Chapter 7
Solubilization of Phosphorus by Soil Microorganisms

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7.1 Introduction

Agricultural production remains highly reliant on the application of phosphorus (P) fertilizers derived from phosphate rock. Due to increasing demand and dwindling stocks, it is predicted that current global reserves of phosphate rock may be depleted within 50–100 years (Cordell et al. 2009). Furthermore, continued agricultural expansion has led to co-saturation of many ecosystems with both N and P, resulting in the degradation of terrestrial, freshwater and marine resources (Tilman et al. 2001). This concern has highlighted the imperative need to better understand the plant–soil–microbial P cycle, with an aim of reducing our reliance on mineral fertilizers. This has led to increased interest in the harnessing of microorganisms to support P cycling in agroecosystems. It is well known that some microbes in soil have the potential to greatly enhance the rate of organic P (P_o) or inorganic (P_i) cycling (i.e. by solubilizing insoluble organic- and mineral-bound P). This chapter aims to identify which P solubilizing organisms (PSM) exist in soil, the types of P they can utilize, the mechanisms by which this occurs and the potential for managing them in an agricultural context. Our aim is to encompass all types of soil microorganisms; however, we will not cover mycorrhizas as these are comprehensively covered by Jansa et al. (2011).

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E.K. Bünemann et al. (eds.), *Phosphorus in Action*, Soil Biology 26,
DOI 10.1007/978-3-642-15271-9_7, © Springer-Verlag Berlin Heidelberg 2011

7.2 P in the Soil Environment

Compared to other essential macronutrients (with the exception of N), P is one of the less-abundant elements in the lithosphere (0.1% of total). However, sufficient P nutrition is of crucial importance for all microorganisms due to its central role in energy transfer (e.g. ATP), cell structure (phospholipids), metabolism and signaling (see Bünemann et al. 2011; Frossard et al. 2011). In soils, concentrations of available P in soil solution are typically low ($<$0.01 to 1 mg L^{-1} in highly fertile soils) due to the comparatively low content of P in the parent material, but also due to the high reactivity of P_i that results in strong retention by the soil's mineral matrix. This has led to microorganisms developing a wide range of strategies to enhance P availability in soil. Although plants can only take up P_i (i.e. HPO_4^{2-}, $H_2PO_4^{-}$), fungi and bacteria can also potentially take up low molecular weight (LMW) organic P (P_o) (e.g. sugar-P; Schwöppe et al. 2003). In contrast, protozoa can take up and assimilate high molecular weight (HMW) P_o, implying that there are only a few microbially unavailable organic P pools in soil and suggesting that different P sources can potentially provide ecological niches for different species (Foster and Dormaar 1991). To date, most research has focussed on the biological manipulation of P_i availability in soil rather than P_o.

In a recent review of P chemistry in soils, Sims and Pierzynski (2005) identified the major processes of the soil P cycle that affect soil solution P concentrations as (1) dissolution–precipitation (mineral equilibria), (2) sorption–desorption (interactions between P in solution and soil solid surfaces), and (3) mineralization–immobilization (biologically mediated conversions of P between inorganic and inorganic forms). With a significant proportion of total soil P being organically bound, the role of microorganisms in P turnover should not be underestimated. Furthermore, microbes (like plants) actively or passively release protons, CO_2 and secondary organic metabolites (e.g. sugars, organic acid anions, amino acids, siderophores, enzymes, phenols) that may all contribute to the solubilization of P from soil minerals (via processes 1 and 2). Overall, between 1–50% of soil bacteria and 0.5–0.1% of soil fungi can be classified as P-solubilizing microorganisms (PSM) (Gyaneshwar et al. 2002; Kucey et al. 1989). Although the number of bacteria in soil classed as PSM generally outnumber those of fungi, the fungal isolates generally exhibit a greater P-solubilizing capacity in both liquid and solid media (Banik and Dey 1982; Gyaneshwar et al. 2002).

7.2.1 *Sources of Soil P Capable of Microbial Solubilization*

The chemical and physical form of P in soil is clearly an important regulator of the efficiency (i.e. gross release and/or solubilization) of PSM to mobilize P bound in the soil's solid phase. For example, phosphate rock contains different types of P minerals with variable solubility. Typically, PSM are selected for their ability to dissolve phosphate rock in vitro; however, phosphate rock may not reflect the form of P found in many soils. This is probably one of the main reasons why PSM show differential responses in situ. Here, we briefly describe the dominant forms of P in soil.

7.2.1.1 Inorganic P

Total P content in top soils (0–15 cm) typically ranges from 50 to 3,000 mg kg^{-1} depending on parent material, soil type, vegetation cover and soil management (Sims and Pierzynski 2005), with P_i comprising 35–70% of total soil P (Sample et al. 1980). The chemical forms of P in soil differ not only with parent material, soil pH and vegetation cover, but also with time and the extent of pedogenesis (Walker and Syers 1976; Foth and Ellis 1997; Fig. 7.1). The organic P pool increases with soil development but tends to decline again in highly weathered, older soils. Consequently, soil development and therefore the distribution of P between the P_o and P_i pools, as well as the composition of P forms, have a major impact on P accessibility for the microbial community, which ultimately determines the success of PSM in the field.

Calcium-phosphates (mainly different forms of apatites, such as fluoroapatite [$Ca_5(PO_4)_3F$], hydroxyapatite [$Ca_5(PO_4)_3OH$], and francolites [carbonate-fluorapatites of variable chemical composition $(Ca, Mg, Sr, Na)_{10}(PO_4, SO_4, CO_3)_6F_{2-3}$]; Benmore et al. 1983) represent the primary mineral source of P_i in unweathered or moderately weathered soils with neutral to alkaline pH, whereas Fe and Al

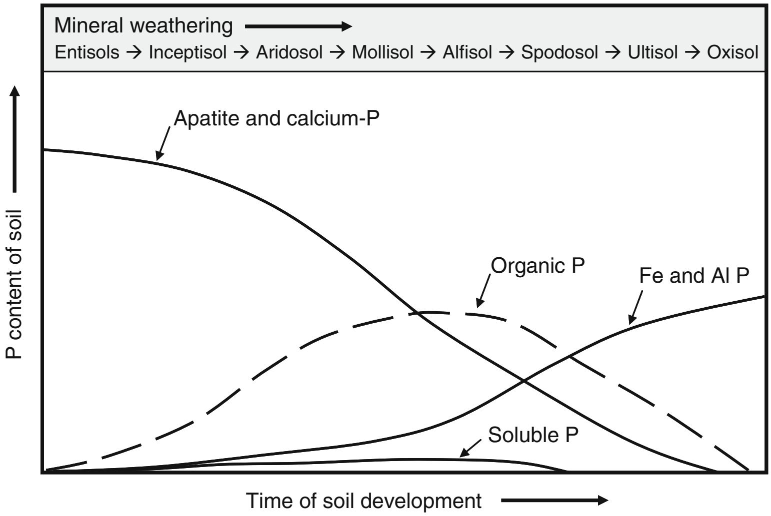


Fig. 7.1 Relative distribution of the major forms of soil P as related to soil development and the major US Soil Taxonomy Orders over a timeframe of millions of years. Adapted from Foth and Ellis (1997)

phosphates and P_i bound and/or occluded by Fe and Al oxy(hydr)oxides predominate in acidic and more progressively weathered soils (Sims and Pierzynski 2005).

