mechanisms like N_2 fixation, by providing various growth-regulating substances to plants (Wani et al. 2007a; Mittal et al. 2008; Ahemad and Khan 2011b), such as siderophores (Oves et al. 2009; Ahemad and Khan 2012) and antibiotics (Lipping et al. 2008; Khan et al. 2010), and by protecting plants from pathogen damage (Hamadali et al. 2008). Documented results have shown that microphos (microbial cultures with PS activity) having such vast and varied activities when used either alone (Chen et al. 2008; Poonguzhali et al. 2008) or as mixture with other plant growth-promoting rhizobacteria (PGPR), a modifier of soil fertility and facilitator of plant establishment (Zaidi and Khan 2006; Wani et al. 2007b; Vikram and Hamzehzarghani 2008; Khan et al. 2009a, b) increased the biological and chemical characteristics of plants grown in various agro-ecosystems (Rodríguez et al. 2006; Khan et al. 2009b; Ahemad and Khan 2011b).

10.2 Mechanism of P-Solubilization and Development of Inoculant: A Brief Account

Naturally abundant yet unavailable insoluble forms of P such as tricalcium phosphate $(Ca_3PO_4)_2$, aluminum phosphate (Al_3PO_4), and iron phosphate (Fe_3PO_4) may be converted to soluble P by P-solubilizing bacteria inhabiting different soil ecosystems (Song et al. 2008; Khan et al. 2010; Ahemad and Khan 2011a). Soil microorganisms in this regard have generally been found more effective in making P available to plants from both inorganic and organic sources by solubilizing (Toro 2007; Wani et al. 2007b) and mineralizing difficultly available P (Bishop et al. 1994; Ponmurugan and Gopi 2006), respectively. Several workers have documented their findings in order to better understand as to how the microbial populations including bacteria cause the solubilization of insoluble P (Cunningham and Kuiack 1992; Illmer and Schinner 1995; Buch et al. 2008; Song et al. 2008). Of the various strategies adopted by microbes, the involvement of low molecular mass organic acids (OA) secreted by microorganisms has been well recognized and a widely accepted theory as a principal means of P solubilization (Maliha et al. 2004). The OA produced by bacterial cultures (Table 10.1) in the natural environment or under in vitro conditions chelate mineral ions or decrease the pH to bring P into solution (Maliha et al. 2004; Pradhan and Shukla 2005). Consequently, the acidification of microbial cells and their surrounding leads to the release of P ions from the P mineral by H^+ substitution for Ca^{2+} (Goldstein 1994). However, there are also reports which suggest that insoluble P could be transformed into soluble forms of P without OA production by microbes (Asea et al. 1988; Illmer and Schineer 1992, 1995; Chen et al. 2006). For example, Altomare et al. (1999) while investigating the P-solubilizing ability of plant growth-promoting and biocontrol fungus *Trichoderma harzianum* T-22 did not record OA production (rock P was used as insoluble P source) under in vitro condition. It was concluded from this study that the insoluble P could be solubilized by mechanisms other than acidification process. Also, the fungal-solubilizing activity was credited both to chelation and to reduction processes, which may be useful in the management of phytopathogens. Apart from the OA theory, some of the inorganic acids (Reyes et al. 2001; Richardson 2001) such as HCl (Kim et al. 1997), nitric acid, and sulfuric acids (Dugan and Lundgren 1965) produced by chemoautrophs and the H^+ pump, for example, in *Penicillium rugulosum*, have also been reported to solubilize the insoluble P (Reyes et al. 1999). The inorganic acids convert tri-calcium phosphate to di- and monobasic phosphates with the net result of an enhanced availability of the element to plants.

The advent of P-solubilizing potentials among renewable resources like the bacterial populations has been one of the most important biological traits that have resulted in reducing the dependence on synthetic P fertilizers and consequently preserving soil fertility and environmental safety from chemical toxicity. And therefore, the use of PS bacteria as an alternative to chemical fertilizer has attracted greater attention of agronomists than microbiologists in recent times. In order to develop microphos, organisms with P-solubilizing activity may be isolated from either conventional or derelict environment using standard methods. The isolated bacterial cultures showing greatest P-solubilizing activity (Fig. 10.1) on any media designed especially to select P-solubilizing bacteria, for example, Pikovskaya medium (Pikovskaya 1948) are selected and used to develop as microbial inoculants following standard procedure (Fig. 10.2). Subsequently, the microphos are tested both under pot house and field environment using seed treatment, seedling dipping, or soil application methods for their ultimate transfer to practitioner/farmers for application in agricultural practices as a cheap and viable phosphatic option.

