Chapter 21
Improving Plant Phosphorus (P) Acquisition by Phosphate-Solubilizing Bacteria

Muhammad Saleem Arif, Sher Muhammad Shahzad, Tahira Yasmeen, Muhammad Riaz, Muhammad Ashraf, Muhammad Arslan Ashraf, Muhammad Salman Mubarik, and Rizwana Kausar

Abstract Phosphorus (P) is an essential plant nutrient required for sustainable production of food and bioenergy crops. A sufficient supply of P to the crop plants is necessary in order to meet global and regional food security challenges. However, limited mobility of P in the soil and its high fixation capabilities within the soil matrix necessitate the use of P fertilizers, which are again prone to fixation, thereby reducing the availability of this crucial element for plant nutrition. Rhizosphere is an intricate zone under the influence of plant roots and harbours variety of microbial species which confer growth and nutrition benefits to the crop plants. Phosphate solubilizing bacteria (PSB) play a crucial role in solubilizing various forms of phosphorus in soil and making them available for plant uptake. The bacterial phosphate solubilization process is mainly triggered by the secretions of organic acids, siderophores, exopolysaccharides, and enzyme (phytase-phosphatase) activities. The bacterial metabolites either solubilize the inorganic forms of phosphorus or mobilize the organic sources of phosphorus through enhanced enzyme activities. In this chapter, we attempt to provide

M.S. Arif (✉) • T. Yasmeen • M. Riaz
Department of Environmental Sciences and Engineering, Government College University Faisalabad, Faisalabad 38000, Pakistan
e-mail: msarif@outlook.com

S.M. Shahzad • M. Ashraf
Department of Soil & Environmental Sciences, University College of Agriculture, University of Sargodha, Sargodha, Pakistan

M.A. Ashraf
Department of Botany, Government College University Faisalabad, Faisalabad 38000, Pakistan

M.S. Mubarik
Centre of Agricultural Biochemistry and Biotechnology (CABB), University of Agriculture, Faisalabad 38040, Pakistan

R. Kausar
Soil and Water Testing Laboratory for Research, Sargodha, Punjab, Pakistan

M. Naeem et al. (eds.), *Essential Plant Nutrients*,
DOI 10.1007/978-3-319-58841-4_21

an overview about the potential contribution of PSB in improving plant P nutrition. Moreover, we also discussed the action mechanism involving PSB and key features that make it a useful value-added product for sustainable agriculture.

Keywords Phosphorus aquaisition • Bacteria • Fertilizers • Alkaline soils

21.1 Introduction

Phosphorus (P) is a fundamental and non-substitutable nutrient element in food production system. Plant phosphorus uptake can be a difficult proposition and thus often considered an important yield limiting factor in most agriculture systems of the world (Ringeval et al. 2017). Even though phosphorus is abundant in soils (organic and inorganic forms), its availability to plant is often restricted due to the formation of insoluble phosphate complexes in soil (Adesemoye and Kloepper 2009). The application of P fertilizer is the most sought out option to counteract phosphorus limitation in crop plants. However, about 80% of applied P fertilizer can be lost due to the fixation and adsorption processes (Lopez-Bucio et al. 2000), either in the form of Fe/Al phosphate in acidic soils or in the form of Ca phosphate in neutral to alkaline soils (Bertrand et al. 2003). Therefore, most of the applied P fertilizer rapidly becomes unavailable to plants that led to reduced production potential of crop plants.

The phosphorus fertilizers are primarily produced from mined rock phosphate; a nonrenewable and geographically restricted resource. The majority of rock phosphate reserves ~85% are found in Morocco, which is the leading world phosphorus producer. Though estimated amounts are not likely running out in the short term, rock phosphate will become scarce, at least in terms of pricing due to increased demand (van de Wiel et al. 2016). In addition, anthropogenic influences such as excessive mining, growing demand, increasing price, geopolitical constraints, excessive wastage, and high discharge to water bodies tend to hinder the sustainable management of the global P resource (Chowdhury et al. 2017).

These arising concerns have led to look for other viable options of phosphorus nutrition in crop plants. One of the alternatives and emerging solution to solve this problem is to exploit the microhabitat of plant under the influence of root (rhizosphere). Rhizosphere is characterized as nutrient-rich niche of immense microbial activity. Certain culturable root zone bacteria have intrinsic ability to aggressively colonize the host plant and improve plant growth and development (plant growth-promoting rhizobacteria (PGPR)). There are number of reports that entail promising effect of these PGPR on crop productivity under various soil conditions (Arif et al. 2016a, b; da Silva et al. 2017). Among these PGPR inoculants, several bacteria are able to mobilize and/or solubilize insoluble P into soluble form by releasing acidic metabolites, chelation, and ion exchange reaction which makes P available for crop plants (Chung et al. 2005; Jorquera et al. 2008). These naturally occurring phosphate-solubilizing bacteria (PSB) are unique environmentally friendly alternative that could offer a sustainable P nutrition for various crop plants. In addition, the application of these P bioinoculant could also negate the depressing effect of P fertilizer on ecosystem health.

21.2 Rock Phosphate-P Fertilizer-Food Security: A Crucial Nexus

The main source of phosphorus fertilizer is the geological deposits of phosphate rock. Morocco holds the phosphate monopoly with approximately 85% of global rock phosphate reserves. Other important rock phosphate-producing countries are China, the USA, Russia, Brazil, and Canada. Global fertilizer sector has seen a dramatic rise (about 430%) of P fertilizer production during the past 50 years (Fig. 21.1a). Extensive population growth and diversified food demand are chief contributors behind this mammoth increase of P fertilizer production. Currently >80% of extracted rock phosphate is being utilized to manufacture P fertilizer for agriculture, which raised questions and concerns about the depletion timeline of these reserves (Ibrahim et al. 2010).

The world food production system need to produce 70 more food (FAO 2009), and securing food sufficiency by 2050 is one of the top most priority to meet the global future food demand of approximately 9.1 billion people. Increased food production

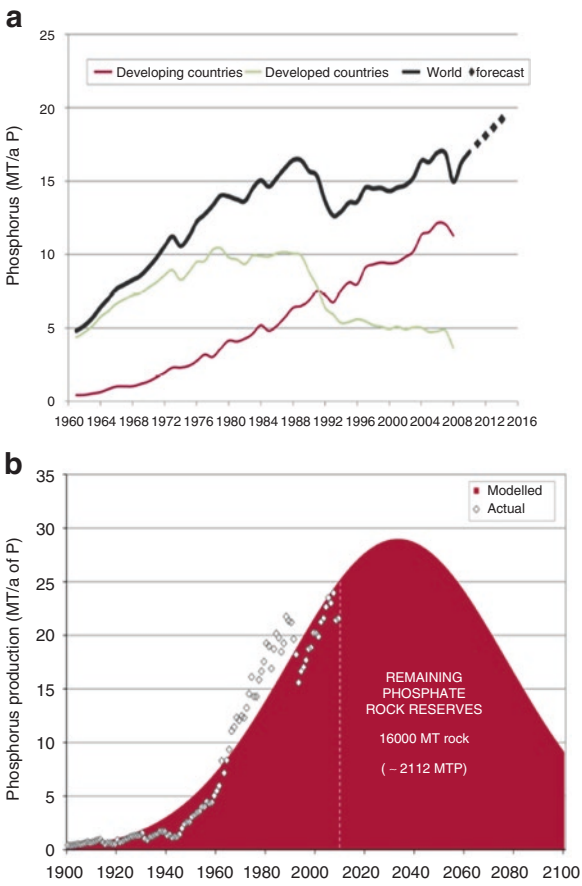

Fig. 21.1 (**a**) Global phosphorus fertilizer consumption between 1961 and 2006 (in million tons P). The figure indicates that while demand in the developed world reached a plateau and then declined around 1990, fertilizer demand has been steadily increasing in the developing world (IFA 2009). (**b**) Peak phosphorus curve indicating a peak in production by 2033, derived from the US Geological Survey and industry data (Cordell et al. 2009)

will come from higher crop yields and an expansion in harvested land, both of which will necessitate greater fertilizer use. At a time when intensive cultivation practices are depleting soil fertility, crop yield improvements continue to decelerate. Considering population growth and rising food demand, it is anticipated that the use of phosphate fertilizer will soar up manifold to achieve higher yield and quality crop product. Based on these trends, the International Fertilizer Industry Association (IFA) is projecting medium-term growth in fertilizer demand of about 1.7% per year, with total fertilizer demand exceeding 200 million metric tons of N, P_2O_5, and K_2O by 2020.

Phosphorus has received only limited attention compared to other important agricultural inputs such as nitrogen and water. Because of the vital role of phosphorus in food production, any consideration of food security needs to include an informed discussion concerning more sustainable use of P due to its limited resource base. Keeping in view the increasing global demand for phosphorus fertilizers, the ongoing debate over the long-term availability of phosphate rock, lack of adequate phosphorus accessibility by many of the world's poor farmers from developing world, shortage of P recycling system, and injudicious phosphorus fertilization warrant careful planning and consideration for P in sustainable agriculture. Moreover, detailed exploratory research is also required to provide reliable, global-scale quantification of the amount of phosphorus available for food production. A global phosphorus assessment, including further insights from scientists and other experts, policy-makers, and other stakeholders, could contribute to improving fertilizer accessibility, waste management in urban settings, and recycling of phosphorus from food waste products.

The long-term availability of phosphorus for global food production is of fundamental importance to the world population. Given the diversity of issues surrounding phosphorus, only an integrated set of policy options and technical measures can ensure its efficient and sustainable use. Environmental solutions that improve nutrient management and recycling minimize phosphorus losses due to soil erosion, and foster sustainable production and consumption also promote wise use of a finite resource. This could be the basis for fostering environmental innovation and other actions at local, national, regional, and international levels to improve phosphorus management. The future of this resource will also depend on governance with regard to its extraction and distribution around the world. There is a need for accurate information about the extent of global reserves, new technologies, infrastructure, institutions, attitudes, and policies to meet the challenge of sustainably feeding a rapidly growing global population while maintaining a healthy and productive environment.

21.2.1 Phosphorus in Soil-Plant System

21.2.1.1 Significance of Phosphorus for Plant

Phosphorus (P) is an essential element to all life forms of the earth ecosystem. In particular, phosphorus is key primary macronutrient necessary for plant growth and development along with nitrogen and potassium. P entry into plant is facilitated by root hairs, root tips, and the outermost layer of root cells. Plants typically take up P

in inorganic form either as primary orthophosphates ($H_2PO_4^-$) or secondary orthophosphates (HPO_4^{2-}) ion from soil solution. The dynamic balance of P availability and its absorption in soil plant system is tightly coupled with its pH. Once P surpassed the plant roots, absorbed inorganic P is either stored in the root or transported into the aerial plant parts through various mechanisms (Schachtman et al. 1998). Phosphorus is the structural component of several fundamental macromolecules and mainly involved in genetic, regulatory, signal transduction, and metabolic processes. In certain conditions, P can get incorporated into multitude of organic compounds ranging from smaller macromolecule (nucleotide, phospholipid, sugar phosphates) to larger macromolecule (DNA, RNA, phosphoprotein, ADP/ATP) of phosphorus (Turner et al. 2002; Condron et al. 2005). High energy phosphate forms that constitute adenosine diphosphate (ADP) and triphosphate (ATP) molecules drive several biochemical process within the plant. Energy transfer through phosphate carrier ADP and ATP to other molecular component of the cell (phosphorylation) controls many key biochemical process in plants (Baginsky 2016). Phosphorus also exists as phytin, a major P reserve of seeds and fruits, required for seed formation and early developmental stages of embryonic plant. Nearly half of total P in legumes seed and two-third in cereal grain are synthesized in the form of phytin. Hence, P deficiency appeared to reduce seed size, seed number, and viability. Moreover, inorganic and organic phosphates in plants also serve as buffers in the maintenance of cellular pH.

21.2.1.2 Soil Phosphorus Cycle

Unlike carbon, oxygen, and nitrogen, global P cycle is a sedimentary cycle that originates from phosphate-bearing mineral deposit and crustal rock sediments. The global occurrence of P cycle in soil followed a dynamic flow of different P forms involving soil, plants, and microorganisms. P enters into the biosphere almost entirely from soil through numerous ways. In natural system, various soil processes control different pools and fluxes of P and subsequently drive soil P cycle in the ecosystem.

21.2.1.3 Forms of Soil Phosphorus

Soil phosphorus forms can be broadly categorized into "sorbed P," "mineral P," and "organic P," and all these P forms diffused into solution P collectively as orthophosphate for plant uptake. Sorbed P matrix is comprised of P adsorbed onto the surface of iron and aluminum oxyhydroxides and $CaCO_3$ by electrostatic and covalent bonding (Moody et al. 2013). Phosphorus also exists in mineral form as a part of the structure of a wide variety of soil minerals, such as rock phosphate, present as fluorapatite [$Ca_5(PO_4)_3F$] or hydroxyapatite [$Ca_5(PO_4)_3OH$]. Soil inorganic P forms are not found in any typical ratios and pattern; they can be formed by sorbed/precipitated P on amorphous Fe and Al oxides and hydrous oxides. In addition, soil pedological processes and/or the reaction products of added P fertilizers also favored the formation of mineral P matrix.

Phosphorus fertilizers are the major inorganic P pool in agricultural soils and contribute approximately 70–80% of inorganic P share in these soils. In agriculture system, typical P fertilizer granule soon after its application predominantly dissolved into soluble inorganic P ($H_2PO_4^-$, HPO_4^{2-}) forms by available soil moisture. Most of soluble phosphates may not be readily available for plant as they are negatively charged and rapidly immobilized by sorption onto the positively charged soil mineral surfaces (Fe^{3+}, Al^{3+}, Ca^{2+}), or fixation into soil organic matter complexes (Frossard et al. 2000; Shen et al. 2013). Organic P largely exists as an inositol polyphosphate fraction and accounts for ~50% of the total organic P in soil (Koopmans et al. 2003) Additionally, phospholipids (~1%) and nucleic acid (5–10%) and their degradation products make up the remaining organic P fraction. Phospholipids and nucleic acids that enter the soil are degraded rapidly by soil microorganisms. Inositol polyphosphates are usually associated with high molecular weight molecules extracted from the soil, suggesting that they are an important component of humus (Dao 2004).