Due to the increasing stability of Ca-P minerals at acidic pH, localized acidification by PSM can result in the solubilization of Ca phosphates and the release of P_i (see also Sect. 7.3.1). Consequently, various acidifying PSM have been applied to accelerate dissolution of phosphate rock (i.e. collective term for igneous, metamorphous or marine sedimentary rock containing Ca-P-bearing minerals) prior to addition to soil (e.g. through the addition of microbial consortia in composts or via addition of individual PSM; Arcand and Schneider 2006; Odongo et al. 2007; Aria et al. 2010).

In neutral and particularly in acidic soils, Al and Fe oxides and hydroxides exert a great impact on P availability, because various identified Fe and Al phosphates, such as wavellite [$Al_3(OH)_3(PO_4)_2 \cdot 5H_2O$], variscite ($AlPO_4 \cdot 2H_2O$), strengite ($FePO_4 \cdot 2H_2O$), etc. (for an extensive review see Harris 2002) are generally rare in occurrence. Due to the increased positive surface charge of the Fe and Al oxides with decreasing pH, strong covalent bonds (chemisorption) are formed with the negatively charged P, rendering it rather recalcitrant to exchange reactions. Nevertheless, LMW organic anions (e.g. gluconate, oxalate, etc.) released by PSM are capable of competing with P_i for sorption sites. Also, changes in pH might directly or indirectly affect the oxides' surface potential and consequently P_i solubility (see also Sects. 7.3.1 and 7.3.2).

7.2.1.2 Organic P

Soil Organic Matter

On average, between 30% and 65% of total P is present as P_o in mineral soils. In organic soils (>20–30% organic matter), P_o can approach up to 90% of the total P. The main identified P_o compounds in soil are inositol phosphates, phospholipids and nucleic acids (Quiquampoix and Mousain 2005; Turner et al 2002). The abundance of inositol phosphates is highly variable; however, they frequently represent the dominant form of P_o in soil ($\geq$80% of P_o; Dalal 1977). They comprise a sequence of phosphate monoesters, from inositol monophosphate to insositol hexakisphosphate in various stereoisomeric variations (*myo, scyllo, neo,* D-*chiro*) (Celi and Barberis 2005). They are characterized by high acidity and are often found as components of polymers or insoluble complexes with proteins and lipids (Harrison 1987). The stability of inositol phosphates is closely linked to the number of phosphate groups, rendering esters of higher order more recalcitrant to biodegradation and consequently more abundant. The most common stereoisomer in soil is *myo*-inositol hexakisphosphate (also known as phytic acid).

Phospholipids usually comprise 0.5–7.0% of total P_o (Dalal 1977), with phosphoglycerides being the most dominant form. Nucleic acids and their derivatives account for less than 3% of total P_o; they are rapidly mineralized, re-synthesized, combined with other soil constituents or incorporated into microbial biomass

(Anderson and Malcolm 1974). Other, less abundant forms of P_o include sugar-P (Anderson 1961), monophosphorylated carboxylic acids (Anderson and Malcolm 1974) and teichoic acids (a major cell wall component of many Gram-positive bacteria; Zhang et al. 1998).

A major characteristic of P biogeochemistry is that only 1% of the total soil P (ca. 400–4,000 kg P ha^{-1} in the top 30 cm) is incorporated into living plant biomass during each growing season (ca. 10–30 kg P ha^{-1}), reflecting its low availability for plant uptake (Blake et al. 2000; Quiquampoix and Mousain 2005). Concentrations of microbial P in soils can range between 0.75 (sandy Spodosol, fertilized pine plantation) and 106 mg kg^{-1} (calcaric Regosol, permanent grassland) in mineral top soils and between 50 (haplic Podzol, Norway spruce forest) and 169 mg kg^{-1} (typic Udivitrand, indigenous New Zealand forest) in organic litter layers, and have been found to comprise between 0.5% and 26% of total soil P (Oberson and Joner 2005). Microbial P generally decreases with increasing soil depth and decreasing soil organic matter (SOM) content. The P-containing compounds in microorganisms are reviewed extensively elsewhere (Bünemann et al. 2011). Briefly, P-containing compounds in bacteria and fungi have been found to include nucleic acids (30–65% of total microbial P), phospholipids, acid-soluble P_i and P_o compounds (i.e. phosphate esters, phosphorylated coenzymes, 15–20%), polyphosphates, as well as teichoic acid (only Gram-positive bacteria). Both polyphosphates and teichoic acid have been reported to serve as P storage compounds (Alexander 1977; Gächter and Meyer 1993). Several authors have reported that immobilization of P by microbes is regulated more by C limitation than by P limitation (Bünemann et al. 2004; Oehl et al. 2001a). Therefore, P concentrations in the microbial biomass seem to be closely linked to C dynamics in soil (Achat et al. 2009). Fertilization with P often results in a decline in microbial P (Clarholm 1993; Grierson et al. 1998), whereas other authors have reported the opposite trend (Joergensen and Scheu 1999) or observed rather small or no effects (Bünemann et al. 2004). Furthermore, apart from substrate-driven changes, it appears that seasonal variations in microbial P are mostly related to changes in gravimetric water content in the soil (Chen et al. 2003), causing reduced microbial biomass P during dry periods.