Table 10.1 Organic acid production and P solubilisation by PS bacteria

PS bacteria	Organic acid produced	Initial pH	Final pH	Amount of P solubilised (μg/ml)	Time (h)	Reference
Pseudomonas trivialis (BIHB 769)	GA, 2-KGA, LA, SA, FA, MA	7 ± 0.2	3.70	806.4 ± 2.3	120	Vyas and Gulati (2009)
P. poae (BIHB 808)	GA, 2-KGA, SA, CA, MA	7 ± 0.2	3.58	821.4 ± 1.7	120	Vyas and Gulati (2009)
P. fluorescens (BIHB 740)	GA, 2-KGA, SA, FA, CA, MA	7 ± 0.2	3.97	768.3 ± 2.6	120	Vyas and Gulati (2009)
Pseudomonas spp. (BIHB 751)	OA, GA, 2-KGA, FA, MA	7 ± 0.2	4.20	318.7 ± 2.0	120	Vyas and Gulati (2009)
Enterobacter Hy-401	OA, GA, MA, LA, CA, SA, FuA	7–7.5	4.32±0.02	623.6 ± 23.0	120	Yi et al. (2008)
Arthrobacter Hy-505	OA, GA, LA, CA	7–7.5	5.50 ± 0.04	428.9 ± 15.3	120	Yi et al. (2008)
Azotobacter Hy-510	OA, GA, TA, LA, SA, FuA	7–7.5	4.69 ± 0.05	229.03 ± 15.2	120	Yi et al. (2008)
Enterobacter Hy-402	OA, GA, TA, CA, SA, FuA	7–7.5	4.51 ± 0.02	111.73 ± 8.07	120	Yi et al. (2008)
Rhodococcus erythropolis(CC-BC11)	GA	7–6.8	5.3	186.9	72	Chen et al. (2006)
Bacillus megaterium (CC-BC10)	CA, LA, PA	7–6.8	5.1	270.2	72	Chen et al. (2006)
Arthrobacter sp. (CC-BC03)	CA, LA	7–6.8	4.9	519.7	72	Chen et al. (2006)
A. ureafaciens (CC-BC02)	CA	7–6.8	5.0	316.1	72	Chen et al. (2006)
Serratia marcescens (CC-BC14)	CA, GA, SA, LA	7–6.8	4.9	421.8	72	Chen et al. (2006)
Delftia (CC-BC21)	SA,	7–6.8	4.9	346.1	72	Chen et al. (2006)
Chryseobacterium (CC-BC05)	CA	7–6.8	6.0	298.9.	72	Chen et al. (2006)
Phyllobacterium myrsinacearum (CC-BC19)	GA	7–6.8	5.2	201.2	72	Chen et al. (2006)
Gordonia (CC-BC07)		7–6.8	6.0	31.5	72	Chen et al. (2006)
Enterobacter intermedium	2-KGA	8	2.8	65×10^3	240	Hwangbo et al. (2003)
Bacillus amyloliquefaciens	AA, IBA, IVA, LA, SA	ND	ND	60 (approx)	24	Vazquez et al. (2000)

B. atrophaeus	PA, IBA, IVA, VA, ISA, SA	ND	ND	110 (approx)	24	Vazquez et al. (2000)
B. licheniformis	IBA, VA, LA, FuA, SA	ND	ND	105 (approx)	24	Vazquez et al. (2000)
V. proteolyticus	AA, LA	ND	ND	475 (approx)	24	Vazquez et al. (2000)
P. macerans	IBA, IVA, LA, SA	ND	ND	85 (approx)	24	Vazquez et al. (2000)
X. agilis	IBA, IVA	ND	ND	190 (approx)	24	Vazquez et al. (2000)

GA Gluconic acid, *2-KGA-2α* ketogluconic acid, *LA* Lactic acid, *SA* Succinic acid, *FA* Formic acid, *MA* Malic acid, *CA* Citric acid, *OA* Oxalic acid, *FuA* Fumaric acid, *TA* Tartaric acid, *PA* Propionic acid, *AA* Acetic acid, *IBA* Isobutyric acid, *IVA* Isovaleric acid, *VA* Valeric acid, *ISA* Isocaproic acid, *ND* not determined

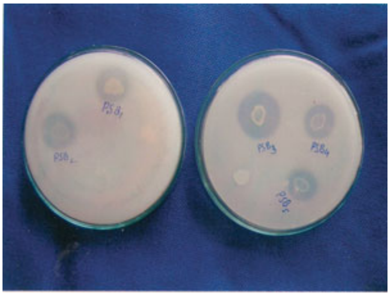

Fig. 10.1 Halo formation by phosphate-solubilizing bacteria on Pikovskaya agar plate

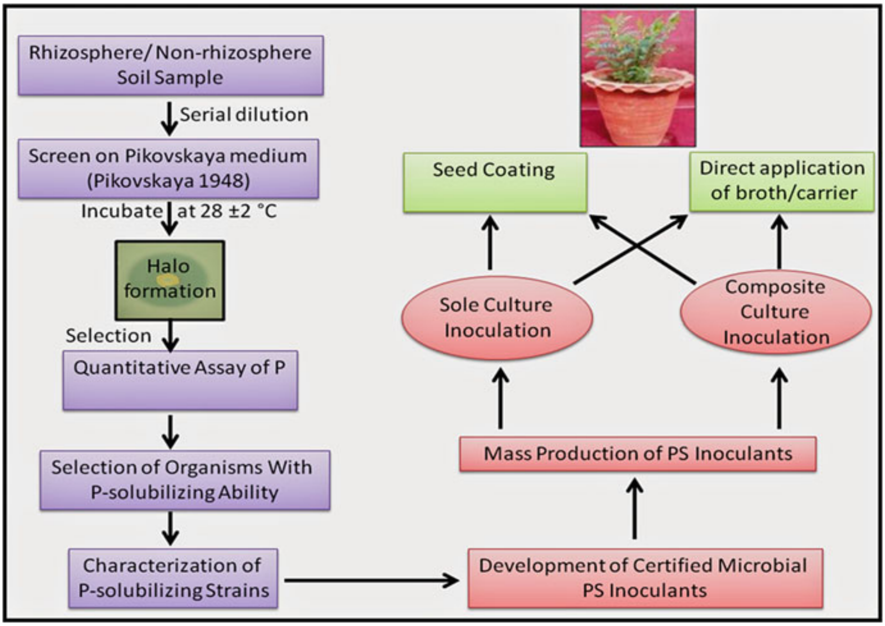

Fig. 10.2 Isolation, selection and formulation of PS bacteria (Modified from Zaidi et al. 2009a, b)

10.3 Functional Diversity Among Phosphate-Solubilizing Bacteria

Principally, P-solubilizing microorganisms in general are widely known to increase the overall performance by providing soluble P to plants in different production systems. However, they also benefit plants by other mechanisms (Fig. 10.3). They exhibit multifunctional properties (Vikram et al. 2007a; Singh et al. 2010; Vassileva et al. 2010; Yadav et al. 2011), for example, they are known to synthesize siderophores (Matthijs et al. 2007; Hamadali et al. 2008; Viruel et al. 2011),