A wide range of soil microorganisms are capable of mineralizing organic phosphates into inorganic orthophosphate via phosphate-specific enzyme activity (Dobbelaere et al. 2003). The enzymes involved in the hydrolysis of phosphate from organic P resources are collectively called as phosphatases. Microorganisms have tendency to produce both acid and alkaline phosphatases, but plant can solely secrete acid phosphatase (Tarafdar 1989). Mineralized pool of inorganic P from organic fraction enters the soil solution phase and might be taken by microbes and plants, adsorbed onto the solid matrix or rarely lost by leaching and run off. Phosphorus released from organic P fraction is highly dependent on soil moisture and temperature conditions (Adhya et al. 2015).

21.2.1.4 Phosphorus Equilibrium in Soil

Soil solution P is the ultimate source of P supply to the plant, primarily through the process of root diffusion, influenced by many factors, i.e., P concentration gradient between the root surface and the bulk soil solution, rate of P re-supply to solution P after its withdrawal, soil water content, soil P buffer capacity (change in the quantity of soil P for a change in solution P concentration), and the connectivity of water films in soil pores (tortuosity factor) (Nye 1980). Both biotic and abiotic factors control the ultimate fate of P in soil solution. Weathering of sedimentary rocks (rock phosphate) containing P minerals primarily apatite [$(Ca_5 (PO_4)_3(F, Cl, OH)$] is the principle source of P to the soil. In general, apatite deposits are distributed across the globe. Individual mineral P (apatite) deposits are mostly of sedimentary origin, but some igneous reserves also exist in lesser amount (Cisse and Mrabet 2004). The dissolution of these P-bearing minerals is synergistically driven by both biotic and abiotic processes which ultimately lead to the release of mineral phosphate. The main mechanism underlying P mineral dissolution involves the release of acidic metabolites usually from microbial activity (e.g., Frossard et al. 1995; Welch et al. 2002). Solubilized phosphate is bioavailable P pool that is taken up by plants and assimilated into different plant parts and potentially can be recycled back to soil by plant residue (Damon et al. 2014).

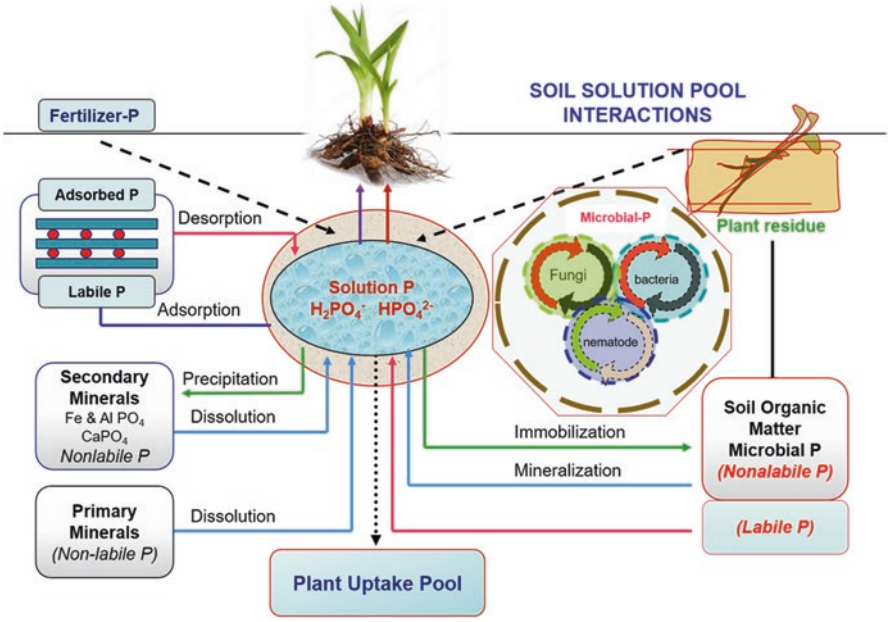

Fig. 21.2 An overview phosphorus cycle

Soil microorganisms act as sink and source of phosphorus (P) and mediate key processes in the soil P cycle, e.g., P mineralization and immobilization (Oberson and Joner 2005). P released into the soil solution from the mineralization of organic compounds might be taken up by soil microbial population, taken up by growing plants, and transferred to soil inorganic pool (Fig. 21.1). Over time, some P fraction that undergo microbial immobilization can affect P availability by removing inorganic P from the soil solution (Olander and Vitousek 2004). Most of inorganic P pool entering soil solution, either by mineralization or P fertilizer addition, is rapidly converted into insoluble P due to sorption and precipitation reactions. The sorption of inorganic P from solution is closely related to the presence of iron and aluminum oxides and hydrous oxides (Tian et al. 2016) and $CaCO_3$ (Pizzeghello et al. 2011). The P concentration of the soil solution at equilibrium state will provide maximum P for plant uptake, highest at the slightly acidic to neutral pH range and are reduced considerably in strongly acidic or alkaline soil conditions (Fig. 21.2).

In calcareous soil, the amount of $CaCO_3$ affects soil solution P equilibrium as reduced P solubility is often associated with the presence of excessive lime ($CaCO_3$) (Mahdi et al. 2011). The reaction of phosphorus with $CaCO_3$ was initially favored P sorption on these surfaces followed by rapid precipitation of soil solution P as Ca–P minerals (Sharpley et al. 1989). The formation and precipitation of these low solubility calcium phosphate compounds depressed P mobility and availability in these soils. In acidic soil, P sorption to Al and Fe oxides may be of equal or greater consideration than P sorption to $CaCO_3$ and other similar compounds. In organic P may adsorb on hydrous oxides and oxides of aluminum and iron of clay mineral surfaces (Syers et al. 2008a, b), and P is precipitated as insoluble Fe and Al phosphate complexes.

The balance between P adsorption and desorption maintains the equilibrium between solid phase and P in solution phase. The amount of P adsorbing or desorbing from surfaces depends on the number of sorption sites and the energy of adsorption (Moody et al. 2013). This equilibrium is termed P buffer capacity and is measured as the quantity of P that is adsorbed or desorbed for a unit change in solution P concentration. All of these P pools are in equilibrium with orthophosphate ($H_2PO_4^-$, HPO_4^{2-}) in the soil solution and govern soil P cycle by the processes of desorption-sorption (in the case of adsorbed P), dissolution-precipitation (in the case of mineral P), and mineralization-immobilization (in the case of organic P).

21.3 Rhizosphere: Ecological Hot Spot of Soil Microbiota

A narrow interfacial region between plant roots and surrounding soil, and characterized by intense biochemical and microbial activities, is called rhizosphere. Hiltner (1904) described rhizosphere as soil compartment influenced by plant growth that harbors microbial activity more than that of its surrounding soil. Rhizosphere, as a unique site of interaction between host plant and its biotic component, is mainly driven by the release of organic resources in the form of plant metabolites (root exudates) and plant debris (dead cells, mucilage). These organic resources served as food reserves for the microbes and support the growth and development of microbial population. These rhizodeposits represent a substantial part of photosynthetically fixed carbon (20–40%) and total plant nitrogen (10–16%) allocated to the underground root system, largely depending on plant species and plant age (Jones et al. 2009). The net sequestration of organic carbon and nitrogen by roots is thought to stimulate soil microbial multiplication in the vicinity of root tissues, because (a) most known soil bacteria are organotrophs, i.e., they derive the energy for growth from organic substrates, and (b) the accessibility and availability of organic compounds are limited in most soils (Alden et al. 2001; Demoling et al. 2007).

Rhizosphere microbiota is attracted by these organic resources and exerts numerous effects on plant growth and soil fertility (Antoun and Prevost 2005). As distinct microbial activity is usually associated with intense biochemical changes close to soil-root interface, therefore, it is also characterized as “microbial hot spot” (Reinhold-Hurek et al. 2015). These interactions are part of complex exchanges between roots and microorganisms and establish either beneficial, detrimental, or neutral relationships regulated by complex molecular signaling (Dardanelli et al. 2010). The beneficial interaction may favor plant growth, protect them from pathogens, and consequently have positive influence on crop productivity.

The rhizosphere, which is the narrow soil zone of soil that is influenced by plant roots and its released metabolites, can contain up to 10^{11} microbial cells per gram root (Egamberdiyeva et al. 2008) and more than 30,000 prokaryotic species (Mendes et al. 2011). In general, the microbial population densities in the rhizosphere are 10–100 higher than in the surrounding bulk soil (Spaepen et al. 2009). As microbial activity dwell on to the close proximity (~50 μm) of root surface, plant rhizodeposi-

tion of (approx. 50–100 mg per g root) is sufficient to support the growth of 2×10^{10} bacterial cells (Foster 1983).

An increasing body of evidence signifies the importance of this root microbiome, which consists of the entire complex of rhizosphere-associated microbes, their genetic elements and complex interactions in determining plant growth and health. The rhizosphere microbial population are usually characterized by rapid growth rate and utilize available substrates (chitin, mucilage, dead cells, and root exudates) that helps in maintaining the dynamic equilibrium of rhizosphere and controls its associated competition (Dessaux et al. 2016). Rhizosphere microbial populations are the most vibrant, highly competitive, and aggressive colonizer of the plant roots (Bouizgarne 2013; Mommer et al. 2016).

21.3.1 Plant Growth-Promoting Rhizobacteria (PGPR)

Rhizosphere microbial communities are increasingly understood to interact extensively with plants, and this association is very crucial to the overall plant health and development. A group of bacteria (PGPR) are known to establish an active synergy with plants through aggressive root colonization that subsequently confer plant growth-promoting benefits to the plants (Hartman et al. 2008; Shahzad et al. 2013). These bacteria can be found within and on roots and in soil associated with roots. The role of PGPR in promoting plant growth depends strongly on their survival and growth under variable field conditions (Rivera et al. 2008). Concerning soil heterogeneity, PGPR potency to compete, proliferate, and improve plant growth is predominantly fueled by root exudates and other organic substrates (Khalid et al. 2006; Yuan et al. 2015). Additionally, PGPR traits such as motility, chemotaxis, attachment, growth, and stress resistance also contribute to the overall competence of bacteria to survive in the rhizosphere and successfully colonize plant tissues.

A more feasible classification of PGPR is their separation as extracellular (e-PGPR) to denote those existing in the rhizosphere, on the rhizoplane, and intracellular (i-PGPR) and to denote bacteria that exist in the spaces between the cells of the root cortex or in specialized nodular structures (Gray and Smith 2005). On similar lines, Ambrosini et al. (2016) also classified soil beneficial bacteria and their association with plant roots, i.e., symbiotic (inside leguminous nodules), endophytic (intercellular spaces), associative (root surface adhered), and rhizospheric (root-soil interface associated). Unlike PGPR, certain free living soil bacteria are opportunistic in their association with plants, as they have loosely bound acclimation to the rhizosphere. These bacterial communities dwell around rhizosphere only in the presence of substantial organic substrate availability and in turn benefit plant in numerous ways. In another study, Bulgarelli and his colleagues (Bulgarelli et al. 2013) explored aboveground plant exterior surfaces as a habitat for microbes. According to their view, aerial plant parts (leave and stem surfaces) are thought to represent one of the largest but less explored microbial habitats called as phyllosphere. Compared with fungi and archaea, bacteria are the most prevalent

phyllosphere-colonizing microbes, with bacterial titers averaging approximately 10^6–10^7 microbial cells per square centimeter of leaf area (Lindow and Brandl 2003). A benefiting plant-microbe interaction always involved several molecular signaling events that establish growth-promoting association with plant (Weiland-Bräuer et al. 2015). Such relationships vary according to plant genotypes and bacterial strains and with respect to the degree of proximity between the roots and surrounding soil as well as with the abilities of bacteria to improve plant growth.

There are several mechanisms by which PGPR can promote plant growth and development. Lugtenberg and Kamilova (2009) outlined tripartite contribution of PGPR toward plant growth, i.e., biofertilizer, phytostimulators, and stress controllers (Pereira and Castro 2014; Kurepin et al. 2014; Shahzad et al. 2014). PGPR use various mechanisms which may take place simultaneously or sequentially at different plant growth stages. The action mechanisms of plant growth promotion by PGPR can be grouped into two major categories, i.e., direct and indirect mode of plant growth promotion (Lugtenberg and Kamilova 2009; Bhattacharyya and Jha 2012; Ashraf et al. 2013). Direct plant growth-promoting activities mainly involve an improvement of nutrient availability to the plant by the fixation of atmospheric nitrogen, production of iron-chelating sideroaphores, organic matter mineralization (thereby meeting the nitrogen, sulfur, phosphorus nutrition of plants), and solubilization of insoluble phosphates (Martinez-Viveros et al. 2010; Chauhan et al. 2015; Etesami and Alikhani 2016). Another important direct mechanism involves the production of plant growth hormones and growth-regulating enzyme 1-aminocyclopro pane-1-carboxylate (ACC) deaminase (Shahzad et al. 2013). PGPR can also promote plant growth indirectly by inhibiting plant pathogen growth. This can also be achieved by the synthesis of enzymes that hydrolyze fungal cell walls, production of HCN, and lytic enzymes and induced systemic resistance by producing various antibiotic metabolites (Yuttavanichakul et al. 2012; Pieterse et al. 2014; Bensidhoum et al. 2016).

21.3.1.1 Phosphate-Solubilizing Bacteria (PSB)

Phosphorus is the most important nutrient after N that affects growth and metabolism processes of plant (Widawati and Suliasih 2006). The mobility of phosphate ions ($H_2PO_4^-$ and HPO_4^{2-}) in soil is very low because of their high retention in soil. But as a result of adsorption, precipitation and conversion to organic forms, only 10–30% of the applied phosphate mineral fertilizer can be recovered by the crops grown after the fertilization (Holford 1997; Syers et al. 2008a, b). The remaining 70–90% is accumulated in soil or in the form of immobile that is bound by Al or Fe in acid soils, or Ca and Mg in alkaline calcareous soils (Prochnow et al. 2006; Yang et al. 2010). While plants cannot absorb P in bound form, the P must be converted into available form. Phosphate-solubilizing bacteria (PSB) can play an important role in dissolving both of fertilizer P and bound P in the soil that is environmentally friendly and sustainable (Khan et al. 2007). The exploration of phosphate-solubilizing bacteria has been conducted by many researchers from soils

(Chen et al. 2006; Widawati and Rahmansyah 2009; Gupta et al. 2013) and rhizosphere (Poonguzhali et al. 2008; Khan et al. 2013).