Organic Soil Additives

In an effort to enhance soil quality and divert waste from landfill, the application of organic waste (e.g. treated municipal sewage sludge – so-called biosolids, compost, animal manures) to land has significantly increased in recent years. Organic soil amendments may increase P nutrition of plants and microbes; however, P availability in these heterogeneous materials is highly dependent on the chemical forms of P present, as well as on the complex interaction of the added material with the soil. There is increasing interest in the potential beneficial interaction of biofertilizers (i.e. PSM) with these organic wastes to provide optimal nutrient delivery to crops. Synchrotron-based analysis of selected biosolids and manure originated from various animal stocks revealed that P in biosolids was mainly present as P_i in the form of variscite (Al-P, 86% of total P) and the less-soluble hydroxylapatite (Ca-P, 14%). Manure contained dicalcium phosphate dehydrate (12–65%), struvite (ammonium magnesium phosphate, 12–68%) and variscite (0–18%) (Ajiboye et al. 2007). Organic P was mainly present as Ca-phytate (20–70%) (Ajiboye et al. 2007). The P_i fraction in compost is bound to Ca as apatite or octacalcium-phosphates (Frossard et al. 2002). Furthermore, the distribution of P_i between Al, Fe and Ca fractions in organic amendments also depends on further additives such as lime and metal salts [e.g. $FeCl_3$, $Al_2(SO_4)_3$]. Despite their reducing effect on potential heavy metal toxicity, these additives have been found to effectively reduce P solubility (Maguire et al. 2006). Metal salts induce P sorption to precipitated Al or Fe hydroxides rather than immobilization as Al or Fe phosphate. The addition of lime induces the formation of recalcitrant Ca phosphates (e.g. hydroxylapatite, tricalcium phosphate) and, consequently, reduces P sorption to Fe hydroxide surfaces (Shober and Sims 2009). The solubility of P in organic soil amendments when applied to soils will be mainly governed by the soil solution equilibrium and the soil and substrate pH, rendering Fe and Al phosphates more, and Ca phosphates less, recalcitrant with decreasing pH. The chemical form of P in the biosolids can also be manipulated to improve their use in the field (e.g. through the addition of stabilizing agents such as CaO, $FeSO_4$ etc.; Huang et al. 2008). Nevertheless, despite being an additional potential P source, organic amendments provide a significant amount of easily available carbon and nitrogen, resulting in an almost direct response in increasing microbial activity (biomass build up, turnover, respiration and substrate mineralization) (Giller et al. 1998; Kao et al. 2006; Saha et al. 2008), accelerating dynamics not only in C- and N-, but also in P cycling. The increasing microbial activity may potentially solubilize organic as well as inorganic P contained in the additives, but also P forms present in the indigenous soil.

7.3 P-Solubilizing Mechanisms

Availability of P_i in soil is mainly governed by the dissolution properties of the P-bearing minerals (which are determined largely by pH) as well as by solution equilibrium reactions (sorption and desorption). In contrast, the availability of P derived from P_o is mainly governed by microbial activity (mineralization and enzymatic hydrolysis). Like higher plants, microorganisms have the potential to modify their immediate chemical environment via the uptake and release of organic and inorganic ions and molecules. The main P solubilization mechanisms employed by soil microorganisms include: (1) release of complexing or mineral dissolving compounds (e.g. organic acid anions, siderophores, protons, hydroxyl ions, CO_2), (2) liberation of extracellular enzymes (biochemical P_o mineralization) and (3) the release of P_o during substrate degradation (biological P_o mineralization) (McGill and Cole 1981). P incorporated in the microbial biomass may be temporarily immobilized but remains in a bioavailable form that can be released via microbial turnover (re-mineralization). Therefore, microorganisms play an important role in all three major components of the soil P cycle (i.e. dissolution–precipitation, sorption–desorption, and mineralization–immobilization).

Microbial P mobilization strategies, uptake and subsequent release, as well as redistribution of P in soil may all affect the success of PSM in improving plant growth. In particular, PSM may also compete with plants for any P released. Soil solution P only increases when P solubilization (from soil minerals) and gross mineralization (mineralization of SOM, re-mineralization of P_o and P_i held in the microbial biomass) exceed P immobilization (uptake and incorporation in the biomass) and sorption to soil minerals. All these processes are driven by a wide range of chemical and physical soil properties (e.g. mineral composition, SOM, texture, structure, temperature, water content) and vegetation properties, making temporal and spatial predictions of P availability in soil from added PSM difficult. The mechanisms and processes involved in P mobilization by PSM in soil are discussed in Sects. 7.3.1–7.3.6.

7.3.1 P Release Mediated by Changes in pH

The release of protons or hydroxide ions by microorganisms can significantly alter the soil solution pH in the close vicinity of the exuding organisms, inducing changes in mineral nutrient availability. Whereas only a few reports of microbial P solubilization by alkalinization exist, microbial P solubilization via acidification is well documented for several fungi and bacterial species (Gyaneshwar et al. 1999; Illmer and Schinner 1992; Ben Farhat et al. 2009) and is often found to be particularly successful when P is associated with Ca. Typically, the release of protons is also linked to the extrusion of organic acid anions into the external media (Arvieu et al. 2003; Casarin et al. 2003). The amount of protons released into the external medium is often significantly influenced by N supply. In general, a greater reduction in pH together with more solubilized P can be observed with NH_4^+ as the sole N source compared to NO_3^-, due to the extrusions of protons to compensate for NH_4^+ uptake (Roos and Luckner 1984; Illmer et al. 1995; Sharan et al. 2008). In contrast, Reyes et al. (1999) found a decrease in P solubilization by *Penicillium rugulosum* from various P-bearing minerals (hydroxyapatite, $FePO_4$, $AlPO_4$) when higher concentrations of NH_4^+ were supplied. The authors attributed these findings to the repressive effect of easily metabolized N sources on secondary metabolic biosynthesis in fungi. The same study also showed that the assimilation of amino acids (in this case arginine) as the sole N source can also lead to a decrease in pH and enhanced mobilization of P.

For some microorganisms, NH_4^+-driven proton release seems to be the sole mechanism to promote P solubilization. Asea et al. (1988) tested two fungi, *Penicillium bilaii* and *Penicillium fuscum*, for their ability to solubilize phosphate rock in the presence of NH_4^+ or without N addition, and showed that only *P. bilaii* maintained the ability to decrease the pH and mobilize P when no N was supplied.

In a study of *Pseudomonas fluorescens*, the form of C supply (e.g. glucose versus fructose) rather than N supply (e.g. NH_4^+ versus NO_3^-) had the greatest effect on proton release (Park et al. 2009). This indicates that for different species, different mechanisms are responsible for proton release, only partly depending on the presence of NH_4^+. Furthermore, Asea et al. (1988) reported a direct relationship between mobilized P and pH for *P. fuscum*, whereas *P. bilaii* solubilized more P than could be accounted for by pH change, indicating the presence of an additional solubilization mechanism.