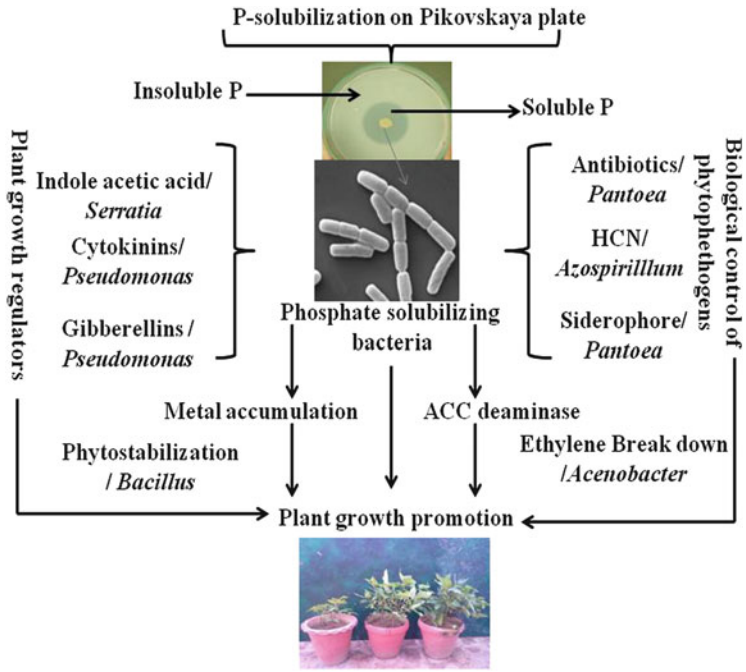

Fig. 10.3 An illustration depicting functional diversity among PS bacteria (Modified from Oves et al. 2009; photograph of PSB, courtesy M. Oves)

indoleacetic acid (IAA), and gibberellic acid (Sattar and Gaur 1987; Souchie et al. 2007; Viruel et al. 2011). Phosphate-solubilizing bacteria such as Gram-negative *P. fluorescens*, *P. aeruginosa*, and *Chromobacterium violaceum* also secretes cyanide, a secondary metabolite which is ecologically important (Siddiqui et al. 2006; Wani et al. 2007a), and gives a selective advantage to the producing strains (Rudrappa et al. 2008). Besides strict P solubilizers, a few genera of rhizobia, for example, *Bradyrhizobium* and *Rhizobium*, have also been found to solubilize P and secrete IAA (Pandey and Maheshwari 2007; Badawi et al. 2011). Interestingly, the ability of PSB, for example, *Serratia marcescens*, to secrete siderophores and cyanide is critical in managing various diseases inflicted by the plant pathogens (Vassilev et al. 2006) and indirectly promoting the plant growth (Badawi et al. 2011). Some of the compounds synthesized by P-solubilizing bacteria with possible effect on plant growth promotion are listed in Table 10.2.

Table 10.2 Examples of plant growth-promoting substances released by phosphate-solubilizing bacteria

Phosphate-solubilizing bacteria	Plant growth-promoting substances	Reference
Pseudomonas fluorescens, *P. putida*	IAA, siderophore, ACC deaminase	Zabihi et al. (2011)
Serratia nematodiphila	IAA, siderophore, HCN	Dastager et al. (2011a)
Pontibacter niistensis	IAA, HCN, ACC deaminase and siderophore	Dastager et al. (2011b)
Klebsiella spp.	IAA, siderophore, HCN, ammonia, EPS	Ahemad and Khan (2011b)
Pantoea agglomerans	IAA	Mishra et al. (2011)
Arthrobacter, *Bacillus*	IAA, antifungal activity, HCN, NH_3	Banerjee et al. (2010)
Paenibacillus alvei, *Bacillus cereus*	IAA, siderophore	
Pantoea	IAA, siderophore, antifungal activity	Taurian et al. (2010)
Pseudomonas aeruginosa	IAA, siderophore, antifungal activity, HCN, EPS	Ahemad and Khan (2010)
P. mendocina, *P. stutzeri* and *P. putida*	IAA, gibberellic acid, trans-zeatin riboside and abscisic acid	Naz and Bano (2010)
Enterobacter aerogenes, *E. cloacae*, *E. asburiae*	IAA, siderophore, HCN	Deepa et al. (2010)
P. alvei	IAA	Hassen and Labuschagne (2010)
Pseudomonas sp.	ACC deaminase, IAA, siderophore	Poonguzhali et al. (2008)
Serratia marcescens	IAA, siderophore, HCN	Selvakumar et al. (2008)
Acinetobacter sp., *Pseudomonas* sp.	ACC deaminase, IAA, antifungal activity, N_2-fixation	Indiragandhi et al. (2008)
Enterobacter sp.	ACC deaminase, IAA, siderophore	Kumar et al. (2008)
Burkholderia	ACC deaminase, IAA, siderophore	Jiang et al. (2008)
Pseudomonas jessenii	ACC deaminase, IAA, siderophore	Rajkumar and Freitas (2008)
P. aeruginosa	ACC deaminase, IAA, siderophore	Ganesan (2008)
Azotobacter sp., *Pseudomonas* sp., *Bacillus* sp.	IAA, siderophore, antifungal activity, ammonia production, HCN	Ahmad et al. (2008)
Fluorescent pseudomonas	IAA, siderophores, HCN, antifungal activity	Shweta et al. (2008)
Pseudomonas vancouverensis	IAA, HCN, siderophore, antifungal activity	Mishra et al. (2008)
Bacillus sp.	IAA, siderophores, ammonia production, HCN	Wani et al. (2007a, 2007b)
Klebsiella oxytoca	IAA, nitrogenase activity	Jha and Kumar (2007)

10.4 Importance of Phosphate-Solubilizing Bacteria in Crop Improvement

Phosphate-solubilizing bacteria among biological materials are one of the most important soil constituents which play a central role in maintaining soil fertility. Consequently, they support plants to grow in a well-directed manner because starting from seed germination until the seed production or maturation stages, plants remain in close proximity with PSB. Considering the vast and varied activities, researchers around the world have either attempted or included the use of this novel group of economically feasible biological materials in agronomic operation for sustainable crop production with variable results (Tables 10.3 and 10.4). The role of PSB in maintaining soil fertility vis-a-vis increasing crop productivity is briefly discussed in the following section.