Some bacterial species have mineralization and solubilization potential for organic and inorganic phosphorus, respectively (Hilda and Fraga 2000; Khiari and Parent 2005). Phosphorus-solubilizing activity is determined by the ability of microbes to release metabolites, such as organic acids, which through their hydroxyl and carboxyl groups chelate the cation bound to phosphate, the latter being converted to soluble forms (Khan et al. 2013; Sharma et al. 2013a, b). Phosphate solubilization takes place through various mechanisms including organic acid production and proton extrusion (Nahas 1996; Khan et al. 2009; Marra et al. 2011). A wide range of microbial P solubilization mechanisms exist in nature, and much of the global cycling of insoluble organic and inorganic soil phosphates is attributed to bacteria and fungi (Banik and Dey, 1982). Phosphorus solubilization is carried out by a large number of rhizobacteria acting on sparingly soluble soil phosphates, mainly by chelation-mediated mechanisms (Whitelaw, 2000; Reyes et al. 2001). Inorganic P is solubilized by the action of organic and inorganic acids secreted by PSB in which hydroxyl and carboxyl groups of acids chelate cations (Al, Fe, Ca) and decrease the pH in basic soils (Kpomblekou and Tabatabai 1994; Stevenson 2005). The PSB dissolve the soil P through the production of low molecular weight organic acids mainly gluconic and keto gluconic acids (Goldstein 1995; Deubel et al. 2000), in addition to lowering the pH of rhizosphere. The pH of rhizosphere is lowered through biotical production of proton/bicarbonate release (anion/cation balance) and gaseous (O_2/CO_2) exchanges. The phosphorus solubilization ability of PSB has direct correlation with pH of the medium. The release of root exudates such as organic ligands can also alter the concentration of P in the soil solution (Hinsinger 2001). Organic acids produced by PSB solubilize insoluble phosphates by lowering the pH, chelation of cations, and competing with phosphate for adsorption sites in the soil (Nahas, 1996). Inorganic acids, e.g., hydrochloric acid can also solubilize phosphate, but they are less effective compared to organic acids at the same pH (Kim et al. 1997). In certain cases, phosphate solubilization is induced by phosphate starvation (Gyaneshwar et al. 1999; Khan et al. 2007).

The mineralization of soil organic P (Po) plays an imperious role in P cycling of a farming system. Organic P may constitute 4–90% of the total soil P. Almost half of the microorganisms in soil and plant roots possess P mineralization potential under the action of phosphatases. Alkaline and acid phosphatases use organic phosphate as a substrate to convert it into inorganic form (Beech et al. 2001). Principal mechanism for mineralization of soil organic P is the production of acid phosphatases (Hilda and Fraga 2000). The release of organic anions and production of siderophores and acid phosphatase by plant roots/microbes (Yadaf and Tarafdar, 2001) or alkaline phosphatase (Tarafdar and Claasen 1988) enzymes hydrolyze the soil organic P or split P from organic residues. The largest portion of extracellular soil phosphatases is derived from the microbial population (Dodor and Tabatabai 2003).

21.4 Methodological Advancement for the Isolation of PSB

A diversity of growth mediums are being used in laboratories for cultivation, isolation, characterization, and subsequently selection of P-solubilizing bacteria. Most of the PSB growth media have differential chemical composition and also characterized with varied growth efficiency both on liquid and solid cultures (Table 21.1). Biological phosphate solubilization activity of root zone microbe was first described by Gerretsen (1948), who explained microbial mediated solubilization of insoluble inorganic P and its resultant effects on plant growth promotion. In the beginning, PSB isolation was primarily administered by plate screening assay and based on visual detection of clear halo zone formation as PSB colony niche in the presence of insoluble mineral P source (tricalcium phosphate/hydroxyapatite) (Pikovskaya 1948; Katznelson et al. 1962; Gupta et al. 1994). The selected method was adopted and generally considered a reliable approach for preliminary isolation and characterization of PSB (Katznelson et al. 1962; Goldstein and Liu 1987; Illmer and Schinner 1995).

However, Gupta et al. (1994) developed some modifications for PSB isolation using a Pikovskaya's medium with bromophenol blue supplementation. These modifications were primarily designed to improve the visibility of halo zone, which were formed by acidic metabolites of PSB and associated pH changes. In some cases, it appears that there was quite a distinct functional mismatch between plate halo detection and P solubilization activity in liquid culture of these so-called PSB. Several workers reported no visible clear halo zone formation on inorganic P supplement could still go on to solubilize various types of insoluble inorganic phosphate in liquid medium (Louw and Webley 1959; Das 1963). This may be because of varying diffusion rates of different organic acids secreted by an organism (Johnson 1959). Nautiyal (1999) emphasized the importance of defined media for screening-efficient PSB and associated P solubilization activity. He formulated National Botanical Research Institute's Phosphate (NBRIP) growth medium containing bromophenol blue as a pH indicator. Once the efficient PSB are selected, they are tested for their ability to solubilize insoluble P under liquid culture medium. Finally, the efficient P-solubilizing bacteria are selected and used for the advancement of inoculants whose efficacy is tested under natural environment against various crops. Similarly, Bashan et al. (2013) argued the vitality of Pikovskaya medium containing tricalcium phosphate (TCP) as the sole P source is used for screening of P-solubilizing bacteria. However, the lack of reliable evidence of TCP-P solubilizer, absence of metal-P source, and increase in the use of rock phosphate as P fertilizer emphasized the need to design a novel medium that could support the growth of P-solubilizing bacteria. They also raised halos zone-based selection concerns for screening P solubilizer as PSB colony growth is often without halos even after the media is replaced several times. They also suggested the adoption of modified liquid broth for the isolation and screening of efficient PSB solubilizer in different soil and culture conditions.

Table 21.1 Plant association and growth-promoting characteristics of PGPR in agriculture

Vegetation type	Host plant	Dominant exudation	Identified microbiota	References
Legumes	Soybean [Glycine max (L.) Merr.]	Phosphate solubilization, N-fixation, siderophores production, protease production	*Bacillus amyloliquefaciens* LL2012, *Bradyrhizobium japonicum*	Masciarelli et al. (2014)
	Chickpea (*Cicer arietinum* L.)	Siderophores production, chitinase activity, ACC-deaminase activity, exopolysaccharide production, phosphate solubilization, HCN production	*Serratia marcescens* (SF3) and *Serratia* spp. (ST9) + *M. ciceri*	Shahzad et al. (2014)
	Mung bean (*Vigna radiata* L.)	ACC-deaminase activity, Auxin production, phosphate solubilization antibiotic resistance	*Pseudomonas fragi* P5, *Pseudomonas jesseni* P10 and *Rhizobium leguminosarum* Z22	Iqbal et al. (2012)
Cereals	Wheat (*Triticum aestivum* L.),	IAA, HCN, siderophores	*Serratia marcescens*	Selvakumar et al. (2008)
	maize (*Zea mays* L)	Acid phosphatase, alkaline phosphatase, IAA production	*Azospirillum brasilense CNPSo 2083*, *Rhizobium tropici CIAT 899*	Marks et al. (2015)
	Rice (*Oryza sativa* L.)	IAA production, gibberellic acid production	*Enterobacter* spp. and *Azospirillium* spp.	Hasan et al. (2014)
	Oat (*Avena sativa* L.) and barley (*Hordeum vulgare* L.)	IAA production, siderophores production, phosphate solubilization	*Sinorhizobium meliloti L3Si*, *Pseudomonas* sp. LG *Azotobacter chroococcum* AV, *Enterobacter sp. E1*,	Stajković-Srbinović et al. (2014)
	Oat (*Avena sativa* L.)	ACC deaminase, HCN, IAA production, phosphate solubilization	*Sinorhizobium meliloti*, *Azotobacter* sp., *Pseudomonas* sp.	Delić et al. (2012)
	Sugarcane (*Saccharum officinarum* L.)	Production of IAA, phosphate solubilization, Induced systemic resistance,	*Azospirillum* sp.	Moutia et al. (2010)
	Sugarcane (*Saccharum officinarum* L.)	Phosphate solubilization, HCN production, IAA production	*Bacillus megaterium*	Sundara et al. (2002)

(continued)

Table 21.1 (continued)

Vegetation type	Host plant	Dominant exudation	Identified microbiota	References
Oil seed	Turnip mustard (*Brassica rapa* L.)	IAA, ACC deaminase, Siderophores	*Pseudomonas* sp.	Poonguzhali et al. (2008)
	Mustard (*Brassica campestris* L.)	HCN production, IAA production	*Mesorhizobium loti* MP6	Chandra et al. (2007)
	Canola (*Brassica napus* L.)	Siderophores, IAA, salicylic acid, ACC deaminase	*Dyella ginsengisoli, Burkholderia kururiensis, Pandoraea* sp. ATSB30	Anandham et al. (2008)
	Sunflower (*Helianthus annuus* L.)	Siderophores production and IAA production	*Pseudomonas fluorescens* biotype F and *Pseudomonas fluorescens* CECT 378^T	Shilev et al. (2012)
Trees	*Pinus roxburghii*	Siderophores production and IAA production	*Bacillus subtilis*	Singh et al. (2008)
	Italian stone pine (*Pinus pinea* L.)	Phosphate solubilization, IAA, exopolysaccharide production, organic acid production	*Bacillus licheniformis CECT 5106 and Bacillus pumilus CECT 5105*	Probanza et al. (2001)
	Teak (*Tectona Grandis*) and Indian redwood (*Chukrasia Tabularis*)	Nitrogen fixation, phosphate solubilization, siderophores production	*Azotobacter sp. DCU26 and Bacillus megaterium A3.3*	Aditya et al. (2009)
Grasses	Canary grass (*Phalaris minor* L.)	IAA production, Nitrogen fixation, HCN production	*Azotobacter* and *Azospirillum*	Zaefarian et al. (2012)
	Bermuda grass (*Cynodon dactylon* L.)	Phosphate solubilization, Exopolysaccharide production, ACC-deaminase activity, HCN production,	*Serratia sp.*—TRY2 and *Bacillus sp.*—TRY4	Sarathambal and Ilamurugu (2013)
	Barnyard grass (*Echinochloa crus-galli* L.), Italian ryegrass (*Lolium multiflorum* L.)	Phosphate solubilization, HCN production, IAA production, antifungal, HCN production,	*Bacillus*, *Arthrobacter*, *Stenotrophomonas*, *Acinetobacter*, and *Pseudomonas*	Sturz et al. (2001)
	Nut grass (*Cyperus rotundus* L.)	Phosphate solubilization, Organic acids production, siderophores production, HCN production	*Enterobacter* sp. Arh 1, *Pseudomonas* sp. Bro 5	Diogo et al. (2010)

(continued)

Table 21.1 (continued)

Vegetation type	Host plant	Dominant exudation	Identified microbiota	References
Vegetables	Red pepper (*Capsicum annuum* L.)	Gibberellic acid, IAA production	*Bacillus cereus* MJ-1	Joo et al. (2005)
	Mint (*Mentha piperita* L.)	Phosphate solubilization, siderophores production, IAA production	*Agrobacterium rubi* A16, *Burkholderia gladii* BA7, *P. putida* BA8, *B. subtilis* OSU142, *B. megaterium* M3	Kaymak et al. (2008)
	Cabbage (*Brassica oleracea* L.)	IAA production, Phosphate solubilization, HCN production, Organic production	*Bacillus megaterium* TV-91C, *Pantoea agglomerans* RK-92 *and B. subtilis* TV-17C	Turan et al. (2014)
	Tomato (*Solanum lycopersicum* L.)	IAA production, antagonistic behavior, HCN production, siderophores production, Gibberellic acid production	*Pseudomonas putida*, *P. fluorescens*, *Serratia marcescens*, *Bacillus subtilis*, *B. amyloliquefaciens*, and *Bacillus cereus*	Almaghrabi et al. (2013)
	Cucumber	Antagonistic effect, HCN production, siderophores production, Phosphate solubilization,	*Bacillus* sp.	Stout et al. (2002)
	Bitter gourd (*Momordica charantia* L.)	Phosphate solubilization, Nitrogen fixation, siderophores production, HCN production, ACC deaminase activity	*Azospirillum*, *Pseudomonas fluorescens*, and *Bacillus subtilis*	Kumar et al. (2012)

Quantitative estimation of biologically solubilized P as dissolved reactive phosphorus (most readily available P) is usually measured by molybdate colorimetric test (Murphy and Riely, 1962). This method was based on the observation that ammonium heptamolybdate and antimony potassium tartrate react with dilute orthophosphate solution in an acidic medium to form an antimony-phospho-molybdate complex. The reduction of the complex by ascorbic acid gives it an intense blue color that is proportional to the orthophosphate concentration.

21.4.1 Mechanisms of P Solubilization

21.4.1.1 Organic Acid Production

Phosphorus-solubilizing bacteria have characteristics ability to release acidic metabolites such as organic acids. These acidic secretions have the tendency to enhance mobility and/or solubility of inorganic P compounds (Son et al. 2006). On quantitative basis, the ability of PSB to solubilize insoluble phosphate in liquid culture medium is investigated by a number of researchers (Narula et al. 2000; Whitelaw, 2000). The solubilization of soil P in liquid medium by PSB has often been resulted due to the excretion of organic acids. In general, PSB produce variety of organic acids, i.e., acetic acid, gluconic acid, oxalic acid, citric acid, and lactic acid in liquid culture filtrates, and usually analyzed by thin layer chromatography or by high-performance liquid chromatography (HPLC). In addition, certain enzymatic methods are also employed for an accurate identification of unknown organic acids (Gyaneshwar et al. 1998).

These organic acids can either directly dissolve the mineral phosphate as a result of anion exchange of PO_4^{2-} by acid anion or can chelate both iron and aluminum ions associated with phosphate (Omar, 1998). In certain cases phosphate solubilization is induced by phosphate starvation (Gyaneshwar et al. 1999). The role of organic acids produced by PSB in solubilizing insoluble phosphate mainly attributed to the lowering of pH, chelating of cations, and competing with phosphate for adsorption sites in soil (Nahas 1996). Some inorganic acids, i.e., hydrochloric acid and sulfuric acid can also solubilize phosphate, but they are less effective compared with organic acids at the same pH (Kim et al. 1997). Effective P mobilization and/or solubilization by organic acid metabolites is related to the number and structure of the carboxyl groups, general order of carboxyl group effectiveness: tricarboxylate (e.g., citrate^{3-}) > dicarboxylate (e.g., malate^{2-}) > monocarboxylates (e.g., acetate $^{1-}$) (Ryan et al. 2001, 2012). The ability of organic acid secretions is gene-regulated mechanism but can also be influenced by prevailing environmental conditions. Soil nutrient content, i.e., C, N could affect the nature of organic acid secretions and P solubilizer (Narsian and Patel, 2000). Moreover, chelating ability of various organic acids has also been shown as an efficient mechanism of P solubility in P-deficient environment (Chapin et al. 2012).