Despite the demonstration of pH changes as a potential P solubilization mechanism, we must keep in mind that most published studies are carried out in vitro and that conditions in the field may not be as conducive to significant acidification occurring (e.g. due to a lack of labile N and C, which limits their activity in the bulk soil). Furthermore, particularly calcareous soils possess a high pH buffer capacity, which could limit the P-solubilizing effect. Gyaneshwar et al. (1999) showed that the numbers of culturable microorganisms inducing a pH-reduction zone in the growth medium were drastically reduced (from 10^4–10^6 to 10^2) when a buffered medium with phosphate rock was used as the sole P source. Furthermore, the buffered culture medium resulted in a reduced recovery of PSM, with only one out of ten soil samples containing PSM. This indicates that early estimates of effective PSM in soil (e.g. 10^3–10^6 g^{-1}; Kucey et al. 1989) might significantly overestimate reality. On the other hand, the majority of soil microbes cannot be cultured but might potentially be capable of solubilizing different forms of P_i, making real numbers of effective PSM in soil hard to predict. Nevertheless, since microbial abundance and activity is particularly high in the rhizosphere, the combined effort of proton (or hydroxide) extrusion by plants and microbes might be sufficient to increase P availability for both groups of organisms. Additionally, higher concentrations of CO_2 in the rhizosphere originated from plant root and microbial respiration might also contribute to a local drop in pH.

7.3.2 P Release Mediated by Organic Acid Anions

Acidification alone often does not fully explain the solubilization of mineral P (Asea et al. 1988; Whitelaw et al. 1999). LMW organic acid anions (carboxylates) released by microbes have been frequently found in P_i solubilization studies (Illmer et al. 1995; Reyes et al. 1999; Patel et al. 2008). Reported organic acid anions secreted by PSM include gluconic, 2-ketogluconic, citric, malic, malonic, oxalic, succinic, lactic, tartaric and glycolic acids (Kucey et al. 1989; Gyaneshwar et al. 2002). Though they are commonly referred to as organic "acids" in the literature, it has been pointed out by many authors that organic anions would be the more appropriate terminology (Hinsinger 2001; Jones et al. 2003; Parker et al. 2005). Due to the low acid dissociation constants (pK_a) values of many organic acid anions (Table 7.1), these LMW compounds are present as dissociated anions in the cytosol of cells (pH ~7), as well as in soil across a wide pH range. Nevertheless, organic

Table 7.1 Acid dissociation constants (pK_a) of some organic acids implicated in P solubilization

Acid	Number of carboxylic groups	pK_a 1	pK_a 2	pK_a 3
Citric	3	3.15	4.77	6.40
Malic	2	3.40	5.13	–
Oxalic	2	1.27	4.28	–
Gluconate	1	3.86	–	–

Table 7.2 Stability constants of some organic acid–metal complexes determined at a 1:1 metal–ligand ratio at 25°C and zero ionic strength

Organic anion	Number of carboxylic groups	Fe^{3+}	Al^{3+}	Ca^{2+}
Citrate	3	11.5	7.9	4.9
Malate	2	7.1	6.0	2.7
Oxalate	2	7.5	6.1	4.9
Gluconate	1	37.2	2.0	1.2

Adapted from Martell and Smith (1977) and Jones (1998)

anion release is often found to be accompanied by medium acidification, but it is important to note that it is not the organic anions that cause acidification, because they are already in their dissociated forms when released into the soil. It is rather the secretion of protons compensating the loss of net negative charges that can cause a drop in pH.

The P-solubilizing effect of organic anions is either caused by their negative charge or by their metal complexation properties (Table 7.2). Being anions, they can mobilize P_i from metal oxide surfaces via ligand exchange or by ligand enhanced dissolution of Fe or Al oxides and Ca phosphates, where the weakening of mineral bonds due to prior organic anion adsorption and/or chelation liberates the occluded P. Additionally, organic anion adsorption on metal oxide surfaces decreases the positive surface potential (Filius et al. 1997), facilitating the release of adsorbed P.

Gluconic and 2-ketogluconic acid are frequently reported to be released by bacteria (Rodriguez and Fraga 1999), and *Gluconacetobacter diazotrophicus* mutants lacking their production capacity have been shown to partially lose their P mobilization ability (Intorne et al. 2009). In contrast, gluconic, citric and oxalic acid are often found to be released by fungi (Reyes et al. 1999; Whitelaw et al. 1999). In general, tri-carboxylic anions such as citrate show a higher potential in solubilizing P_i than do di-carboxylic acids (gluconate, oxalate, etc.). There is increasing evidence that the mobilization of P_i by particularly citrate (other organic acid anions to a minor extent) is accompanied by a significant increase of Fe and Al in the solution, indicating that mineral dissolution is the main mobilizing mechanism (Gerke et al. 2000; Oburger and coworkers, unpublished data). Furthermore, oxalate has been shown to be particularly efficient in mobilizing P in calcareous soils (Ström et al. 2005) due to its high affinity to form Ca precipitates. To our knowledge, the behaviour of gluconic acid and 2-ketogluconic acid (unlike citric and oxalic acid) in soils has not yet been thoroughly investigated.

The P mobilization efficiency of organic anions released by microbes and plants is determined largely by soil properties (e.g. sorption sites, pH), as well as by the quantity and characteristics of the compounds released. Reported concentrations of organic acid anions released by cultured PSM range from a few micromolar (Illmer et al. 1995) to 100 mM (Reyes et al. 1999; Gyaneshwar et al. 1999; Patel et al. 2008). Detected concentrations in bacterial and fungal cultures differ greatly with incubation conditions (Illmer et al. 1995) and with different C sources (Reyes et al. 1999; Patel et al. 2008). It should be noted that organic acid anion exudation patterns might be completely different in soil (e.g. due to the lack of available C to synthesize the organic acid anions). In soil, sorption to metal oxide surfaces will decrease the free organic anion concentration in solution, making predictions of actual soil solution concentrations difficult. It has also been shown that the P-solubilizing effect of organic acid anions is significantly reduced in soils rich in carbonate or in Fe and Al (hydr)oxides (Ström et al. 2005; Oburger et al. 2009). Additionally, LMW carboxylates produced by microbes (and plant roots) can also serve as a labile C substrate for the microbial community, thus removing them from solution and reducing their P mobilization potential. The half-life of organic acid anions in soil typically ranges from 0.5 to 12 h, suggesting that organic acid anions need to be continually produced by PSM to maintain P dissolution over the lifetime of a crop (Jones et al. 2003). However, microbial breakdown of organic acid anions have been found to be drastically reduced in high-sorbing soils (Oburger et al. 2009; Oburger and Jones 2009; van Hees et al. 2003), indicating the importance of sorption processes to organic acid bioavailability and functional efficiency. Alongside the direct stimulation of microbial growth and P solubilization from inorganic sources, organic acid anions such as citrate, malate and oxalate can improve the solubility of P_o (e.g. phytate) making it more susceptible to enzymatic hydrolysis (Otani and Ae 1999; Tang et al. 2006).