10.4.1 Phosphate Solubilizers–Legume Interactions: Current Perspective

The sole or composite application of PSB for raising legume production has received considerable attention worldwide (Zaidi et al. 2004; Vikram et al. 2007b; Shaharoona et al. 2008; Collavino et al. 2010). Considering the success of PSB application achieved so far in agronomic practices, we have attempted in the following section to focus on the role of PSB exclusively in the improvement of legumes grown in different agro-ecosystems.

10.4.1.1 Impact of Monoculture of PSB on Legume Improvement

Phosphate-solubilizing fluorescent pseudomonads isolated from the groundnut (*Arachis hypogaea*) rhizosphere, when used as phosphatic biofertilizer against groundnut plants, enhanced germination by 30 % while it increased grain yield by 77 %. To test the biocontrol potential of this PSB strain, a plant pathogen *Macrophomina phaseolina* alone was also included, which, however, decreased the grain yield substantially by 57 %. The increase in the yield of ground following PSB application, however, suggested that *Pseudomonas* strains used in this study had two basic traits (1) pseudomonads acted as biocontrol agent against *M. phaseolina* and (2) that they provided available form of P and consequently enhanced the yield of groundnut (Shweta et al. 2008). Dey et al. (2004) in yet another study observed a significantly higher pod yields, haulm yield, and nodule dry weight in PSB (*P. fluorescens*)-inoculated peanut plants compared to those recorded for un-inoculated plants grown in pots and field trials. The seed bacterization also resulted in higher N and P contents in soil. In addition, the pod yields were increased by 23–26 %; other plant characteristics such as root length, pod number,

Table 10.3 Examples of phosphate solubilizing bacteria used for raising crop production

Phosphate-solubilizing bacteria	Crop tested	Botanical name	Reference
Pantoea agglomerans	Maize	*Zea mays*	Mishra et al. (2011)
Pseudomonas fluorescens, *B. cepacia*, *Aeromonas vaga*	Mung bean	*Vigna radiata*	Jha et al. (2012)
Pseudomonas fluorescens, *P. putida*	Wheat	*Triticum aestivum* L.	Zabihi et al. (2011)
Bacillus	Rice	*Oryza sativa*	Panhwar et al. (2011)
Serratia nematodiphila	black pepper	*Piper nigrum* L	Dastager et al. (2011a)
Pseudomonas chlororaphis, *Bacillus cereus* and *P. fluorescens*	Walnut	*Juglans siggillata* L	Yu et al. (2011)
Enterobacter aerogenes	Kidney bean	*Phaseolus vulgaris*	Collavino et al. (2010)
Pseudomonas, *Bacillus*	Alfalfa	*Medicago sativa* L	Guiñazú et al. (2010)
Pantoea	Peanut	*Arachis hypogaea*	Taurian et al. (2010)
P. aeruginosa	Green gram	*Vigna radiata* (L.) Wilczek	Ahemad and Khan (2010)
E. aerogenes, *E. cloacae*, *E. asburiae*	Cowpea	*Vigna unguiculata* (L.)	Deepa et al. (2010)
Pseudomonas synxantha, *Burkholderia gladioli*, *Enterobacter hormaechei* and *Serratia marcescens*	Chinese aloe	*Aloe barbadensis*	Mamta et al. (2010)
Bacillus megaterium var. *phosphaticum*	Flax	*Linum usitatissimum* L	El-Nagdy et al. (2010)
Bacillus simplex, *B. megaterium*, *B. cereus*, *Paenibacillus alvei*	Tomato, wheat	*Lycopersicon esculentum* Mill.	Hassen and Labuschagne (2010)
B. amyloliquefaciens and *B. pumilus*	Tomato	*Solanum lycopersicum*	Adesemoye et al. (2009)
B. megaterium, *B. subtilis*, *Pseudomonas corrugate*	Rice	*Oryza sativa*	Trivedi et al. (2007)

100-kernel mass, shelling out-turns, and nodule numbers were also increased following bacterial inoculation. Seed treatment with *P. fluorescens* also depressed incidence of soil-borne fungal diseases, like collar rot and charcoal rot of peanut (Bhatia et al. 2008), caused by *A. niger*. While considering the overall improvement in inoculated peanut, it was inferred that the increase was due to (1) the synthesis of IAA, ACC-deaminase and siderophore, and (2) antifungal activity against various fungal pathogens. Similar increase in the biological and chemical characteristics and quality of pea (*Pisum sativum*) and chickpea (*Cicer arietinum*) under both controlled conditions and field environment following P-solubilizing, auxin, ACC deaminase, ammonia, and siderophore-producing strains of *Acinetobacter*

Table 10.4 Examples of sole and composite inoculation effects of phosphate-solubilizing bacteria on biological and chemical characteristics of different plants