21.4.1.2 Siderophores Production

It is well known that certain microbes secrete organic ligand to solubilize Fe from poorly available sources. Microbial siderophores are low molecular weight organic ligand produced as a scavenging agent to combat iron limitation. Siderophores production is usually not a widely investigated mechanism for phosphate solubilization. Many PSB have the ability to forage Fe from mineral complex into soluble Fe^{3+} form that is taken up by active transport carrier mechanism (Collavino et al. 2010). Siderophores production by PSB has indirect potential to improve P availability as these ligands can also extract Fe from ferric citrate and ferric phosphate (Zaidi et al. 2009). Approximately, 500 different siderophores structure are known to be produced by several gram-positive and gram-negative bacteria.

Very few works have been carried out to evaluate siderophores production as a method of P solubilization. Reid et al. (1985) showed 13-fold increments in P diffusion when compared with water. In view of mineral dissolution ascendency over ligand exchange by organic acids as a P-solubilizing mechanism, the probable siderophores contribution to improve P availability should be more pronounced.

21.4.1.3 Exopolysaccharides Production

The role of low molecular weight organic acids in the solubilization of mineral P is well documented. However, the knowledge on the role of high molecular weight microbial exudates (nonenzymatic mucilage) on P solubilization is limited. Exopolysaccharide (EPS) and biosurfactants are produced by bacteria largely in response to biofilm formation and stress. Microbial exopolysaccharides are polymers of carbohydrates excreted by bacteria on the outer side of their cell walls. The structural composition of exopolysaccharides is quite heterogenous (homo- or heteropolysaccharides) and may possess various organic and inorganic substituents (Sutherland, 2001). Some earlier studies have shown that the exopolysaccharides have the ability to form complexes with metals in soil (order of affinity to form complexes $Al^{3+} > Cu^{2+} > Zn^{2+} > Fe^{3+} > Mg^{2+} > K^{+}$) (Ochoa-Loza et al. 2001) that implicates their role of P solubilization in soil. Microbial exopolysaccharides have shown to stimulate the dissolution of tricalcium phosphate (TCP) in synergy with organic anions (Yi et al. 2008). Further the rate of dissolution was showed dependent on microbial source and concentration of EPS. Recently, Taktek et al. (2017) showed that exopolysaccharide-producing rhizobacteria solubilized igneous phosphate rock through secretions of viable biofilm cells and release of organic acids. They also found concomitant effect on plant P nutrition and yield of maize.

Phosphorus also releases from complex organic P compounds in soil by enzymatic activities; (a) phosphatases (Bandick and Dick 1999), which perform dephosphorylation of phospho-ester or phosphoanhydride bonds in organic matter; (b) phytases (Maougal et al. 2014), which particularly cause P release from phytic acid; (c) phosphonatases and C–P lyases, enzymes that exhibit C–P cleavage in organophosphonates.

21.4.1.4 Phosphatases Activity

Phosphatases are broad range of hydrolytic enzymes which showed strong affinity to catalyze the hydrolysis of both organic phosphate esters and anhydrides of H_3PO_4. Organic P is an important component of global phosphorus cycle. The P enzyme activities drive the mineralization of organic P into available inorganic form of P that easily assimilable by plants (Nannipieri 2011).

Interest in soil enzymes activity has increased manifold during the last decade because of their significance in P cycling (Beech et al. 2001; Rodríguez et al. 2006). Many bacteria having phosphatases release inorganic phosphate from organophosphate complexes. However, activities of these P-cycling enzymes largely depend upon their pH and are classified as either alkaline (pH > 7) or acid (pH < 6) phosphatase.

These enzymes catalyze the hydrolysis of many different phosphate systems including those of primary, secondary, cyclic, and sugar alcohols as well as phenols and amines.

Acid phosphatases are widely distributed hydrolase and primarily a plant origin enzyme exhibiting minimal substrate specificity (Duff et al. 1994). Several acid phosphatase genes from gram-negative bacteria have been isolated and characterized (Rossolini et al. 1998). Some of them code for acid phosphatase enzymes that are capable of performing well in soil. For example, the acpA gene isolated from *Francisella tularensis* expresses an acid phosphatase with optimum action at pH 6 with a wide range of substrate specificity (Reilly et al. 1996; Beech et al. 2001).

Alkaline phosphatases are group of hydrolases originally released by microbes under alkaline and neutral soil conditions. They can potentially hydrolyze up to 90% of total organic P into available P source in soil (Jarosch et al. 2015). This enzyme catalyzes the hydrolysis of a wide variety of phosphomonoesters and diesters excluding inositol phosphate (Kageyama et al. 2011). According to previous studies, PSB inoculation acts as an orderly stimulus with higher alkaline phosphatase activity that eventually lead to improve soil P status and plant P nutrition (Shahzad et al. 2014; Kaur and Reddy 2014).

21.4.1.5 Phytases Activity

Mostly phytases (myoinositol hexakisphosphate phosphohydrolases) belong to high molecular weight acid phosphatases. In its basic form, phytate is the primary source of inositol and the major stored form of phosphate in plant seeds and pollen. Most genetic engineering studies have focused on the search for phytases that are optimal for improving animal nutrition. Another attractive application of these enzymes that is not currently exploited is solubilization of soil organic phosphorus through phytate degradation. Phytate is the major component of organics forms of P in soil (Rodríguez et al. 2006). The ability of plants to obtain P directly from phytate is very limited. However, the growth and P nutrition of *Arabidopsis* plants supplied with phytate were improved significantly when they were genetically transformed with the phytase gene (phyA) (Richardson et al. 2001). This resulted in improved P nutrition, such that the growth and P content of the plant were equivalent to control plants supplied with inorganic phosphate. In relation to plant P availability, inoculation with phytate-mineralizing rhizobacteria improved P nutrition in cereals crop without P fertilization under Chilean Andisol (Martínez et al. 2015). Extracellular phytase-producing rhizobacteria have also been identified (Kumar et al. 2013; Li et al. 2013).

21.5 Recent Advances and Future Prospects of PSB

Based on above discussions, it is explicitly concluded that limited plant available P as well as low solubility of applied P fertilizer in soil are the major constraint in most agroecosystem. P deficiency can cause some serious concerns for overall

growth, development, and yield of crop plants. However, the impediment caused by P limitation on plant growth can be dispelled and/or minimized by naturally occurring microorganisms capable of solubilizing P such as PSB.

Recently, proteomic-based techniques have emerged as an effective tool to disclose genotypic adaptation mechanisms involved in various crop plants under P deficiency. Various phosphate starvation responsive proteins have been identified in plant using these approaches, and using these proteins and their corresponding genes, it is now possible to improve plant P acquisition capacity by an upregulation of plant system for an efficient P uptake in the near future. The identification of metabolic genes regulating bioacidulation (principle mode of P solubilization) mechanism and its linked traits in PSB would advance our understanding about the underlying molecular basis of solubilized P fraction in soil. So far most of the studies involving PSB are originally in vitro which lack rigor and reliability to select an efficient PSB as a deliverable product for field trials. Thus, the work will further bridge the existing knowledge gap related to unclear role of PSB inoculant under varied soil environment. Another potential option is to develop transgenic plants encoding the genes of particular traits related to bacterial P solubilization. The literature shows that these transgenic plants have the adaptive capacity to counteract limited nutritional reserves. However, such studies are very limited in number and are at very early stage which warrants some elaborative validations before performing extensive experimentation. Moreover, information about the molecular mechanisms regulating P deficiency in crop plants is also scarce. Overall, future research should be focused (1) to mediate PSB-based metabolite engineering under P-deficient environments, (2) to explore multiple mechanistic traits of P solubilization in PSB, (3) to identify target P responsive genes for promoting growth under P starvation, and (4) the transference of targeted genes for efficient P utilization in plants through biotechnology.

21.6 Conclusion

Various modern agro-biotechnological interventions are being used to boost up plant P acquisition under P-limited conditions. One of the most emerging tools to negate P solubility and availability concerns for crop plant is the use of PSB as P bioinoculant. PSB play an important role in phosphorus nutrition by enhancing its availability to plants through solubilization and mineralization of inorganic and organic phosphates in soil. Therefore, plant beneficial microbes (including phosphate-solubilizing bacteria, i.e., PSB) and their associative interaction with host plant are key determinant of overall plant growth, development, and yield of crops under P-limited conditions. However, efficiency of PSB as a value-added P biofertilization approach further necessitates a more rigorous selection criteria for quality PSB formulation, which requires considerable attention of the scientists to overcome such challenges (Tables 21.2, 21.3, 21.4, 21.5 and 21.6).

Table 21.2 Effectiveness of PGPR for plant growth regulation under varied soil type

PGPR	Source/experimental soil	Host plant	Botanical name	Plant growth regulation	References
Bacillus firmus NCIM 2636	Heavy loam	Paddy	*Oryza* Spp.	Increased root biomass and phytohormones in plant (e.g., auxin, gibberellins, cytokinins, etc.)	Datta et al. (1982)
B. megaterium + *G. fasciculatum* and *G. fasciculatum*	Clay loam soil	Banana	*Musa paradisiaca*	Increased fresh biomass and phosphorous intake in plant as compared to uninoculated control	Patil et al. (2002)
Pseudomonas striata	Sandy loam	Chickpea, soybean	*Glycine max*	Increased the number of nodules per plant, dry and fresh weight of nodules and grain yield legumes	Son et al. (2006)
P. Fluorescence + *Bacillus megaterium*	Sandy clay loam soil	Chickpea	*Cicer arietinum*	Improving seedling growth, phosphorus uptake, total chlorophyll content, fresh and dry weight of roots	Sharma et al. (2007)
Pseudomonas putida	Heavy loam	Barley	*Hordeum vulgare*	Increased total chlorophyll contents in plant leaf	Mehrvarz et al. (2008)
Enterobacter gergoviae J107, *P. fluorescens* J108, *S. proteamaculans* J119 and *C. koseri* J120	Sandy clay loam	Chickpea	*Cicer arietinum*	Out of these, J119 strain was found to be the most effective PGPR in improving root and shoot growth, nodulation and grain yield of chickpea than control in growth pouches, pot and field trials	Shahzad et al. (2010)

PGPR	Source/experimental soil	Host plant	Botanical name	Plant growth regulation	References
G. etunicatum + *Burkholderia cepacia* BAM 6	Loam soil	Wheat	*Triticum aestivum*	Increased biomass, phosphorous uptake in plants and total grain yield	Minaxi et al. (2013)
Pseudomonas thivervalensis STF3 and *Serratia marcescens* STJ5	Sandy clay loam	Maize	*Zea mays* L.	Bacterial isolates, with 75 and 100% CF, significantly improved the growth, yield and NPK uptake in maize than control. The growth and yield promoting effect of STF3 strain with 75% CF were similar to CF alone. But with 100% CF, same strain significantly increased total biomass, grain yield and chlorophyll content than control	Shahzad et al. (2013)
Pseudomonas tolaasii IEXb, *Pseudomonas koreensis* SP28	Silt loam	Maize	*Zea mays* L.	Both strains showed a positive effect on plant growth. A significant increase in plant height (45%), shoot dry weight (40%) was observed in plants treated with IEXb, while SP28 has significantly increased P content than uninoculated control	Viruel et al. (2014)

(continued)

Table 21.2 (continued)

PGPR	Source/experimental soil	Host plant	Botanical name	Plant growth regulation	References
S. marcescens (SF3) and Serratia spp. (ST9) + M. ciceri	Sandy clay loam (irrigated area), sandy loam (rain-fed area)	Chickpea	*Cicer arietinum*	Significantly increased the nodules per plant, grain yield, protein content, P uptakes under irrigated and rain-fed conditions than sole inoculation. Integrating PEC with co-inoculation gave an additive effect on the nodulation and growth of chickpea under both farming systems	Shahzad et al. (2014)
Klebsiella sp. Br1, *Klebsiella pneumoniae* Fr1, *Bacillus pumilus* S1r1 and *Acinetobacter* sp. S3r2	Clay loam	Maize	*Zea mays* L.	Significantly improved the dry biomass of top, root and ear, total N and P content of maize roots due to PGPR inoculation. In particular, the plants inoculated with *B. pumilus* S1r1 generally out performed those with the other treatments	Kuan et al. (2016)

PGPR	Source/experimental soil	Host plant	Botanical name	Plant growth regulation	References
Bacillus megaterium RC01 and *Bacillus* M-13	loam soil	Barley	*Hordeum vulgare* L.	Seed inoculation of barley significantly increased the root weight, shoot weight and P uptakes by 32.1%, 54.2% and 39.6%, respectively, over uninoculated control	Cakmakcı et al. (2007)
Bacillus M-13	Silt clay loam	Sunflower	*Helianthus annuus* L.	Inoculation with PSB significantly enhanced the head diameter, 1000 seed weight, kernel ratio and oil content and led to seed and oil yield increases of 15.0 and 24.7% over control respectively	Ekin (2010)
Burkholderia sp. PS-01, *Bacillus* sp. PS-12, *Pseudomonas* sp. PS-32, *Flavobacterium* sp. PS-41 and *Pseudomonas* sp. PS-51	Sandy clay loam	Maize	*Zea mays* L.	Inoculation significantly increased the plant height, root length, shoot dry weight, root dry weight and grain yield were observed which were up to 16, 11, 42, 29 and 33%, respectively, over control in the presence of FYM at 16 Mg ha^{-1}	Hussain et al. (2013)

(continued)

Table 21.2 (continued)

PGPR	Source/experimental soil	Host plant	Botanical name	Plant growth regulation	References
Pseudomonas aurantiaca and *Pseudomonas fluorescens*	Sandy loam	Paddy	(*Oryza sativa* L.)	Inoculation with PSB significantly improved the plant height, shoot and root dry weight, P and N uptake and net photosynthetic rate of walnut seedlings. Application of these two PSB strains also improved soil quality, as indicated by increased activities of dehydrogenase, neutral phosphatase and urease in the soil	Yu et al. (2014)

Table 21.3 Culture media and their chemical composition used for P-solubilizing bacteria

Chemical composition of media	PVK	NBRIP	NBRIY	YEM	Ashby's
Ammonium sulfate	0.50	0.10	0.50		
Bromophenol blue (BPB)		0.03			
Calcium carbonate				2.00	5.00
Dipotassium hydrogen phosphate				0.50	0.20
Ferrous sulfate	0.00				
Glucose	10.00	10.00	10.00		
Iron(III) chloride			0.002		
Magnesium chloride hexahydrate		5.00			
Magnesium sulfate heptahydrate	0.10		0.10	0.20	0.20
Manganese sulfate	0.25	0.25	0.00		
Mannitol				10.00	20.00
Potassium chloride	0.20	0.20	0.20		
Potassium sulfate					0.10
Sodium chloride	0.20		0.20		