7.3.3 Exopolysaccharide-Mediated Release of P

To our knowledge, the role of HMW (non-enzymatic) microbial exudates (i.e. mucilage, exopolysaccharides) in P solubilization from soil constituents has not yet been directly investigated in situ. Gaume et al. (2000) showed that maize root mucilage adsorbed onto synthetic ferrihydrite significantly decreased consecutive P adsorption, but the investigated mucilage components were not able to mobilize significant amounts of already adsorbed P. Nevertheless, microbial mucilages can have an indirect effect on P availability through their important role in soil aggregation and in increasing pore connectivity in soil (Aspiras et al. 1971), thereby facilitating soil water retention and movement (Ionescu and Belkin 2009). Exopolysaccharides (EPS) and biosurfactants are produced by microorganisms largely in response to biofilm formation and stress. Studies on microbially produced EPS have shown their ability to complex metals in soil ($Al^{3+} > Cu^{2+} > Zn^{2+} > Fe^{3+} > Mg^{2+} > K^{+}$; Ochoa-Loza et al. 2001), from which it can be deduced that they must in some way influence P solubility in soil. In pure culture, microbial EPS has been shown to stimulate the dissolution of tricalcium phosphate synergistically with organic acid anions (Yi et al. 2008). Furthermore, the rate of dissolution appears dependent on the microbial source and concentration of EPS. Although there is some evidence to suggest that EPS production is stimulated under P deficiency, this does not appear to be a universal phenomenon in bacteria (Dephilippis et al. 1991, 1993). Furthermore, EPS production seems to be more dependent on the rate of N supply than on available P (Danhorn and Fuqua 2003; Wielbo and Skorupska 2008).

7.3.4 Siderophore-Mediated Release of P

Siderophores are complexing agents that have a high affinity for iron and are produced by almost all microorganisms in response to iron deficiency. There are approximately 500 known siderophores, with the majority of them being used by a wide range of microorganisms and plants and some of them being exclusively used by the microbial species and strains that produce them (Crowley 2007). Many studies have reported the release of siderophores from PSM (Vassilev et al. 2006; Caballero-Mellado et al. 2007; Hamdali et al. 2008c); however, siderophore production has not been widely implicated as a P-solubilization mechanism. Considering the dominance of mineral dissolution over ligand exchange by organic acid anions as a P-solubilizing mechanism (Parker et al. 2005), the potential role of siderophores in enhancing P availability should be obvious. However, there is an impressive body of literature concerning Fe mobilization by microbial siderophores, but to the best of our knowledge only one study exists that has investigated the effect of microbial siderophores on P availability. More than two decades ago, Reid et al. (1985) investigated the ability to increase Fe and P diffusion of two siderophores (desferrioxamine-B, desferriferrichrome) and the iron-chelating agent EDDHA as compared to water using a root simulation technique. They found that desferriferrichrome increased P diffusion 13-fold compared to water whereas different concentrations of desferrioxamine-B exhibited only a small effect (Fig. 7.2). Considering the occurrence of Fe phosphates in soil and, probably even more important, the large P sorption capacity of Fe (hydr)oxides and considering the needs of microorganisms for Fe, the lack of knowledge about siderophore-enhanced P solubilization is quite surprising.

7.3.5 Enzyme-Mediated Release of P

The biochemical mineralization of P_o is mediated by either cell-wall-bound or free phosphatase enzymes, whose release is mainly driven by P demand. The role of these enzymes in P cycling is reviewed extensively elsewhere (Nannipieri et al. 2011); however, here we aim to present evidence relevant to the behaviour of PSM in soil. Typically, extracellular phosphatases rather than intracellular or membrane-

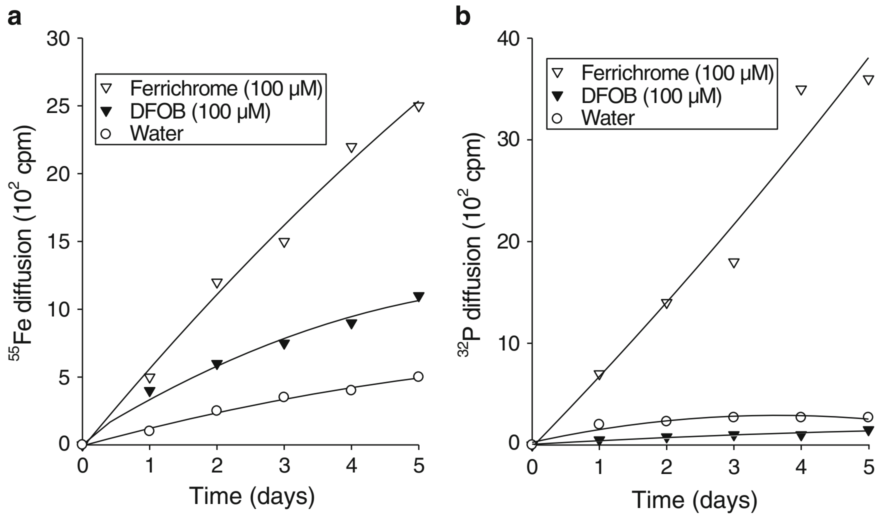


Fig. 7.2 Effects of the microbial siderophores desferrioxamine-B (*DFOB*) and ferrichrome on the diffusion of (**a**) ^{55}Fe or (**b**) ^{32}P towards a root in a low pH soil. Water is shown as a control. Fe and P were added to the soil as $FeCl_3$ and KH_2PO_4, respectively. Overall the results indicate that some microbial siderophores (e.g. ferrichrome) can stimulate both Fe and P solubilization in soil. Adapted from Reid et al. (1985)

bound phosphatases are thought to be responsible for inducing large changes in soil solution P concentration. However, experimental differentiation between exo- and endo-enzyme activity still remains problematic.

Phosphatases or phosphohydrolases describe a broad group of enzymes that catalyze the hydrolysis of both esters and anhydrides of H_3PO_4 (Tabatabai 1994). Its activities have been shown to be inhibited by increasing concentrations of orthophosphate (end-product) as well as other polyvalent anions (e.g. MoO_4^{2-}, AsO_4^{3-}) and high concentrations of several metals [Zn, Hg, Cu, Mn (II), Fe (II)]. Lower concentrations of divalent cations (e.g. Ca, Mg, Zn, Co) have been found to act as enzyme activators (Quiquampoix and Mousain 2005). Furthermore, adsorption to soil mineral or organomineral surfaces can also significantly alter enzyme conformation and activity. Although sorption to the solid phase reduces enzymatic activity, it can also help protect the enzymes from microbial attack or thermal inactivation (Huang et al. 2005). Typically, phosphatases are held most strongly to clay-sized particles. These results clearly show that the activity of enzymes released from PSM are not simply related to their release rate but are also strongly influenced by soil properties such as mineral composition, SOM and pH.