Organisms applied				
Sole	Composite	Crop	Plant attributes	Reference
P. agglomerans NBRISRM		Maize, chickpea	Shoot length, leaves, seed, N, P and K uptake	Mishra et al. (2011)
P. chlororaphis, *P. fluorescens*, *B. cereus*		Walnut	Plant height, root and shoot dry weight, P, N and K uptake	Yu et al. (2011)
P. fluorescens, *P. putida*		Wheat	Plant height, tillers, number of grains/ spike, 1,000-grain weight, grain and straw yield, N, P and K uptake	Zabihi et al. (2011)
Enterobacter sp		Cowpea	Root and shoot length, dry biomass, seedling length	Deepa et al. (2010)
P. fluorescens, *Pantoea*		Peanut	Plant length, Dry weight, N and P content	Taurian et al. (2010)
P. aeruginosa		Green gram	Plant height, plant dry weight, nodulation, chlorophyll, leghaemoglobin, N and P content, seed yield	Ahemad and Khan (2010)
Citrobacter, *Pantoea*, *Klebsiella and Enterobacter*		Pigeon pea	Shoot P content, dry shoot/root ratio, dry weight	Patel et al. (2010)
Bacillus sp.		Chickpea	Root and shoot length, nodulation, dry weight	Wani and Khan (2010)
Burkholderia gladioli, *Enterobacter aerogenes* and *Serratia marcescens*		*Stevia rebaudiana*	Shoot and root length, leaf and stem dry weight, shoot biomass and glycoside contents	Mamta et al. (2010)
A. calcoaceticus SE370		Cucumber, Chinese cabbage and Crown daisy	Shoot length, plant height, dry weight	Kang et al (2009)
Pseudomonas aeruginosa	*Sinorhizobium meliloti*	Mustard	Root and shoot fresh weight and dry weight, yield	Maheshwari et al. (2011)
Pontibacter niistensis		Cowpea	Root and shoot weight, dry weight, seedling growth	Dastager et al. (2011b)

(continued)

Table 10.4 (continued)

Organisms applied				
Sole	Composite	Crop	Plant attributes	Reference
P. fluorescens	*Burkholderia cepcia, Aeromonas vaga*	Mung bean	Root and shoot length, dry weight, leaf area, photosynthetic yield, P content in leaf	Jha et al. (2012)
Pseudomonas	*Bacillus*	Strawberry	Fruit yield and weight, vit. C, reducing sugar	Esitken et al (2010)
Bacillus, Pseudomonas	*Sinorhizobium meliloti*	Alfalfa	Root and shoot dry weight, root length, N content in shoot	Guiñazú et al (2010)
Paenibacillus alvei	*Bacillus simplex, Bacillus cereus*	Wheat	Shoot and root biomass and total root length	Hassen and Labuschagne (2010)
Bacillus megaterium	*Bacillus simplex, Bacillus cereus*	Tomato	Shoot and root biomass and total root length	Hassen and Labuschagne (2010)
P. putida	*B. japonicum*	Soybean	Root and shoot dry weight, nodulation	Rosas et al. (2006)
P. putida	*S. meliloti*	Alfalfa	Root and shoot dry weight, nodulation	Rosas et al. (2006)

rhizosphaerae and *Mesorhizobium mediterraneum* (PECA21) has been reported (Peix et al. 2001; Gull et al. 2004; Gulati et al. 2009). Likewise, inoculation of green gram [*Vigna radiata* (L.) Wilczek] seeds with PSB demonstrated an extensive nodulation and increased shoot dry matter and total dry matter, P-content, and P uptake in green gram plants 45 days after sowing relative to either rock phosphate (RP) or single super phosphate (SSP) application (Vikram and Hamzehzarghani 2008).

10.4.1.2 Synergistic Effect of Phosphate-Solubilizing Bacteria with Other PGPR/AM-Fungi

Even though P is available in plenty in many soils, application of phosphatic fertilizers is essentially required to cover up losses caused due to P fixation by soil constituents and phosphate runoff in P-loaded soil (Goldstein 1986; Del Campillo et al. 1999). On the contrary, the use of phosphate solubilizers to provide exclusively P to plants and also along with other compatible PGPR for increasing quality of crops have been studied intensively (Zaidi and Khan 2006; Afzal et al. 2010; Zaidi et al. 2010). The beneficial microbes involved in P solubilization in addition to P can also enhance plant growth by improving the efficiency of BNF, by accelerating the availability of other trace elements, and by production of phytohormones (Wani et al. 2007a). Accordingly, increase in yield of various legumes have been observed following seed or soil inoculation with N_2-fixing organisms, PSB, or PSB when used with nodule bacteria (Maheshwari et al. 2011) and AM fungus (Zaidi and Khan 2006; Khan and Zaidi 2007).

Like other PGPR, PSB within soil forms a close relationship with microbes and play important role in improving crop yields additively or synergistically. For example, the composite application of N_2-fixing *Sinorhizobium meliloti* and P-solubilizing bacterium *Bacillus* sp. M7c and *Pseudomonas* sp. FM7d significantly enhanced the N-fixing efficiency of alfalfa plants. Of these, *Pseudomonas* sp. FM7d resulted in enhanced dry matters production in plant organs such as root and shoot, length and surface area of roots, number and symbiotic properties of alfalfa (*Medicago sativa* L.) plants (Guiñazú et al. 2010). It was concluded from this study that *S. meliloti* B399 and *Bacillus* sp. M7c proved effective for developing mixed phosphatic inoculants. In a similar experiment, Bansal (2009) observed a dramatic increase in nodulation and grain yield of mung bean treated simultaneously with *Rhizobium*, PGPR, and PSB. The tripartite treatments were followed by dual inoculation of *Rhizobium* with PGPR and *Rhizobium* alone in terms of nodulation and grain yield increases in *kharif* seasons. The pooled analysis also gave significantly highest number of nodules/plant (21/plant), dry weight of nodules/plant (87.7 mg), and grain yield (12.9 q/ha) following combined inoculation of *Rhizobium*, PGPR, and PSB. The increase in yield (12 q/ha) was at par with *Rhizobium* used with PGPR. In a follow-up study, Dutta and Bandyopadhyay (2009), while conducting a field experiment during the winter seasons, observed that P and biofertilizers, phosphobacterin (*Pseudomonas striata*) and co-inoculation of *Rhizobium* with phosphobacterin, when applied together, enhanced the early vegetative growth, symbiotic properties like nodule production and excessive synthesis of leghaemoglobin in nodules, nitrogenase activity (NA), and yield components such as seed yields, harvest index (HI), and P uptake by chickpea cultivar Mahamaya-2 plants grown in entisol (laterite soil) under rainfed conditions. Of the various combination treatments, seed inoculation of phosphobacterin with *Rhizobium* was significantly better than that of rest of the treatments.