PVK Pikovskaya's medium (Pikovskaya, 1948), *NBRIP* National Botanical Research Institute's phosphate growth medium (Nautiyal 1999), *NBRIY* National Botanical Research Institute's phosphate growth medium devoid of yeast extract medium (Nautiyal 1999), *YEM* yeast extract mannitol broth (Holt et al. 1994), Ashby's medium (SubbaRao 1977)

Table 21.4 Effects of different types of phosphate-solubilizing bacterial inoculant on plant performance

Type of P bacteria	Name	Source	Host plant	Botanical name	Response	Conditions	References
Free living	*Arthrobacter* sp. and *Bacillus subtilis*	Soil	Wheat	*Triticum aestivum* L.	Increases dry weight up to 26% and P uptake up to 19% when co-inoculated at 2 dS $m^{-1}$of salinity level and 40 and 34% when co-inoculated at 6 dS m^{-1} of salinity level	Pot	Upadhyay et al. (2011)
	Serratia liquefaciens, *Bacillus sp.Pseudomonas sp.*	Soil	Maize	*Zea mays* L.	Grain yield increased up to 14% when they were inoculated as consortia over control. In sole inoculation, *S. liquefaciens* increased the dry weight of maize respect to control more than 10%, *Bacillus* sp. more than 7% and *Pseudomonas* sp. more than 10%	Pot (Green house)	Lalande et al. (1989)

Type of P bacteria	Name	Source	Host plant	Botanical name	Response	Conditions	References
Associative	*Pseudomonas putida* R-168, *Pseudomonas fluorescens* R-93, *P. fluorescens* DSM 50090, *A. lipoferum* DSM 1691,	Root	Maize	*Zea mays* L.	Plant height, seed weight, number of seed per ear and leaf area, shoot dry weight and phosphorus content significantly increased over control	Field	Gholami et al. (2009)
	Pseudomonas fluorescens PGPR1, *PGPR2*, *PGPR4*	Root	Peanut	*Arachis hypogaea* L.	Significantly enhanced pod yield, haulm yield, nodule dry weight and P uptake over the control	Pot and field	Dey et al. (2004)
	Enterobacter sakazakii 8MR5, *Pseudomonas sp.* 4MKS8, *Klebsiella oxytoca* 10MKR7	Root	Maize	*Zea mays* L.	Inoculation increased growth parameters and NP uptake	Pot	Babalola et al. (2003)

(continued)

Table 21.4 (continued)

Type of P bacteria	Name	Source	Host plant	Botanical name	Response	Conditions	References
Rhizobia	*Mesorhizobium* sp. RC3	Nodule	Chickpea	*Cicer arietinum* L.	Increased the dry matter accumulation, number of nodules, seed yield, P content and grain protein by 71%, 86%, 36%, 23%, and 16%, respectively, over uninoculated control plants	Pot	Wani et al. (2008)
	Bradyrhizobium MRM6	Nodule	Green gram	*Vigna radiata* (L.) Wilczek	When herbicide-tolerant *Rhizobium* strain MRM6 was used with herbicide, it increased the growth parameters at all tested concentrations of herbicides (quizalafop-p-ethyl and clodinafop)	Pot	Ahemad and Khan (2012)
	Mesorhizobium strain MRC4	Nodule	Chickpea	*Cicer arietinum* L.	Significantly increased symbiotic properties (nodulation and leghemoglobein content), root N, shoot N, root P, shoot P, seed yield, and seed protein	Pot	Ahemad and Khan (2010)

Type of P bacteria	Name	Source	Host plant	Botanical name	Response	Conditions	References
Endophytes	*Enterobacter agglomerans*	Tissue	Tomato	*Solanum lycopersicum* L.	Significantly increased the P concentration in shoot and fruit parts than control plants	Pot	Kim et al. (1998)
	Pseudomonas mutant CRPF7	Tissue	Mung bean	*Vigna radiata* L.	Significantly enhanced the nodulation, P in shoot and grain seed yield, and seed protein than uninoculated plants	Field	Das et al. (2003)
Phyllosphere	*Azotobacter chroococcum* REN 2 and *Beijerinckia indica* JN1	Leaf	Wheat	*Triticum aestivum* L.	Gave significantly increase in number of tiller, fresh biomass, grain yield, protein content, and P content in shoot and grain as compared to respective control	Field	Pati and Chandra (1981)

Table 21.5 P-solubilizing bacterial metabolites and plant growth promotion

Bacterial name	Activity	Host plant growth	Botanical name	References
Pseudomonas putida	Organic acids	Enhanced chlorophyll content and P uptake in plants	*Hordeum vulgare* L.	Mehrvarz et al. (2008)
Paenibacillus lentimorbus B-30488	Organic acids	Enhanced plant growth due to biofilm formation and phosphate solubilization	*Zea mays* L.	Khan et al. (2011)
Pseudomonas striata	Phosphatase	Increased the number of nodules, fresh and dry weights of nodules, and grain yield and improve the P uptake in grain	*Cicer arietinum* L. and *Glycine max* L.	Son et al. (2006)
Pseudomonas fluorescence + *Bacillus megaterium*	Phosphatase	Enhanced seedling growth and phosphorus content in plants in comparison to uninoculated plants	*Cicer arietinum* L.	Sharma et al. (2013a, b)
Enterobacterium with *Sinorhizobium meliloti*	Phosphatase	Increased P uptake, fresh biomass and grain yield than uninoculated plants	*Cicer arietinum* L. and *Pisum sativum* L.	Hynes et al. (2008)
Bacillus sp. with *Rhizobium*	Phytase	Co-inoculation improved pod and straw yield; increased the root length, root mass, and number of nodule and mass; and enhanced the nutrient concentration in mash plant and grains	*Vigna mungo* L.	Qureshi et al. (2012)

(continued)

Table 21.5 (continued)

Bacterial name	Activity	Host plant growth	Botanical name	References
A. chroococcum	Phytase	Enhanced plant growth due to phosphate solubilization, auxin production, and catalase activity	*Zea mays* L.	Rojas-Tapias et al. (2012)
Acinetobacter sp. (PSGB04), *Pseudomonas* (PRGBB06)	Exopolysaccharide	Increased root length, shoot length, seedling vigor, dry mass/ IAA, salicylic acid, N-fixation, and P uptake in seedlings	*Brassica napus*, Tomato	Indiragandhi et al. (2008)
Pseudomonas aeruginosa	Siderophores	Improving root and shoot growth of plant under water stress and increase P uptake in plant as compared to untreated plants	Black gram	Ganesan (2008)
Enterobacter sp.	Siderophores	Increasing chlorophyll content and iron and phosphorus content in leaves than uninoculated plants	*Brassica juncea*	Kumar et al. (2008)

Table 21.6 Types and functional expression of P-solubilizing genes in plant beneficial bacteria

Identified Gene	Source	Function/mineral P solubilized	References
pKG3791	*Serratia marcescens*	PQQ biosynthesis, produce gluconic acid, and solubilizes P mineral/TCP	Krishnaraj and Goldstein (2001)
gabY	*Pseudomonas cepacia*	Produces gluconic acid and also having phosphatase activity/TCP	Babu-Khan et al. (1995)
pqqE	*Erwinia herbicola*	Produces gluconic acid and solubilizes P mineral/TCP	Vikram et al. (2007)
pqqED genes	*Rahnella aquatilis*	Produces gluconic acid and acetic acid and solubilizes P mineral/HAP	Kim et al. (1998)
Unknown	*Enterobacter agglomerans*	Produces gluconic acid and solubilizes P mineral/DCP	Kim et al. (1997)
pqqABCDEF genes	*Enterobacter intermedium*	Produces citric acid, gluconic acid, and solubilizes P mineral/HAP	Kim et al. (2003)
Ppts-gcd, *P gnlA-gcd*	*E. coli*	Produces gluconic acid and solubilizes P mineral/TCP	Sashidhar and Podile (2009)
gabY putative PQQ transporter	*Pseudomonas cepacia*	Produces gluconic acid	Babu-Khan et al. (1995)
gltA/citrate synthase	*E. coli* K12	Produces citric acid and solubilizes P mineral/DCP	Buchet et al. (1999)
Unknown	*Synechocystis* PCC 6803	Produces gluconic and acetic acids and solubilizes P mineral/RP	Gyaneshwar et al. (2002)
gad/gluconate dehydrogenase	*P. putida* KT2440	Produces gluconic and 2-Ketobutyric acids and solubilizes P mineral/RP	Kumar et al. (2013)
nap A	*Burkholderia cepacia IS-16*	Increased extracellular alkaline phosphatases and solubilizes P mineral/CP	Fraga et al. (2001)

References

Adesemoye, A., & Kloepper, J. (2009). Plant–microbes interactions in enhanced fertilizer use efficiency. *Applied Microbiology and Biotechnology, 85*, 1–12.

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

Aditya, B., Abhrajyoti Ghosh, A., & Chattopadhyay, D. (2009). Co-inoculation effects of nitrogen fixing and phosphate solublising microorganisms on teak (*Tectona grandis*) and indian redwood (*Chukrasiatu bularis*). *Journal of Biological Sciences, 1*, 23–29.

Ahemad, M., & Khan, M. S. (2010). Ameliorative effects of Mesorhizobium sp. MRC4 on chickpea yield and yield components under different doses of herbicide stress. *Pesticide Biochemistry and Physiology, 98*, 183–190.

Ahemad, M., & Khan, M. S. (2012). Productivity of greengram in tebuconazole-stressed soil, by using a tolerant and plant growth–promoting *Bradyrhizobium* sp. MRM6 strain. *Acta Physiologiae Plantarum, 34*, 245–254.

Alden, L., Demoling, F., & Baath, E. (2001). Rapid method of determining factors limiting bacterial growth insoil. *Applied and Environmental Microbiology, 67*, 1830–1838.

Almaghrabi, O. A., Massoud, S. I., & Abdelmoneim, T. S. (2013). Influence of inoculation with plant growth promoting rhizobacteria (PGPR) on tomato plant growth and nematode reproduction under greenhouse conditions. *Saudi Journal of Biological Sciences, 20*, 57–61.

Ambrosini, A., Souza, R., & Passaglia, L. M. P. (2016). Ecological role of bacterial inoculants and their potential impact on soil microbial diversity. *Plant and Soil, 400*, 193–207.

Anandham, R., Gandhi, P. I., Madhaiyan, M., & Sa, T. (2008). Potential plant growth promoting traits and bioacidulation of rock phosphate by thiosulfate oxidizing bacteria isolated from crop plants. *Journal of Basic Microbiology, 48*, 439–447.

Antoun, H., & Prevost, D. (2005). Ecology of plant growth promoting rhizobacteria. In Z. A. Siddiqui (Ed.), *PGPR: Biocontrol and biofertilization* (pp. 1–38). Dordrecht: Springer.

Arif, M. S., Riaz, M., Shahzad, S. M., Yasmeen, T., Akhtar, M. J., Riaz, M. A., Jassey, V. E. J., Bragazza, L., & Buttler, A. (2016a). Associative interplay of plant growth promoting rhizobacteria (*Pseudomonas aeruginosa* QS40) with nitrogen fertilizers improves sunflower (*Helianthus annuus* L.) productivity and fertility of Aridisol. *Applied Soil Ecology, 108*, 238–247.

Arif, M. S., Riaz, M., Shahzad, S. M., Yasmeen, T., Ali, S., & Akhtar, M. J. (2016b). Phosphorus mobilizing plant growth promoting rhizobacteria (*Bacillus cereus* GS6) improved symbiotic efficiency of soybean (*Glycine max* L.) in compost amended aridisol. Pedosphere (submitted).

Ashraf, M. A., Asif, M., Zaheer, A., Malik, A., Ali, Q., & Rasool, M. (2013). Plant growth promoting rhizobacteria & sustainable agriculture: A review. *African Journal of Microbiology Research, 7*, 704–709.

Babalola, O. O., Osir, E. O., Sanni, A., Odhaimbo, G. D., & Bulimo, W. D. (2003). Amplification of 1-aminocyclopropane-1-carboxylic (ACC) deaminase from plant growth promoting rhizobacteria in Striga-infested soils. *African Journal of Biotechnology, 2*, 157–160.

Babu-Khan, S., Yeo, T. C., Martin, W. L., Duron, M. R., Rogers, R. D., & Goldstein, A. H. (1995). Cloning of a mineral phosphate-solubilizing gene from *Pseudomonas cepacia*. *Applied and Environmental Microbiology, 61*, 972–978.

Baginsky, S. (2016). Protein phosphorylation in chloroplasts–A survey of phosphorylation targets. *Journal of Experimental Botany, 67*(13), 3873–3882. doi:10.1093/jxb/erw098.

Bandick, A. K., & Dick, R. P. (1999). Field management effects on soil enzyme activities. *Soil Biology and Biochemistry, 31*, 1471–1479.

Banik, S., & Dey, B. K. (1982). Available phosphate content of an alluvial soil as influenced by inoculation of some isolated phosphate solubilizing microorganisms. *Plant and Soil, 69*, 353–364.

Bashan, Y., Kamnev, A. A., & de-Bashan, L.E. (2013). A proposal for isolating and testing phosphate-solubilizing bacteria that enhance plant growth. *Biology and Fertility of Soils, 49*, 1–2.

Bashan, Y., & Holguin, G. (1998). Proposal for the division of plant growth promoting rhizobacteria into two classifications: Biocontrol–PGPB plant growth–promoting bacteria, and PGPB. *Soil Biology and Biochemistry, 30*, 1225–1228.

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, UK: BioLine.

Bensidhoum, L., Nabti, E., Tabli, N., Kupferschmied, P., Weiss, A., Rothballer, M., Schmid, M., Keel, C., & Hartmann, A. (2016). Heavy metal tolerant *Pseudomonas protegens* isolates from agricultural well water in northeastern Algeria with plant growth promoting, insecticidal and antifungal activities. *European Journal of Soil Biology, 75*, 38–46.

Bertrand, I., Holloway, R. E., Armstrong, R. D., & McLaughlin, M. J. (2003). Chemical characteristics of phosphorus in alkaline soils from southern Australia. *Australian Journal of Soil Research, 41*, 61–76.

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

Bouizgarne, B. (2013). Bacteria for plant growth promotion and disease management. In D. K. Maheshwari (Ed.), *Bacteria in agrobiology: Disease management* (pp. 15–47). Berlin Heidelberg: Springer-Verlag.

Buchet, A., Nasser, W., Eichler, K., & Mandrand-Berthelot, M. A. (1999). Positive co-regulation of the *Escherichia coli* carnitine pathway *cai* and *fix* operons by CRP and the CaiF activator. *Molecular Microbiology, 34*, 562–575.