Among the variety of phosphatase enzyme classes released by PSM, phosphomonoesterases (often just called phosphatases) are the most abundant and best studied. Depending on their pH optima, these enzymes are divided into acid and alkaline phosphomonoesterases and both can be produced by PSM depending upon the external conditions (Kim et al. 1998; Jorquera et al. 2008). Typically, acid phosphatases predominate in acid soils, whereas alkaline phosphatases are more abundant in neutral and alkaline soils (Eivazi and Tabatabai 1977; Juma and Tabatabai 1977, 1988; Renella et al. 2006). Although plant roots can produce acid phosphatases they rarely produce large quantities of alkaline phosphatases, suggesting that this is a potential niche for PSM (Juma and Tabatabai 1988; Criquet et al. 2004). Laboratory studies have shown a gross mineralization potential of 1–4 mg P kg^{-1} soil day^{-1} (Lopez-Hernandez et al. 1998; Oehl et al. 2001b); however, so far it has proved impossible to distinguish between enzymatic (biochemical) and biological (microbial turnover) mineralization. It is also difficult to differentiate between root- and PSM-produced phosphatases (Richardson et al. 2009a, b) but some evidence suggests that phosphatases of microbial origin possess a greater affinity for P_o compounds than those derived from plant roots (Tarafdar et al. 2001). The relationship between PSM introduced into soil, phosphatase activity and the subsequent mineralization of P_o still remains poorly understood (Chen et al. 2003). Controversial results have been reported about the correlation between increased phosphatase activity and P_i concentrations in soil solution, with several authors reporting no relationship between the two (Criquet et al. 2002, 2004; Olander and Vitousek 2000). Other groups found a positive correlation (Tate and Salcedo 1988; Rojo et al 1990; George et al. 2002) and some observed a negative relation between P_i concentrations and phosphatase activity (Ali et al. 2009). Considering the interactive complexity of biological, chemical and biochemical processes of P mobilization in soils, these controversial findings are not surprising but highlight the uncertainty about predicting the benefits of PSM introduced into soil.

7.3.6 Release of P Held in P-Solubilizing Microorganisms

Although some of the P released by PSM will be captured by plants and other soil organisms, it is inevitable that a large proportion will be immobilized in the PSM. Release of P immobilized by PSM primarily occurs when cells die due to changes in environmental conditions, starvation or predation. Environmental changes, such as drying–rewetting or freezing–thawing, can result in so-called flush-events, a sudden increase in available P in the solution due to an unusually high proportion of microbial cell lysis (Turner et al. 2003; Butterly et al. 2009). Grierson et al. (1998) found that about 30–45% of microbial P (0.8–1 mg kg^{-1}) was released in a sandy spodosol in an initial flush after drying–rewetting cycles within the first 24 h. However, the availability of P after these flush events is also likely to be highly dependent on the P sorption properties of the soil because a large proportion could become subsequently immobilized on the solid phase.

P is also released when microorganisms are grazed by microbivores (e.g. nematodes, protozoa). Cole et al. (1978) showed that significant net P mineralization occurred within 1 week in the presence of bacterial grazers, whereas the absence of predators resulted in a constantly high P immobilization and no net P release after more than 3 weeks. SOM availability and its C:P ratio has also been shown to have a significant impact on microbial P immobilization/re-mobilization dynamics (Chauhan et al. 1979, 1981). Fresh organic matter inputs, particularly easily available C sources, tend to increase microbial P followed by a subsequent decline and increase in soil solution P if the substrate is depleted. However, the time elapsed between P immobilization and re-mineralization is determined by substrate quality and soil properties, with dynamics being less pronounced with more recalcitrant organic matter (Oehl et al. 2001a, b). Overall, however, the release of P held in PSM is poorly understood and certainly warrants further research.

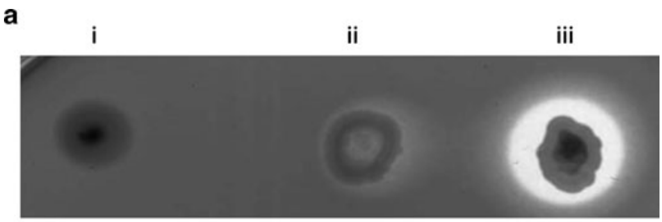
7.4 P-Solubilizing Organisms

7.4.1 Bacteria

It has been known for a long time that significant variation in the ability to solubilize P in soil exists within the bacterial community. Those that are known to enhance P availability includes species of the common soil bacteria *Pseudomonas*, *Azotobacter*, *Burkholderia*, *Bacillus* and *Rhizobium*. The recent isolation of a supersolubilizer (*Serratia marcescens*) has also suggested that selected bacteria could be used to develop environmentally friendly processes for fertilizer production (Ben Farhat et al. 2009). Recent work on *P. fluorescens* strains isolated from a range of agricultural fields has suggested that significant variation also exists within a single bacterial species (Browne et al. 2009). Interestingly, in the study by Browne et al. (2009) P fertilizer regime and crop type appeared to have little effect on the abundance of pseudomonads in the rhizosphere (Fig. 7.3). However, it was clear that significant variation exists within a single species linked to a single phylogenetic lineage. Identification of the underlying genetic mechanisms, combined with work to enhance their rhizosphere competence, may therefore provide more efficient biofertilizer agents. Evidence from *G. diazotrophicus* also suggests that bacteria may operate more than one P solubilization mechanism simultaneously (Intorne et al. 2009).

A study by Hariprasad et al. (2009) has also indicated that the selection for one bacterial trait may not always be the best use of inoculation technology. For example, they showed that rhizobacteria producing P-solubilizing indole acetic acid (PSIRB) may prove better than either P-solubilizing rhizobacteria (PSRB) or indole-acetic-acid-producing rhizobacteria (IRB) in isolation.