When P (26.2 kg/ha) was also added to the mixture of *Rhizobium* and phosphobacterin, the biological and chemical properties of chickpeas were further improved relative to other levels of P used with biofertilizer. In other parts of the world like Erzurum (29°55′N and 41°16′E with an altitude of 1,950 m), Turkey, a similar investigation was carried out by Elkoca et al. (2008) where they used *Rhizobium*, N_2-fixing *Bacillus subtilis* (OSU-142), and P-solubilizing *B. megaterium* (M-3) to inoculate chickpea plants. Under the field trials, single, dual, and triple inoculations with *Rhizobium*, OSU-142, and M-3 significantly increased plant height, shoot, root, and nodule dry weight, N%, chlorophyll content, pod numbers, seed yield, total biomass yield, and seed protein content compared with the control treatment, equal to or higher than N, P, and NP treatments. Interestingly, the mixture containing *Rhizobium* was comparatively better in terms of nodulation than the sole application of *Rhizobium*. Increase in the seed yield under different inoculation treatments ranged between 18 % (*Rhizobium*) and 31 % (*Rhizobium* with OSU-142 and M-3) over the control whereas N, P, and NP applications corresponds to an increase of 27 %, 11 %, and 33 %, respectively. Dual and triple inoculations in general were more effective than other treatments which could probably be due to P activity of *Enterobacter*.

Coinoculation with rhizosphere PSM and AMF of soils with high phosphate-fixation capacity may overcome the limitation mentioned on the effectiveness of PSM in enhancing plant P uptake. First, mycorrhizal plants can release higher amounts of carbonaceous substance in to rhizosphere (Linderman 1988; Rambelli 1973) than non-mycorrhizal plants. Rhizosphere PSM can use these carbon substrates for their metabolic process, which are responsible for organic acid production in the rhizosphere and/or protein excretion (Azcon and Barea 1996). Second, the extensive mycorrhizal network formed around roots can efficiently take up P released by PSM thus minimizing its re-fixation. Barea et al. (2002) reported that the combined inoculation with PSB, mycorrhizal fungi, and *Rhizobium* increased the P uptake by several legumes fertilized with rock phosphate. Mycorrhizal interaction with PSM has been found beneficial and has shown dramatic improvement in plant P uptake in highly weathered soil in contrast to the results obtained for less-weathered soils. Osorio (2011) in his experiments while using PSM alone and in combination with mycorrhizal fungi in order to assess their impact on growth of *Leucaena leucocephala* found that the overall growth of test plant was highly dependent on the nature of P sorption capacity of soil. The sole application of PSM significantly increased plant growth of *Leucaena* in low P sorption soil, while in high P sorption soil mixture of PSM and AMF was significantly greater than single application of PSM. This finding suggested that the effectiveness of PSM in increasing plant P uptake and growth is controlled by the P sorption capacity. In soils with low P sorption ($P_{0.3} < 100$) capacity, though PSM inoculation alone can increase plant growth but in soils with medium and high P sorption ($100 < P_{0.2} < 500 < P_{0.2}$), PSM alone is less effective or even ineffective, their effectiveness depends on the presence of mycorrhizal association.

In other study, Osorio (2008) observed that PSM could desorb P from mineral and soil samples, but this was controlled by the P desorption (higher P desorption at low $P_{0.2}$ value). For minerals, the magnitude on which P desorbed was in the order montmorillonite > kaolinite > goethite > allophone (null description) and consequently for soils the order was mollisol > oxisol > ultisol > andisol. The amount of P desorbed by the PSM was higher when the minerals or soils had higher levels of sorbed P; this is when saturation of sorption sites was higher.

In addition to the PGPR, PSB has been found to form symbiotic relationship with AM fungi (Wang et al. 2011). For example, Toro et al. (2008) conducted an experiment to test the efficacy of composite microbial inoculations such as a wild-type (WT) *R. meliloti* strain, its genetically modified (GM) derivative, the AM fungus *G. mosseae* (Nicol. and Gerd) Gerd and Trappe, and a PSB *Enterobacter* sp. and rock phosphate (RP) on N and P acquisition by alfalfa plants. Interestingly, all the microbial cultures were established well within root tissues and/or in the alfalfa rhizosphere and had no antagonistic effect towards each other. Also, the population of PSB was stimulated following both AM colonization and RP application and GM *Rhizobium* application. Subsequently, there was tremendous improvement in N and P accumulation in alfalfa plants following composite microbial inoculations. Even though the *Enterobacter* application had no noticeable effect on N or P accumulation in soil treated with RP, it showed an obvious effect in the non-RP-amended controls. In addition, ^{15}N:^{14}N ratio in plant shoots indicated enhanced N_2 fixation rates in *Rhizobium*-inoculated AM plants, compared to those obtained by the same *Rhizobium* strain in non-mycorrhizal plants. Regardless of the *Rhizobium* strain and of whether or not RP was added, AM-inoculated plants showed a lower specific activity (^{32}P:^{31}P) than did their comparable non-mycorrhizal controls suggesting that the plant was using otherwise unavailable P sources. The P-solubilizing, AM-associated, microbiota could in fact release P ions, either from the added RP or from the indigenous "less-available" P. Additionally, the proportion of plant P derived either from the labeled soil P (labile P pool) or from RP was similar for AM-inoculated and non-mycorrhizal controls (without *Enterobacter* inoculation) for each *Rhizobium* strain, but the total P uptake, regardless of the P source, was far higher in AM plants which could probably be due to P mobilization by AM fungi.