Bulgarelli, D., Schlaeppi, K., Spaepen, S., Loren, V., van Themaat, E., & Schulze-Lefert, P. (2013). Structure and functions of the bacterial microbiota of plants. *Annual Review of Plant Biology, 64*, 807–838.

Cakmakcı, R., Erat, M., Erdo, U. G., & Donmez, M. F. (2007). The influence of PGPR on growth parameters, antioxidant and pentose phosphate oxidative cycle enzymes in wheat and spinach plants. *Journal of Plant Nutrition and Soil Science, 170*, 288–295.

Chandra, S., Choure, K., Dubey, R. C., & Maheshwari, D. K. (2007). Rhizosphere competent *Mesorhizobium loti* MP6 induces root hair curling, inhibits *Sclerotiniasclerotiorum* and enhances growth of Indian mustard (*Brassica campestris*). *Brazilian Journal of Microbiology, 38*, 128–130.

Chapin, F. S., Maton, P. A., & Vitousel, P. M. (2012). *Principles of terrestrial ecosystem ecology* (p. 436). New York: Springer-Verlag.

Chauhan, H., Bagyaraj, D. J., Selvakumar, G., & Sundaram, S. P. (2015). Novel plant growth promoting rhizobacteria–prospects. *Applied Soil Ecology, 95*, 38–53.

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

Chowdhury, R. B., Moore, G. A., Weatherley, A. J., & Arora, M. (2017). Key sustainability challenges for the global phosphorus resource, their implications for global food security, and options for mitigation. *Journal of Cleaner Production, 140*, 945–963.

Chung, H., Park, M., Madhaiyan, M., Seshadri, S., Song, J., Cho, H., & Sa, T. (2005). Isolation and characterization of phosphate solubilizing bacteria from the rhizosphere of crop plants of Korea. *Soil Biology and Biochemistry, 37*, 1970–1974.

Cisse, L., & Mrabet, T. (2004). World phosphate production: Overview and prospects. *Phosphorus Research Bulletin, 15*, 21–25.

Condron, L. M., Turner, B. L., & Cade-Menun, B. J. (2005). Chemistry and dynamics of soil organic phosphorus. In J. T. Sims & A. N. Sharpley (Eds.), *Phosphorus: Agriculture and the environment* (pp. 87–121). Madison: American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Inc.

Collavino, M. M., Sansberro, P. A., Mroginski, L. A., & Aguilar, O. M. (2010). Comparison of in vitro solubilization activity of diverse phosphate-solubilizing bacteria native to acid soil and their ability to promote *Phaseolus vulgaris* growth. *Biology and Fertility of Soils, 46*, 727–738.

Cordell, D., Drangert, J. O., & White, S. (2009). The story of phosphorus: Global food security and food for thought. *Global Environmental Change, 19*, 292–305.

Damon, P. M., Bowden, B., Rose, T., & Rengel, Z. (2014). Crop residue contributions to phosphorus pools in agricultural soils: A review. *Soil Biology and Biochemistry, 74*, 127–137.

Dao, T. H. (2004). Ligands and phytase hydrolysis of organic phosphorus in soils amended with dairy manure. *Agronomy Journal, J96*, 1188–1195.

Dardanelli, M. S., Manyani, H., Gonzalez-Barroso, S., Rodriguez-Carvajal, M. A., Gil-Serrano, A. M., Espuny, M. R., López-Baena, F. J., Bellogin, R. A., Megías, M., & Ollero, F. J. (2010). Effect of the presence of the plant growth promoting rhizobacterium (PGPR) *Chryseobacteriumbalustinum* Aur9 and salt stress in the pattern of flavonoids exuded by soybean roots. *Plant and Soil, 328*, 483–493.

Das, A. C. (1963). Utilization of insoluble phosphates by soil fungi. *Journal of the Indian Society of Soil Science, 11*, 203–207.

Das, K., Katiyar, V., & Goel, R. (2003). P solubilization potential of plant growth promoting Pseudomonas mutants at low temperature. *Microbiological Research, 158*, 359–362.

Datta, M. S., Banik, M., & Gupta, R. K. (1982). Studies on the efficacy of a phytohormone producing phosphate solubilizing bacillus firmis in augmenting paddy yield in acid soils of Nagaland. *Plant and Soil, 69*, 365–373.

Delić, D., Stajković-Srbinović, O., Kuzmanović, D., Rasulić, N., Maksimović, S., Radović, J., & Simić, A. (2012). Influence of plant growth promoting rhizobacteria on alfalfa, Medicago sativa L. yield by inoculation of a preceding Italian ryegrass, *Lolium multiflorum* Lam. In S. Barth & D. Milbourne (Eds.), *Breeding strategies for sustainable forage and turf grass improvement* (pp. 333–339). Dordrecht, Netherlands: Springer.

Demoling, F., Figueroa, D., & Baath, E. (2007). Comparison of factors limiting bacterial growth in differentsoils. *Soil Biology and Biochemistry, 39*, 2485–2495.

Dessaux, Y., Grandclément, C., & Faure, D. (2016). Engineering the rhizosphere. *Trends in Plant Science, 21*, 266–278.

Deubel, A., Gransee, A., & Merbach, W. (2000). Transformation of organic rhizodeposits byrhizoplane 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 (*Arachish ypogaea* L.) by application of plant growth-promoting rhizobacteria. *Microbiological Research, 159*, 371–394.

Diogo, J., Korenblum, E., Casella, R., Vital, R. L., & Seldin, L. (2010). Polyphasic analysis of the bacterial community in the rhizosphere and roots of *Cyperus rotundus* L. grown in a petroleum contaminated soil. Microbiol. *Biotechnology, 20*, 862–870.

Dobbelaere, S., Vanderleyden, J., & Okon, Y. (2003). Plant growth promoting effects of diazotrophs in the rhizosphere. *Critical Reviews in Plant Sciences, 22*, 107–149.

Dodor, D. E., & Tabatabai, A. M. (2003). Effect of cropping systems on phosphatases in soils. *Journal of Plant Nutrition and Soil Science, 166*, 7–13.

Duff, S. M., Sarath, G., & Plaxton, W. C. (1994). The role of acid phosphatases in plant phosphorus metabolism. *Physiologia Plantarum, 90*, 791–800.

Egamberdiyeva, D., Kamilova, F., Validov, S., Gafurova, L., Kucharova, Z., & Lugtenberg, B. (2008). High incidence of plant growth stimulating bacteria associated with the rhizosphere of wheat grown on salinated soil in Uzbekistan. *Environmental Microbiology, 10*, 1–9.

Ekin, Z. (2010). Performance of phosphate solubilizing bacteria for improving growth and yield of sunflower (*Helianthus annuus* L.) in the presence of phosphorus fertilizer. *African Journal of Biotechnology, 9*, 3794–3800.

Etesami, H., & Alikhani, H. A. (2016). Rhizosphere and endorhiza of oilseed rape (*Brassica napus* L) plant harbor bacteria with multifaceted beneficial effects. *Biological Control, 94*, 11–24.

FAO. (2009). *How to feed the world in 2050*. Rome, Italy: Food and Agriculture Organization.

Fiske, C. H., & Subbarow, Y. (1925). A colorimetric determination of phosphorous. *The Journal of Biological Chemistry, 66*, 375–400.

Foster, R. C. (1983). The fine structure of epidermal cell mucilages of roots. *The New Phytologist, 91*, 727–740.

Fraga, R., Rodriguez, H., & Gonzalez, T. (2001). Transfer of the gene encoding the Nap A acid phosphatase from *Morganellamorganii* to a *Burkholderiacepacia* strain. *Acta Biotechnologica, 21*, 359–369.

Frossard, E., Brossard, M., Hedley, M. J., & Meterell, A. (1995). Reactions controlling the cycling of P in soils. In H. Tiessen (Ed.), *Phosphorus in the global environment* (pp. 107–137). New York: Wiley.

Frossard, E., Condron, L. M., Oberson, A., Sinaj, S., & Fardeau, J. C. (2000). Processes governing phosphorus availability in temperate soils. *Journal of Environmental Quality, 29*, 15–23.

Ganesan, V. (2008). Rhizoremediation of cadmium soil using a cadmium-resistant plant growth-promoting rhizopseudomonad. *Current Microbiology, 56*, 403–407.

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

Gholami, A., Shahsavani, S., & Nezarat, S. (2009). The effect of plant growth promoting rhizobacteria (PGPR) on germination, seedling growth and yield of maize. *International Journal of Biological, Biomolecular, Agricultural, Food and Biotechnological Engineering, 1*, 9–14.

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 *Erwiniaherbicola*. *Biotechnology, 5*, 72–74.

Gray, E. J., & Smith, D. L. (2005). Intracellular and extracellular PGPR: Commonalities and distinctions in the plant–bacterium signaling processes. *Soil Biology and Biochemistry, 3*, 7395–7412.

Gupta, R., Singal, R., Sankar, A., Kuhad, R. C., & Saxena, R. K. (1994). A modified plate assay for screening phosphate solubilizing microorganisms. *The Journal of General and Applied Microbiology, 40*, 255–260.

Gupta, G., Panwar, J., & Jha, P. (2013). Natural occurrence of Pseudomonas aeruginosa, a dominant cultivable Diazotrophic endophytic bacterium colonizing *Pennisetum glaucum* (L) R. Br. *Applied Soil Ecology, 64*, 252–261.

Gyaneshwar, P., Naresh, K. P. G., & Parekh, J. L. (1998). Effect of buffering on the phosphate-solubilizing ability of microorganisms. *World Journal of Microbiology and Biotechnology, 14*, 669–673.

Gyaneshwar, P., Parekh, L. J., Archana, G., Podle, P. S., Collins, M. D., Hutson, R. A., & Naresh, K. G. (1999). Involvement of a phosphate starvation inducible glucose dehydrogenase in soil phosphate solubilization by *Enterobacter asburiae*. *FEMS Microbiology Letters, 171*, 223–229.

Gyaneshwar, P., Kumar, G. N., Parekh, L. J., & Poole, P. S. (2002). Role of soil microorganisms in improving P nutrition of plants. *Plant and Soil, 245*, 83–93.

Hartmann, A., Schmid, M., van Tuinen, D., & Berg, G. (2009). Plant–driven selection of microbes. *Plant and Soil, 321*, 235–257.

Hasan, M., Bano, A., Hassan, S. G., Iqbal, J., Awan, U., Rong-ji, D., & Khan, K. A. (2014). Enhancement of rice growth and production of growth–promoting phytohormones by inoculation with rhizobium and other rhizobacteria. *World Applied Sciences Journal, 31*, 1734–1743.

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

Hiltner, L. (1904). Uber neuere Erfahrungen und Probleme auf dem Gebiet der Bodenbakteriologie und unter besonderer Berucksichtigung der Grundungung und Brache. *Arbeiten der Deutschen Landwirtschaftlichen Gesellschaft, 98*, 59–78.

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.

Holford, I. C. R. (1997). Soil phosphorus: Its measurements and its uptake by plants. *Australian Journal of Soil Research, 35*, 227–239.

Holt, J. G., Krieg, N. R., Sneath, P. H. A., Staley, J. T., & Willams, S. T. (1994). *Bergeys manual of determinative bacteriology* (9th ed.). Baltimore: Williams and Wilkins.

Hussain, M. I., Asghar, H. N., Akhtar, M. J., & Arshad, M. (2013). Impact of phosphate solubilizing bacteria on growth and yield of maize. *Plant, Soil and Environment, 32*, 71–78.

Hynes, L. G. C., Hirkala, D. L., & Nelson, L. M. (2008). Isolation, selection, and characterization of beneficial rhizobacteria from pea, lentil and chickpea grown in Western Canada. *Canadian Journal of Microbiology, 54*, 248–258.

Ibrahim, S. S., El-Midany, A. A., & Boulos, T. R. (2010). Economic preferences of mechanical activation over mineral beneficiation for phosphate rock direct applications. *Physicochemical Problems of Mineral Processing, 44*, 63–78.

Illmer, P., & Schinner, F. (1995). Solubilization of inorganic calcium phosphate solubilization mechanisms. *Soil Biology and Biochemistry, 27*, 257–563.

Indiragandhi, P., Anandham, R., Kim, K., Yim, W. J., Madhaiyan, M., & Sa, T. M. (2008). Induction of defense responses in tomato against *Pseudomonas syringae* pv. tomato by regulating the stress ethylene level with *Methylobacteriumoryzae* CBMB20 containing 1-aminocyclo propane-1-carboxylate deaminase. *World Journal of Microbiology and Biotechnology, 24*, 1037–1045.

International Fertilizer Industry Association (IFA). (2009). IFADATA; IFA: Paris, France. Available online: http://www.fertilizer.org/ifa/ifadata/search. Accessed 22.01.17.

Iqbal, M. A., Khalid, M., Shahzad, S. M., Ahmad, M., Soleman, N., & Akhtar, N. (2012). Integrated use of *Rhizobium leguminosarum*, plant growth promoting rhizobacteria and enriched compost for improving growth, nodulation and yield of lentil (*Lens culinaris* Medik.) *Chilean Journal of Agricultural Research, 72*, 104–110.

Iqbal, S., Khan, M. Y., Asghar, H. N., & Akhtar, M. J. (2016). Combined use of phosphate solubilizing bacteria and poultry manure to enhance the growth and yield of mung bean in calcareous soil. *Soil & Environment, 35*, 146–154.

Jarosch, K. A., Doolette, A. L., Smernik, R. J., Tamburini, F., Frossard, E., & Bünemann, E. K. (2015). Characterisation of soil organic phosphorus in NaOH-EDTA extracts: a comparison of 31P NMR spectroscopy and enzyme addition assays. *Soil Biology and Biochemistry, 91*, 298–309.

Johnson, H. W. (1959). The solubilization of "insoluble" phosphate IV the reaction between organic acids and tricalcium phosphate. *New Zealand Journal of Science, 2*, 215–218.

Jones, D. L., Nguyen, C., & Finlay, R. D. (2009). Carbon flow in the rhizosphere: Carbon trading at the soil-rootinterface. *Plant and Soil, 321*, 5–33.

Joo, G. J., Kim, Y. M., Kim, J. T., & Lee, L. I. J. (2005). Gibberellins-producing rhizobacteria increase endogenous gibberellins content and promote growth of red peppers. *Journal of Microbiology, 43*, 510–515.