Many bacteria can also colonize the surface of mycorrhizal hyphae in soil (hyphosphere) and, therefore, may contribute indirectly to P uptake by mycorrhizas (and ultimately the plant) if they express P-solubilizing activity (Gonzalez-Chavez et al. 2008). These bacteria can be found embedded in hyphal mucilage, on the hyphoplane, between hyphal wall layers and even inside hyphae and are known to include several common PSM species (Mansfeld-Giese et al. 2002). Further work is required to elucidate their quantitative role in supplying P in comparison to the mycorrhizas.



b

Crop type	Barley							
Nutrient input	Low				High			
Field plot	1	2	3	4	5	6	7	8
Strong PS	10	8	1	4	3	5	3	8
Weak PS	22	16	13	16	23	21	20	17
No PS	15	23	33	27	21	21	24	22

Crop type	Wheat							
Nutrient input	Low				High			
Field plot	1	2	3	4	5	6	7	8
Strong PS	6	4	6	3	2	5	8	4
Weak PS	18	23	12	16	19	20	15	18
No PS	23	20	29	28	26	22	24	25

Fig. 7.3 P solubilization by different isolates of *Pseudomonas fluorescens* obtained from agricultural fields receiving either high or low inputs of fertilizer and under either a barley or wheat crop. (**a**) Plate assay demonstrating the three $Ca_3(PO_4)_2$ solubilization phenotypes used to classify isolates: (1) No $Ca_3(PO_4)_2$ solubilization, (2) weak $Ca_3(PO_4)_2$ solubilization and (3) strong $Ca_3(PO_4)_2$ solubilization. All 752 isolated from the field were then spot-inoculated (six repeats) on modified NBRIP agar, incubated for 6 days at 30°C. (**b**) Sampling strategy employed in the study and the numbers of isolates with each P solubilization (*PS*) phenotype (strong, weak, or no P solubilization activity) for each field plot. A total of 47 isolates were evaluated per plot. Adapted from Browne et al. (2009)

7.4.2 Non-mycorrhizal Fungi

A range of non-mycorrhizal soil fungi have been screened and selected for their P-solubilizing capacity. Of those identified, many are commonly found in agricultural soils such as *Penicillium* spp., *Mucor* spp. and *Aspergillus* spp., which has been shown to increase plant growth by 5–20% after inoculation (Dwivedi et al. 2004; Babana and Antoun 2006; Wakelin et al. 2007; Gunes et al. 2009). In addition, a range of *Trichoderma* spp. have also been identified and found to stimulate plant growth both in the laboratory and field (Rudresh et al. 2005). As with many ectomycorrhizal fungi, P-solubilizing non-mycorrhizal fungi (e.g. *Emericella* *rugulosa*, *Penicillium* spp.) appear to employ three strategies for mobilizing soil P, namely acidification of the soil, the release of organic acid anions (e.g. citrate, oxalate, gluconate) and the release of acid and alkaline phosphatases and phytase (Yadav and Tarafdar 2007; Xiao et al. 2009).

7.4.3 Actinomycetes

The P-solubilizing ability of actinomycetes has attracted interest in recent years because this group of soil organisms are not only capable of surviving in extreme environments (e.g. drought, fire etc.) but also possess other potential benefits (e.g. production of antibiotics and phytohormone-like compounds etc.) that could simultaneously benefit plant growth (Fabre et al. 1988; Hamdali et al. 2008a). Numerous P-solubilizing actinomycete species have been isolated from the rhizosphere (Barreto et al. 2008) and their presence in soil has been linked to enhanced efficiency of P use (El-Tarabily et al. 2008). Further, re-inoculation of soil with isolates selected for P solubilization has been shown to stimulate plant growth when supplied with phosphate rock (Hamdali et al. 2008b). Overall, however, the taxonomic groups and mechanisms of P solubilization within the actinomycetes remain poorly elucidated. A study by Hamdali et al. (2008c) has indicted that approximately 20% of actinomycetes can solubilize P, including those in the common genera *Streptomyces* and *Micromonospora*. In contrast to most fungi, most of the P-solubilizing actinomycetes identified to date do not appear to acidify the external medium. However, they do release large quantities of organic acid anions (e.g. citrate, formiate, lactate, malate, succinate), which are implicated in the P dissolution process (Hoberg et al. 2005), and possibly other P dissolution-promoting organic substances (Hamdali et al. 2010). After uptake, the P is stored in polyphosphate within the mycelium (Hamdali et al. 2010). One exception was reported by Abdulla (2009), who showed that P solubilization occurred concomitantly with acidification. A marine study has also suggested that actinomycetes may enhance P availability through the release of phosphatases; however, the significance of this in soil remains unknown (Sahu et al. 2007). Field trials inoculating P-poor soils have shown significant yield benefits, although whether this was due to P or other beneficial effects of the actinomyctes remains unknown. One potential application of actinomycetes is to harness their thermo-tolerant properties to enhance P availability during the composting of municipal and animal wastes (Chang and Yang 2009).

7.4.4 Protozoa

As protozoa represent a major mechanism for regulating bacterial and fungal numbers in soil, they both directly and indirectly influence soil P cycling (Alphei et al. 1996). If P-solubilizing microorganisms are introduced into soil, then protozoal grazing can be expected to dramatically reduce their effectiveness (Rosenberg et al. 2009; Pedersen et al. 2009). Although protozoa have the capacity to take up and assimilate SOM, ultimately making P more bioavailable, the likelihood of managing protozoal numbers in soil to harness this potential remains remote (due to difficulties and cost of mass production of a protozoal biofertilizer and uncertainty surrounding their potentially deleterious impact on microbial food webs in soil).

7.4.5 Mesofaunal Interactions

Mesofauna are known to enhance P availability and cycling in a range of soils; however, due to difficulties in their practical handling they are rarely used as a management tool to directly manipulate nutrient availability in agricultural soils (Lopez-Hernandez et al. 1993). Of significance, however, are the positive interactions that may occur between mesofauna and PSM in soil. For example, Sreenivas and Narayanasamy (2009) showed that the earthworm, *Eisenia fetida*, enhanced the P-solubilizing ability of the fungus *Aspergillus awamori*, resulting in increases in both soluble P_i and soluble P_o. The mechanistic basis for this response currently remains unknown. Similarly, Wan and Wong (2004) showed that earthworms promoted growth and phosphatase production in the P-solubilizing bacteria *Bacillus megaterium* and that this subsequently enhanced P_i availability in soil. Mba (1994, 1997) identified earthworm casts as being a particular site of enhanced PSM activity. In contrast, nematodes can be expected to dramatically reduce the amount of PSM inoculated into soil (Pedersen et al. 2009). Although this may reduce the effectiveness of P solubilization, it may also stimulate the release of P immobilized in the PSM. For more information on P mesofaunal interactions, the reader should consult Chapuis-Lardy et al. (2011).

7.5 Significance of PSM in the Field and Potential for Management

It is notable that the conclusions of many publications on the subject state that PSM hold great potential for development as a biofertilizer that can enhance soil fertility and promote plant growth. In addition, others state that PSM could constitute a novel and non-polluting biofertilizer product useful for the development of sustainable agriculture. Potentially this could be true, however, are we promising too much, too soon? For any PSM product to be a commercial success and to be accepted by farmers, a major perception change will be required within the agrochemical and agricultural industry. Typically, the industry is sceptical of products that cannot demonstrate a clear and positive benefit and that may be technically difficult to administer to fields. For PSM to be accepted requires that the technology is robust enough to be rolled out across wide geographical zones encompassing different soil types, crops and abiotic stresses. Furthermore, there must be a tangible economic benefit for farmer adoption because there are likely to be few legislative drivers to encourage farmer adoption of PSM technology. The costs associated with the environmental licensing of PSM products, particularly if they are genetically engineered, may also be prohibitive. In our view, PSM technology is still in its infancy and requires further optimization and refinement before commercial release, at least into developed world markets. Critical evidence in support of our view is presented below.