10.4.2 Inoculation Effects of Phosphate Solubilizers on Cereal Crops

The use of PSB in agricultural practices dates back to 1950s when some Russian and European scientists applied *Megaterium viphosphateum*, which later on was identified as *Bacillus megaterium* var. *phosphaticum*. The preparation of this bacterium was subsequently called as phosphobacterin (Cooper 1959; Menkina 1963), and when this was used, increased crop yields from 0 % to 70 % in Soviet soils. However, similar experiments conducted in USA failed to produce any significant effect (Smith et al. 1961). Despite conflicting reports on the performance of PSB in variable agro-ecosystem against a multitude of crops (Yarzábal 2010), they have since been applied and have shown promising results in some parts of the world (Chesti and Ali 2007; Baig et al. 2011). For example, in a trial conducted under both pot and field environments, the biomass and total P of winter wheat (*Triticum aestivum*) were significantly increased following sole application of *Phosphobacterium* strain 9320-SD. However, there was no significant difference in height of the test plants (Chen et al. 2006). Similarly, PSB isolated from stressed environment such as cold temperature region contained *Serratia marcescens* with inherent PGP traits such as IAA, HCN, and siderophore production profoundly enhanced the plant biomass and nutrient uptake of wheat seedlings when grown in cold environment (Selvakumar et al. 2008). In a follow-up study, wheat plants inoculated with ACC deaminase-secreting PSB, *P. fluorescens* and *P. fluorescens* biotype F, had higher growth, yield, and nutrient use efficiency, when grown in soil treated simultaneously with varying levels of three major nutrients like N, P, and K (at 0 %, 25 %, 50 %, 75 %, and 100 % of recommended doses). However, the overall growth of inoculated wheat plants decreased both under pot and field trials with increasing concentration of synthetic fertilizers.

Hence, in most of the cases, significant negative linear correlations were recorded between percentage increases in growth and yield parameters of even inoculated wheat plants. The decline in growth and yield of bacterized wheat plants when grown with increasing chemical fertilizers, however, raised certain questions. For example, do the rates of fertilizers greater than recommended ones have any direct impact on composition and functional activities of bacteria or excessive rates have any inhibitory effect on plants metabolism? In this context, it is speculated that low fertilizer application causes reduction in the ACC deaminase activity of PS strains and thereby leads to reduction in the synthesis of stress (nutrient)-induced inhibitory levels of ethylene in the roots through ACC hydrolysis into NH_3 and α-ketobutyrate. Based on this finding, the study suggested that *Pseudomonads* could be used in combination with appropriate doses of fertilizers for better plant growth and savings of fertilizers (Shaharoona et al. 2008) as also observed by Kumar et al. (2009) and Maheshwari et al. (2011). Such increase in cereal production following PSB such as *P. fluorescens* 153, *P. fluorescens* 169, *P. putida* 4, and *P. putida* 108 application has been attributed to both PSA of PSB and their ability to synthesize growth-promoting substances (such as ACC deaminase and IAA-like products) in natural soil ecosystem (Zabihi et al. 2011). Interestingly, *P. putida* 108 among the bacterial cultures displayed enhanced P uptake (96 % and 80 %) and grain yield (58 % and 37 %) in wheat under greenhouse and field conditions, respectively. Even though this finding suggested that *Pseudomonas* sp. could serve as an alternative to expensive P application in wheat production system, the better results can be achieved when a compatible bioinoculant is added as mixture with 50 % (25 kg/ha P_2O_5) P fertilization. In a recent follow-up study, Abbasi et al. (2011) isolated eight PGPR strains and assessed their morphological and cultural characteristics, PSA and their ability to secrete IAA. Invariably all strains produced IAA (ranging from 5.5 to 31.0 mg/ml) while only four of them showed P-solubilizing traits. Subsequently, strains WPR-32, WPR-42, and WPR-51 grouped under PGPR category were used both as single and coculture along with two levels (50 and 100 kg N/ha) of N to evaluate their effect against wheat under greenhouse conditions. As expected, application of PGPR resulted in significant increase in plant height (25 %), shoot fresh weight (45 %), and shoot dry weight (86 %), while it was 27 %, 102 %, and 76 % increase in root length, root fresh and dry weight, respectively, over uninoculated plants. In addition, the number of tillers per plant, 1,000-grain weight, and grain yield were enhanced by 23 %, 48 %, and 59 %, respectively, over control. The nutrient (N and P) uptake by plant organs like shoot was increased threefolds, while K uptake was increased by 58 % following PGPR application.

However, the growth, yields, and nutrient uptake were increased even further when bacterial cultures were used together with varying levels of N. Apart from the direct effect of PGPR on wheat plants, the concentration of NO^{-3}, N, and available P in soil also increased with PGPR application. Moreover, of the varying treatments, mixed bacterial cultures showed better efficiency than the individual ones suggesting that there is no reason to doubt why application of PGPR with N fertilizer cannot increase N contents and N uptake by plants. Also, application of PGPR even with low fertilizer rates could be a more viable option for achieving optimum benefits while reducing the dependence on chemical inputs (Kumar et al. 2009). An interactive and positive effect of PSB, N_2 fixer, and AM fungi on plant vigor, nutrient uptake, and yield in wheat plants was observed following composite application of *Pseudomonas striata* + *Azotobacter chroococcum* + *Glomus fasciculatum*. The available P contents in soil enhanced significantly due to triple inoculation of *A. chroococcum*, *P. striata*, and *G. fasciculatum*. The residual N content of soil, however, did not change appreciably even among the treatments. The density of *A. chroococcum*, PSB, percentage root infection, and spore density of the AM fungus in inoculated treatments increased at 80 days of wheat growth (Zaidi and Khan 2005).