Jorquera, M. A., Hernandez, M. T., Rengel, Z., Marschner, P., & de la Luz, M. M. (2008). Isolation of culturable phosphobacteria with both phytate–mineralization and phosphate–solubilization activity from the rhizosphere of plants grown in a volcanic soil. *Biology and Fertility of Soils, 44*, 1025–1034.

Kageyama, H., Tripathi, K., Rai, A. K., Chaum, S., Waditee-Sirisattha, R., & Takabe, T. (2011). An alkaline phosphatase/phosphodiesterase, PhoD, induced by salt stress and secreted out of the cells of Aphanothece halophytica, a halotolerant cyanobacterium. *Applied and Environmental Microbiology, 77*, 5178–5183.

Katznelson, H., Peterson, E. A., & Rovatt, J. W. (1962). Phosphate dissolving microoganisms on seed and in the root zone of plants. *Canadian Journal of Botany, 40*, 1181–1186.

Kaur, G., & Reddy, M. S. (2014). Influence of P-solubilizing bacteria on crop yield and soil fertility at multi locational sites. *European Journal of Soil Biology, 61*, 35–40.

Kaymak, H. C., Yarali, F., Guvenc, I., & Donmez, M. F. (2008). The effect of inoculation with Plant Growth Promoting Rhizobacteria (PGPR) on root formation of mint (*Mentha piperita* L.) cuttings. *African Journal of Biotechnology, 7*, 4479–4483.

Khalid, A., Arshad, M., & Zahir, Z. A. (2006). Phytohormones: Microbial production and applications. In N. Uphoff, A. S. Ball, E. Fernandes, H. Herren, O. Husson, M. Laing, C. Palm,

J. Pretty, P. Sanchez, N. Sanginga, & J. Thies (Eds.), *Biological approaches to sustainable soil systems* (pp. 207–220). Boca Raton: Taylor and Francis.

Khan, M. S., Zaidi, A., & Wani, P. A. (2007). Role of phosphate solubilizing microorganisms in sustainable agriculture. A review. *Agronomy for Sustainable Development, 27*, 29–43.

Khan, M. S., Zaidi, A., Wani, P. A., Ahemad, M., & Oves, M. (2009). Functional diversity among plant growth–promoting rhizobacteria. In M. S. Khan, A. Zaidi, & J. Musarrat (Eds.), *Microbial strategies for crop improvement* (pp. 105–132). Berlin: Springer.

Khan, N., Khan, N. W., & Khan, S. A. (2011). Combined effect of nitrogen fertilizers and herbicides upon maize production in Peshawar. *Journal of Animal and Plant Sciences, 21*, 1001–1006.

Khan, M. S., Ahmad, E., Zaidi, A., & Oves, M. (2013). Functional aspect of phosphate–solubilizing bacteria. Importance in crop production. In D. K. Maheshwari, M. Saraf, & A. Aeron (Eds.), *Bacteria in agrobiology: Crop productivity* (pp. 237–265). Berlin: Springer.

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., & McDonald, G. A. (1997). Solubilization of hydroxyapatite by *Enterobacter agglomerans*and cloned *Escherichia coli* in culture medium. *Biology and Fertility of Soils, 24*, 347–352.

Kim, K. Y., Jordan, D., & Krishnan, H. B. (1998). Expression of genes from Rahnellaaquatilis that are necessary for mineral phosphate solubilization in *Escherichia coli*. *FEMS Microbiology Letters, 159*, 121–127.

Kim, C. H., Han, S. H., Kim, K. Y., Cho, B. H., Kim, Y. H., Koo, B. S., & Kim, C. Y. (2003). Cloning and expression of pyrroloquinoline quinone (PQQ) genes from a phosphate-solubilizing bacterium *Enterobacter intermedium*. *Current Microbiology, 47*, 457–461.

Koopmans, G. F., Chardon, W. J., Dolfing, J., Oenema, O., Van der Meer, P., & Van Riemsdijk, W. H. (2003). Wet chemical phosphorus-31 nuclear magnetic resonance analysis of phosphorus speciation in a sand soil receiving long-term fertiliser or animal manure applications. *Journal of Environmental Quality, 32*, 287–295.

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

Krishnaraj, P. U., & Goldstein, A. H. (2001). Cloning of a *Serratia marcescens* DNA fragment that induces quinoprotein glucose dehydrogenase–mediated gluconic acid production in Escherichia coli in the presence of stationary phase *Serratia marcescens*. *FEMS Microbiology Letters, 205*, 215–220.

Kuan, K. B., Othman, R., Rahim, K. A., & Shamsuddin, Z. H. (2016). Plant growth–promoting rhizobacteria inoculation to enhance vegetative growth, nitrogen fixation and nitrogen remobilisation of maize under greenhouse conditions. *PloS One, 11*, e0152478. doi:10.1371/journal.pone. 0152478.

Kumar, K. V., Singh, N., Behl, H. M., & Srivastava, S. (2008). Influence of plant growth promoting bacteria and its mutant on heavy metal toxicity in *Brassica juncea* grown in fly ash amended soil. *Chemosphere, 72*, 678–683.

Kumar, A., Kumar, A., Devi, S., Patil, S., Payal, C., & Negi, S. S. (2012). Isolation, screening and characterization of bacteria from rhizospheric soils for different plant growth promotion (PGP) activities: An in vitro study. *Recent Research in Science and Technology, 4*, 01–05.

Kumar, V., Singh, P., Jorquera, M. A., Sangwan, P., Kumar, P., Verma, A. K., & Agrawal, S. (2013). Isolation of phytaseproducing bacteria from Himalayan soils and their effect on growth and phosphorus uptake of Indian mustard (*Brassica juncea*). *World Journal of Microbiology and Biotechnology, 29*, 1361–1365.

Kurepin, L. V., Zaman, M., & Pharis, R. P. (2014). Phytohormonal basis for the plant growth promoting action of naturally occurring biostimulators. *Journal of the Science of Food and Agriculture, 94*, 1715–1722.

Lalande, R., Bissonnette, N., Coutlée, D., & Antoun, H. (1989). Identification of rhizobacteria from maize and determination of their plant-growth promoting potential. *Plant and Soil, 115*, 7–11.

Li, G. E., Wu, X. Q., Ye, J. R., Hou, L., Zhou, A. D., & Zhao, L. (2013). Isolation and identification of phytate-degrading rhizobacteria with activity of improving growth of poplar and Masson pine. *World Journal of Microbiology and Biotechnology, 29*, 2181–2193.

Lindow, S. E., & Brandl, M. T. (2003). Microbiology of the phyllosphere. *Applied and Environmental Microbiology, 69*, 1875–1883.

Lopez-Bucio, J., de la Vega, O. M., Guevara-García, A., & Herrera-Estrella, L. (2000). Enhanced phosphorus uptake in transgenic tobacco plants that overproduce citrate. *Nature Biotechnology, 18*, 450–453.

Louw, H. A., & Webley, D. M. (1959). A study of soil bacteria dissolving certain phosphate fertilizers and related compounds. *The Journal of Applied Bacteriology, 22*, 227–233.

Lugtenberg, B., & Kamilova, F. (2009). Plant–growth–promoting rhizobacteria. *Annual Review of Microbiology, 63*, 541–556.

Mahdi, S. S., Hassan, G. I., Hussain, A., & Rasool, F. (2011). Phosphorus availability issue—Its fixation and role of phosphate solubilizing bacteria in phosphate solubilization. *Research Journal of Agricultural Sciences, 2*, 174–179.

Maougal, R. T., Brauman, A., Plassard, C., Abadie, J., Djekoun, A., & Drevon, J. J. (2014). Bacterial capacitiesto mineralize phytate increase in the rhizosphere of nodulated common bean (*Phaseolus vulgaris*) under P deficiency. *European Journal of Soil Biology, 62*, 8–14.

Marks, B. B., Megías, M., Ollero, F. J., Nogueira, M. A., Araujo, R. S., & Hungria, M. (2015). Maize growth promotion by inoculation with *Azospirillum brasilense* and metabolites of *Rhizobium tropici* enriched on lipochito oligosaccharides (LCOs). *AMB Express, 5*, 71–79. doi:10.1186/s13568-015-0154-z.

Marra, L. M., de Oliveira, S. M., Soares, C. R. F. S., & de Souza Moreira, F. M. (2011). Solubilisation of inorganic phosphates by inoculants strains from tropical legumes. *Scientia Agricola, 68*, 603–609.

Martinez-Viveros, O., Jorquera, M., 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.

Martínez, O. A., Crowley, D. E., Mora, M. L., & Jorquera, M. A. (2015). Short-term study shows that phytatemineralizing rhizobacteria inoculation affects the biomass, phosphorus (P) uptake and rhizosphere properties of cereal plants. *Journal of Soil Science and Plant Nutrition, 15*, 153–166.

Masciarelli, O., Llanes, A., & Luna, V. (2014). A new PGPR co-inoculated with *Bradyrhizobium japonicum* enhances soybean nodulation. *Microbiological Research, 169*, 609–615.

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.

Mendes, R., Kruijt, M., de Bruijn, I., Dekkers, E., van der Voort, M., Schneider, J. H. M., Piceno, Y. M., DeSantis, T. Z., Andersen, G. L., Bakker, P. A. H. M., & Raaijmakers, J. M. (2011). Deciphering the rhizosphere microbiome for disease–suppressive bacteria. *Science, 332*, 1097–1100.

Minaxi, Saxena, J., Chandra, S., & Nain, L. (2013). Synergistic effect of phosphate solubilizing rhizobacteria and *arbuscular mycorrhiza* on growth and yield of wheat plants. *Journal of Soil Science and Plant Nutrition, 13*, 511–525. doi:10.4067/S0718–95162013005000040.

Mommer, L., Kirkegaard, J., & van Ruijven, J. (2016). Root-root interactions: Towards a rhizosphere framework. *Trends in Plant Science, 21*, 209–217.

Moody, P. W., Speirs, S. D., Scott, B. J., & Mason, S. D. (2013). Soil phosphorus tests I: What soil phosphorus pools and processes do they measure? *Crop & Pasture Science, 64*, 461–468.

Moutia, J. F. Y., Saumtally, S., Spaepen, S., & Vanderleyden, J. (2010). Plant growth promotion by *Azospirillum* sp. in sugarcane is influenced by genotype and drought stress. *Plant and Soil, 337*, 233–242.

Murphy, J., & Riely, J. P. (1962). A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta, 27*, 31–36.

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

Nannipieri, P. (2011). Potential impact of climate change on microbial function in soil. In T. J. Sauer, J. M. Norman, & M. V. K. Sivakumar (Eds.), *Sustaining soil productivity in response to global climate change* (1st ed., pp. 199–209). New York: Wiley.

Narsian, V., & Patel, H. H. (2000). *Aspergillus aculeatus* as a rock phosphate solubilizer. *Soil Biology and Biochemistry, 32*, 559–565.

Narula, N., Kumar, V., Behl, R. K., Duebel, A. A., Gransee, A., & Merbach, W. (2000). Effect of P solubilizing *Azotobacter chroococcum* on N, P, K uptake in P responsive wheat genotypes grown under greenhouse conditions. *Journal of Plant Nutrition and Soil Science, 163*, 393–398.

Nautiyal, C. S. (1999). An efficient microbiological growth medium for screening phosphate solubilizing microorganism. *FEMS Microbiology Letters, 170*, 265–270.

Nye, P. H. (1980). Diffusion of ions and uncharged solutes in soils and soil clays. *Advances in Agronomy, 31*, 225–272.

Oberson, A., & Joner, E. J. (2005). Microbial turnover of phosphorus in soil. In B. L. Turner, E. Frossard, & D. S. Baldwin (Eds.), *Organic phosphorus in the environment* (pp. 133–164). Wallingford: CABI.

Ochoa-Loza, F. J., Artiola, J. F., & Maier, R. M. (2001). Stability constants for the complexation of various metals with a rhamnolipid biosurfactant. *Journal of Environmental Quality, 30*, 479–485.

Olander, L. P., & Vitousek, P. M. (2004). Biological and geochemical sinks for phosphorus in soil from a wet tropical forest. *Ecosystems, 7*, 404–419.

Omar, S. A. (1998). The role of rock phosphate solubilizing fungi and vesicular arbuscular mycorrhiza (VAM) in growth of wheat plants fertilized with rock phosphate. *World Journal of Microbiology and Biotechnology, 2*, 211–218.

Pati, B. R., & Chandra, A. K. (1981). Effect of spraying nitrogen-fixing phyllospheric bacterial isolates on wheat plants. *Plant and Soil, 61*, 419–427.

Patil, M. G., Sayyed, R. Z., Chaudhari, A. B., & Chincholkar, S. B. (2002). Phosphate solubilizing microbes: A potential bioinoculant for efficient use of phosphate fertilizers. In S. M. Reddy, S. R. Reddy, & S. Grisham (Eds.), *Bioinoculants for sustainable agriculture and forestry* (pp. 127–138). Jodhpur: Scientific Publisher.

Pereira, S. I. A., & Castro, P. M. L. (2014). Phosphate solubilizing rhizobacteria enhance *Zea mays* growth in agricultural P–deficient soils. *Ecological Engineering, 73*, 526–535.

Pieterse, C. M. J., Zamioudis, C., Berendsen, R. L., Weller, D. M., Van Wees, S. C. M., & Bakker, P. A. H. M. (2014). Induced systemic resistance by beneficial microbes. *Annual Review of Phytopathology, 52*, 347–375.

Pikovskaya, R. I. (1948). Mobilization of phosphorus in soil in connection with the vital activity of some microbial species. *Mikrobiologiya, 17*, 362–370.

Pizzeghello, D., Berti, A., Nardi, S., & Morari, F. (2011). Phosphorus forms and P–sorption properties in three alkaline soils after long–term mineral and manure applications in north–eastern Italy. *Agriculture, Ecosystems & Environment, 141*, 58–66.

Poonguzhali, S., Madhaiyan, M., & Sa, T. (2008). Isolation and identification of phosphate solubilizing bacteria from Chinese cabbage and their effect on growth and phosphorus utilization of plants. *Journal of Microbiology and Biotechnology, 18*, 773–777.

Probanza, A., Mateos, J. L., Lucas-Garcia, J. A., Ramos, B., de Felipe, M. R., & Gutierrez Manero, F. J. (2001). Effects of inoculation with PGPR Bacillus and *Pisolithustinctorius* on *Pinus pinea* L. growth, bacterial rhizosphere colonization, and mycorrhizal infection. *Microbial Ecology, 41*, 140–148.

Prochnow, L. I., Fernando, J., Quispe, S., Artur, E., Francisco, B., & Braga, G. (2006). Effectiveness of phosphate fertilizers of different water solubilities in relation to soil phosphorus adsorption. *Agronomy Journal, 95*, 293–302.

Qureshi, M. A., Iqbal, A., Akhtar, N., Shakir, M. A., & Khan, A. (2012). Co-inoculation of phosphate solubilizing bacteria and rhizobia in the presence of L-tryptophan for the promotion of mash bean (*Vigna mungo* L.) *Soil and Environment, 31*, 47–54.

Reid, R. K., Reid, C. P. P., & Szaniszlo, P. J. (1985). Effects of synthetic and microbially produced chelates on the diffusion of iron and phosphorus to a simulated root in soil. *Biology and Fertility of Soils, 1*, 45–52.

Reilly, T. J., Baron, G. S., Nano, F., & Kuhlenschmidt, M. S. (1996). Characterization and sequencing of a respiratory burst inhibiting acid phosphatase from *Francisella tularensis*. *The Journal of Biological Chemistry, 271*, 10973–10983.

Reinhold-Hurek, B., Bünger, W., Burbano, C. S., Sabale, M., & Hurek, T. (2015). Roots shaping their microbiome: Global hotspots for microbial activity. *Annual Review of Phytopathology, 53*, 403–424.

Reyes, I., Baziramakenga, R., Bernier, L., & Antoun, H. (2001). Solubilization of phosphate rocks and minerals by a wild–type strain and two UV induced mutants of *Penicillium rugulosum*. *Soil Biology and Biochemistry, 33*, 1741–1747.

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

Ringeval, B., Augusto, L., Monod, H., van Apeldoorn, D., Bouwman, L., Yang, X., Achat, D. L., Chini, L. P., Van Oost, K., Guenet, B., Wang, R., Decharme, B., Nesme, T., & Pellerin, S. (2017). Phosphorus in agricultural soils: Drivers of its distribution at the global scale. *Glob Change Biology*. doi:10.1111/gcb.13618.

Rivera, C. M., Trujillo, N. A., Córdova, B. G., Kohler, J., Caravaca, F., & Roldan, A. (2008). Poultry manure and banana waste are effective biofertilizer carriers for promoting plant growth and soil sustainability in banana crops. *Soil Biology and Biochemistry, 40*, 3092–3095.

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

Rojas-Tapias, D., Moreno-Galván, A., Pardo-Díaz, S., Obando, M., Rivera, D., & Bonilla, R. (2012). Effect of inoculation with plant growth-promoting bacteria (PGPB) on amelioration of saline stress in maize (*Zea mays*). *Applied Soil Ecology, 61*, 264–272.

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.

Ryan, P. R., Delhaize, E., & Jones, D. L. (2001). Function and mechanism of organic anion exudation from plant roots. *Annual Review of Plant Physiology and Plant Molecular Biology, 52*, 527–560.

Ryan, M. H., Tibbett, M., Edmonds-Tibbett, T., Suriyagoda, L. D. B., Lambers, H., Cawthray, G. R., & Pang, J. (2012). Carbon trading for phosphorus gain: The balance between rhizosphere carboxylates and arbuscular mycorrhizal symbiosis in plant phosphorus acquisition. *Plant, Cell & Environment, 35*, 2170–2180.

Sarathambal, C., & Ilamurugu, K. (2013). Saline tolerant plant growth promoting diazotrophs from rhizosphere of bermuda grass and their effect on rice. *Indian Journal of Weed Science, 45*, 80–85.

Sashidhar, B., & Podile, A. R. (2009). Transgenic expression of glucose dehydrogenase in *Azotobacter vinelandii* enhances mineral phosphate solubilization and growth of sorghum seedlings. *Microbial Biotechnology, 2*, 521–529.

Schachtman, D. P., Robert, J., & Reid, A. S. M. (1998). Phosphorus uptake by plants: From soil to cell. *Plant Physiology, 116*, 447–453.

Selvakumar, G., Mohan, M., Kundu, S., Gupta, A. D., Joshi, P., Nazim, S., & Gupta, H. S. (2008). Cold tolerance and plant growth promotion potential of *Serratia marcescens* strain SRM (MTCC 8708) isolated from flowers of summer squash (*Cucurbita pepo*). *Letters in Applied Microbiology, 46*, 171–175.

Shahzad, S. M., Khalid, A., Arshad, M., Tahir, J., & Mahmood, T. (2010). Improving nodulation, growth and yield of Cicer arietinum L. through bacterial ACC–deaminase induced changes in root architecture. *European Journal of Soil Biology, 46*, 342–347.

Shahzad, S. M., Arif, M. S., Riaz, M., Ashraf, M., & Iqbal, Z. (2013). PGPR with varied ACC–deaminase activity induced different growth and yield response in maize (*Zea mays* L) under fertilized conditions. *European Journal of Soil Biology, 57*, 27–34.

Shahzad, S. M., Khalid, A., Arif, M. S., Riaz, M., Ashraf, M., & Iqbal, Z. (2014). Co-inoculation integrated with P-enriched compost improved nodulation and growth of chickpea (*Cicer arietinum* L.) under irrigated and rainfed farming systems. *Biology and Fertility of Soils, 50*, 1–12.

Sharma, K. K., Mathur, P. B., & Jatanand, B. (2007). Chickpea (*Cicer arietinum* L). In K. Wang (Ed.), *Agrobacterium protocol, volume 1*, *Methods in molecular biology* (Vol. 343, 2nd ed.). Tootowa NJ: Humana Inc.

Sharma, S., Upadhyaya, H. D., Roorkiwal, M., Varshney, R. K., & Gowda, C. L. L. (2013a). Chickpea. In M. Singh, H. D. Upadhyaya, & I. S. Bisht (Eds.), *Genetic and genomic resources of grain legume improvement* (pp. 81–104). London: Elsevier Inc..

Sharma, S. B., Sayyed, R. Z., Trivedi, M. H., & Gobi, T. A. (2013b). Phosphate solubilizing microbes: Sustainable approach for managing phosphorus deficiency in agricultural soils. *Springerplus, 2*, 587–600.

Sharpley, A. N., Singh, U., Uehara, G., & Kimble, J. (1989). Modeling soil and plant phosphorus dynamics in calcareous and highly weathered soils. *Soil Science Society of America Journal, 53*, 153–158.

Shen, J., Li, C., Mi, G., Li, L., Yuan, L., Jiang, R., & Zhang, F. (2013). Maximizing root/rhizosphere efficiency to improve crop productivity and nutrient use efficiency in intensive agriculture of China. *Journal of Experimental Botany, 64*, 1181–1192.

Shilev, S., Sancho, E. D., & Benlloch-González, M. (2012). Rhizospheric bacteria alleviate salt-produced stress in sunflower. *Journal of Environmental Management, 95*, 37–41.

da Silva, T. F., Vollú, R. E., do Carmo Dias, B., de Lacerda, J. R. M., Marques, J. M., Nishikawa, M. M., de Vasconcelos Goulart, F. R., Alviano, C. S., & Seldin, L. (2017). Cultivable bacterial communities associated with roots of rose–scented geranium (*Pelargonium graveolens*) with the potential to contribute to plant growth. *Applied Soil Ecology, 111*, 123–128.

Singh, N., Pandey, P., Dubey, R. C., & Maheshwari, D. K. (2008). Biological control of root rot fungus *Macrophomina phaseolina* and growth enhancement of *Pinus roxburghii* (Sarg.) by rhizosphere competent *Bacillus subtilis* BN1. *World Journal of Microbiology and Biotechnology, 24*, 1669–1679.

Son, H. J., Park, G. T., Cha, M. S., & Heo, M. S. (2006). Solubilization of insoluble inorganic phosphates by a novel salt- and pH tolerant *Pantoea agglomerans* R-42 isolated from soybean rhizosphere. *Bioresource Technology, 97*, 204–210.

Spaepen, S., Vanderleyden, J., & Okon, Y. (2009). Plant growth-promoting actions of rhizobacteria. In L. C. van Loon, J. C. Ed Kader, & M. Delseny (Eds.), *Advances in botanical research* (Vol. 51, pp. 283–320). Amsterdam, The Netherlands: Elsevier.

Stajković-Srbinović, O., Delić, D., Kuzmanović, D., Protić, N., Rasulić, N., & Knežević-Vukčević, J. (2014). Growth and nutrient uptake in oat and barley plants as affected by rhizobacteria. *Romanian Biotechnology Letters, 19*, 9429–9436.

Stevenson, F. J. (2005). *Cycles of soil: Carbon, nitrogen, phosphorus, sulfur, micronutrients* (p. 448). New York: Wiley.

Stout, M. J., Zehnder, G. W., & Baur, M. E. (2002). Potential for the use of elicitors of plant defense in arthropod management programs. *Archives of Insect Physiology and Biochemistry, 51*, 222–235.

Sturz, A. V., Matheson, B. G., Arsenault, W., & Christie, L. B. R. (2001). Weeds as a source of plant growth promoting rhizobacteria in agricultural soils. *Canadian Journal of Microbiology, 47*, 1013–1024.

SubbaRao (Ed.). (1977). *soil microorganisms and plant growth*. India: Oxford and IBH Publishing Co.

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, 77*, 43–49.

Sutherland, I. (2001). Biofilm exopolysaccharides: a strong and sticky framework. *Microbiology, 147*, 3–9.

Syers, J. K., Johnston, A. E., & Curtin, D. (2008a). *Efficiency of soil and fertilizer phosphorus use FAO*. Rome, Italy: Fertilizer and Plant Nutrition Bulletin 18.

Syers, J. K., Johnston, A. E., & Curtin, D. (2008b). *Efficiency of soil and fertilizer phosphorus: Reconciling changing concepts of soil phosphorus behaviour with agronomic information* (pp. 27–44). Rome, Italy: FAO Fertilizer and Plant Nutrition Bulletin 18.

Taktek, S., St-Arnaud, M., Piché, Y., Fortin, J. A., & Antoun, H. (2017). Igneous phosphate rock solubilization by biofilm forming mycorrhizo bacteria and hyphobacteria associated with *Rhizoglomus irregular* DAOM 197198. *Mycorrhiza, 27*, 13–22.

Tarafdar, J. C. (1989). Use of electrofocussing technique for characterizing the phosphatases in the soil and root exudates. *Journal of the Indian Society of Soil Science, 37*, 393–395.

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.

Tian, G., Cox, A. E., Kumar, K., Granato, T. C., O'Connor, G. A., & Elliott, H. A. (2016). Assessment of plant availability and environmental risk of biosolids–phosphorus in a US mid-west corn–belt soil. *Journal of Environmental Management, 172*, 171–176.

Turan, M., Ekinci, M., Yildirim, E., & Dursun, A. (2014). Plant growth-promoting rhizobacteria improved growth, nutrient, and hormone content of cabbage (*Brassica oleracea*) seedlings. *Turkish Journal of Agriculture and Forestry, 38*, 327–333.

Turner, B. L., Papházy, M. J., & Haygarth, P. M. (2002). Inositol phosphates in the environment. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 357*, 449–469.

Upadhyay, S. K., Singh, J. S., Saxena, A. K., & Singh, D. P. (2011). Impact of PGPR inoculation on growth and antioxidant status of wheat under saline conditions. *Plant Biology, 14*, 605–611.

Van de Wiel, C. C. M., van der Linden, C. G., & Scholten, O. E. (2016). Improving phosphorus use efficiency in agriculture: Opportunities for breeding. *Euphytica, 207*, 1–22.

Vikram, A., Ajjanna, R., Alagawadi, A. P. U., Krishnaraj, A. K. S., & Kumar, M. (2007). Transconjugation studies in *Azospirillum* sp. negative to mineral phosphate solubilization. *World Journal of Microbiology and Biotechnology, 23*, 1333–1337.

Viruel, E., Erazzú, L. E., Calsina, L. M., Ferrero, M. A., Lucca, M. E., & Siñeriz, F. (2014). Inoculation of maize with phosphate solubilizing bacteria: Effect on plant growth and yield. *Journal of Soil Science and Plant Nutrition, 14*, 819–831.

Wani, P. A., Khan, M. S., & Zaidi, A. (2008). Chromium-reducing and plant growth-promoting Mesorhizobium improves chickpea growth in chromium-amended soil. *Biotechnology Letters, 30*, 159–163.

Weiland-Bräuer, N., Pinnow, N., & Schmitz, R. A. (2015). Novel reporter for identification of interference with acyl homoserine lactone and autoinducer–2 quorum sensing. *Applied and Environmental Microbiology, 81*, 1477–1489.

Welch, S. A., Taunton, A. E., & Banfield, J. F. (2002). Effect of microorganisms and microbial metabolites on apatite dissolution. *Geomicrobiology Journal, 19*, 343–367.

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

Widawati, S., & Rahmansyah, M. (2009). The influence of bacteria inoculation to *jarakpagar* (*Jatropha curcas* L) growth. *Jurnal Biologi Indonesia, 6*, 107–117.

Widawati, S., & Suliasih. (2006). Augmentation of potential phosphate solubilizing bacteria (PSB) stimulate growth of green mustard (*Brassica caventis* Ocd) in marginal soil. *Biodiversitas, 7*, 10–14.

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., Ding, G., Shi, L., Xu, F., & Meng, J. (2010). Detection of QTL for phosphorus efficiency at vegetative stage in *Brassica napus*. *Plant and Soil, 339*, 97–111.

Yi, Y., Huang, W., & Ying, G. (2008). Exopolysaccharide: A novel important factor in the microbial dissolution of tricalcium phosphate. *World Journal of Microbiology and Biotechnology, 24*, 1059–1065.

Yu, X., Liu, X., & Zhu, T. (2014). Walnut growth and soil quality after inoculating soil containing rock phosphate with phosphate–solubilizing bacteria. *Science Asia, 40*, 21–27.

Yuan, J., Zhang, N., & Huang, Q. (2015). Organic acids from root exudates of banana help root colonization of PGPR strain *Bacillus amylo liquefaciens* NJN–6. *Scientific Reports, 5*, 134–438.

Yuttavanichakul, W., Lawongsa, P., Wongkaew, S., Teaumroong, N., Boonkerd, N., Nomura, N., & Tittabutr, P. (2012). Improvement of peanut rhizobial inoculant by incorporation of plant growth promoting rhizobacteria (PGPR) as biocontrol against the seed borne fungus, *Aspergillus niger*. *Biological Control, 63*, 87–97.

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.

Zaefarian, F., Vahidzadeh, S., Rahdari, P., Rezvani, M., & Zadeh, H. G. (2012). Effectiveness of plant growth promoting rhizobacteria in facilitating lead and nutrient uptake by little seed canary grass. *Brazilian Journal of Botany, 35*, 241–248.