Inoculation of *Burkholderia vietnamiensis* to rice (*Oryza sativa*) cultivars in two pot and four field trials at different locations of Vietnam showed an enhancement of 33 %, 57 %, 30 %, and 13 % in shoot weight, root weight, leaf area, and number of tillers/hill, respectively, compared to non-inoculated plants. In other study, strain of *Rhodobacter capsulatus* significantly increased the plant dry weight, number of productive tillers, grain and straw yields of rice var. Giza 176, grown in pot treated with different levels of N fertilizer compared to non-inoculated plants (Elbadry et al. 1999). The results of this study concluded that N fertilizer could be saved up to 50 % while applying bacterial fertilizers. Similarly, an increase of 41 %, 12 %, 11.2–20 %, and 18.7 % in root weight, straw yield, grain yield, and total biomass, respectively, due to PGPR inoculation over non-inoculated rice is reported (Sherchand 2000; Mehnaz et al. 1998). The liquid culture (for pot experiments) or carrier-based preparation (for field trials) of three bacterial species, such as *Bacillus megaterium*, *B. subtilis*, and *Pseudomonas corrugata*, isolated from temperate locations in the Indian Himalayan region and exhibiting phosphate-solubilizing activity (PSA) in the order *P. corrugata* $>$ *B. megaterium* $>$ *B. subtilis*, when tested caused a dramatic increase in overall performance of rice. While comparing the effect of three cultures, *B. subtilis* had the most promising effect and increased the grain yield by 1.7- and 1.6-fold in pot and field trials, respectively (Trivedi et al. 2007).

Similar variable effects of PSB on other cereals used either alone or in combination with other chemical fertilizers have been reported (Panhwar et al. 2011; Yazdani et al. 2011). For example, like wheat and cereals, there has also been a substantial increase in the biomass of maize (*Zea mays*) plants inoculated with *S. marcescens* (EB 67) and *Pseudomonas* sp. (CDB 35) (Hameeda et al. 2008). In this experiment, strain EB 67 enhanced the dry matter accumulation by 99 % while it was 94 % by strain CDB 35. Grain yield of inoculated maize increased by 85 % and 64 %, following EB 67 and CDB 35 application, respectively. When applied as mixture with arbuscular mycorrhizal (AM) fungi *Glomus intraradices*, the PSB

Pseudomonas fluorescens (Pf) had a positive impact on plant growth, nutrient uptake, grain yield, and yield components in maize plants. Composite inoculation of the two cultures significantly increased grain yield, yield components, harvest index, grain N and P, soil available P, and root colonization percentage under water stress conditions. However, some of the assayed characteristics under well-watered conditions were nonsignificantly higher in chemical fertilizer treatment compared to those observed for dual inoculation treatments. However, the effect of sole application of *P. fluorescens* (Pf) was poor relative to the composite application of AM fungus with PSB or single application of AM fungi. The measured parameters of inoculated plants were in general higher than un-inoculated plants under water deficit stress conditions. In addition, the characteristics determined for coinoculated plants grown under severe water-stressed conditions were significantly lower than coinoculated plants grown under well-watered and moderate-stressed conditions. This finding suggested that PSB can interact positively with other organism like AM fungi as observed in this study and can be used to facilitate plant growth and P uptake by maize plants, leading to plant tolerance improving under water deficit stress conditions (Ehteshami et al. 2007). In a recent study, Rajapaksha et al. (2011) conducted experiments under both pot and field environment to assess the substitutability of triple superphosphate (TSP) by a P fertilizer mixture (PFM) involving TSP, RP, and PSB inoculants for wetland rice. For these studies, six single and two dual inoculants were formulated with *Enterobacter gergoviae* and five *Bacillus* species. In pot trials, the mixture of *E. gergoviae* and *B. mycoides* and the sole application of *B. subtilis* enhanced yields by 32 % and 25 %, respectively, relative to single application of TSP. The results observed in pot trials were validated under field environment where dual culture of *E. gergoviae* with *B. subtilis* and *E. gergoviae* with *B. pumilus* augmented grain yield by 22–27 % compared to TSP application alone (574 gm^{-2}). Overall, it was suggested that about 50 % of TSP could be saved when RP is applied with *E. gergoviae*, *B. pumilus*, and *B. subtilis*, as seed inoculant for raising the productivity of rice both under pot and field conditions.

10.5 Conclusion and Future Prospects

Considering the documented data and literature presented in this chapter, it seems feasible that the soil nutrient pool especially P using renewable resources like microbes can be increased by (1) careful management of existing microbial populations to optimize their competence to solubilize/mobilize P and (2) applying microbial inoculants especially designed/developed to provide P to plants. Despite repeated claims of making P available to plants or enhancing soil P by PSB, limited success in terms of their wide and regular application in agronomic practices has, however, been achieved so far. The reason for this low popularity of microphos could be both unawareness about the performance of PSB among practitioners or their varying activity under natural but fluctuating environments. Therefore, to make PSM more attractive and cost-effective measures for increasing crop productivity in different agro-ecological regions, we need to have a detailed and meaningful understanding of microbial interactions occurring in soil environment.

Moreover, how soil and farm management practices influence the processes mediated by PSM needs to be elucidated. In this context, molecular tools and metagenomic approaches have provided some insight to uncover the structure and functions of PSM. Genetic manipulation of some PSB and plants for important features such as P mobilization or growth promotion besides generating specific mutants with traits such as organic anion release in *Pseudomonas* spp. could play pivotal roles in deciphering mechanistic basis and evaluating their contribution to increased P availability in soil. Even some success has been achieved here and there by using molecular tools; there is greater need to develop area-specific microphos which may be suitable for application in any specific region. If developed with suitable multiple traits, such microphos can be applied back into the same environment from where they originated. This approach is, therefore, likely to reduce the impact of fluctuating environment on the performance of PSM when used for raising the production of different crops grown in many variable regions across the world.

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