Typically, plant growth response trials with PSM have been carried out under controlled conditions that are rarely representative of those in the field (e.g. in small pots in the absence of mesofauna, under optimal conditions for plant growth and with a high inoculation dose). It is known from bitter experience with plant-growth-promoting rhizobacteria (PGPR) and N_2 fixation inoculants, however, that the positive growth responses obtained in the greenhouse often fail to reflect those subsequently obtained in the field, the latter of which can show zero or even negative yield responses (Streeter 1994). This is highlighted by Okon and Labandera-Gonzalez (1994), who concluded that of the published N_2-fixing *Azospirillum* field trials, 30–40% showed no positive response and, when a response was reported, the yield gain was very low (5–30% in comparison to uninoculated controls). This highlights the uncertain world of microbial inoculants. Success is largely determined by the ability of the inoculum to remain alive long enough in soil to have an appreciable benefit and to be able to compete with the indigenous microbial community (Denton et al. 2003). Despite this, some PSM isolates have been successfully translated from the laboratory to the field whilst others have failed (Fernández et al. 2007). For example, field studies have shown that PSM application can enhance foliar P concentration and increase efficiency of P use (Sud and Jatav 2007; Malboobi et al. 2009). This effect is often dramatic when undertaken with poor soils and low grade phosphate rock fertilizers (Sharma and Prasad 2003). Although not noted by Malboobi et al. (2009), their results revealed a high degree of dependence on geographical location and fertilizer dose. This context-specific view is also taken by Sahin et al. (2004), who showed that the beneficial effects of PSM on plant growth varied significantly depending on environmental conditions, bacterial strains, and plant and soil conditions. The success of PSM has also been shown to be influenced by the use of agrochemicals and the addition of organic fertilizers (Sutaliya and Singh 2005; Das and Debnath 2006). This suggests that blanket recommendation for farmers will be difficult to formulate and that depressions in yield may also be possible, an outcome clearly not welcomed by farmers and that will undermine adoption of the technology. It is also clear that PSM cannot provide a complete replacement for conventional fertilizers but simply a way of reducing our reliance on them (i.e. the use of PSM as part of an integrated nutrient management regime; Jilani et al. 2007; Sharma et al. 2009). Overall, across a range of field trials, PSM application typically results in marginal increases in crop yield

Table 7.3 Effect of the presence (+) and absence (−) of the P-solubilizing microorganism *Penicillium radicum* inoculation on grain yield and protein levels in wheat grown under field conditions

	Grain yield (tons ha^{-1})		Seed protein (kg ha^{-1})	
	(−)	(+)	(−)	(+)
P applied (kg/ha)				
0	2.1	2.3	213	226
5	2.6	3.1	254	299
10	3.2	3.3	328	315
15	3.3	4.1	307	407
20	3.5	4.1	379	375
Statistical analysis				
Least significant difference ($P = 0.05$)				
Phosphate	0.6		64	
P. radicum	0.4		41	
Significance of effects				
Phosphate	$P < 0.001$		$P < 0.001$	
P. radicum	$P < 0.05$		n.s.	
P × *P. radicum*	n.s.		n.s.	

P fertilizer was added as single superphosphate. Values represent mean ($n = 3$). *n.s.* indicates not significant ($P > 0.05$). Adapted from Whitelaw et al. (1997)

(0–20%) (Table 7.3; Sahin et al. 2004; Chen et al. 2008). Although there are only a few reports of the potential savings, some studies have speculated that inoculation with PSM may be equivalent to a saving of between 100 and 150 kg P ha^{-1} in some high-intensity horticultural production systems (Gunes et al. 2009). The potential P savings in more conventional cropping systems, however, are expected to be much less. Cost saving may also be made if the PSM repress fungal diseases, thereby reducing the application of fungicides (Khan and Khan 2001). In a study in India, the application of PSM induced yield increases of 0.1–0.2 tons ha^{-1} in rice and 0.1–0.5 tons ha^{-1} in wheat (Dwivedi et al. 2004).

In the case of legumes in particular there is great potential to co-inoculate with N_2-fixing *Rhizobium* sp. and PSM. Where this has been attempted, synergistic effects have been reported whereby the co-inoculants enhance crop nodulation, growth and nutrient uptake and improve the use and availability of added chemical fertilizers (Sahin et al. 2004; Dadhich et al. 2006; Elkoca et al. 2008; Rugheim and Abdelgani 2009; Sammauria et al. 2009). This co-inoculation improved yield by as much as 30% in soybean and 10% in sugar beet and barley (Sahin et al. 2004; Govindan and Thirumurugan 2005).

Similarly, field trials have indicated that synergistic effects may exist between arbuscular mycorrhizal fungi (AMF) and PSM with co-application consistently increasing crop growth, foliar N and P concentrations, grain quality and yield (Khan and Zaidi 2007). In one of the most successful trials undertaken in Mali, co-inoculating seeds with PSM and AMF showed that it was possible to obtain wheat grain yields comparable to those produced from conventional inorganic N and P fertilizers (Babana and Antoun 2006). However, the uncertainly of the approach is highlighted by Wu et al. (2005), who showed that AMF inhibited any PSM effect.

One of the major problems with interpreting field trial data is that the trials are rarely matched with a mechanistic understanding of soil P cycling (i.e. measurements of P availability and rates of cycling). Consequently, it is often difficult to decide whether any observed increase in yield is due to a direct P-solubilizing effect or some other effect (e.g. repression of pathogens, microbial production of indole acetic acid or siderophores). This is highlighted in a classic study by deFreitas et al. (1997), who showed that P solubilization was not the main mechanism responsible for the positive growth response upon inoculation with PSM. Specifically, PSM might increase root growth and/or mycorrhizal colonization, which subsequently enhances soil exploration and subsequent P capture (Richardson et al. 2009a, b). A more thorough review of the benefits of PGPR on root growth and function is provided in Vessey (2003) and Lugtenberg and Kamilova (2009).

As discussed by Oberson et al. (2011), there is also potential to manage the agronomic regime to influence P dynamics in soil. There is clear evidence that some of these strategies (e.g. organic residue addition) can directly affect the size, activity and structure of the microbial community and its associated P-solubilizing potential (Bolton et al. 1985; Hu et al. 2009). For example, organic manures and composts typically cause an initial stimulation in microbial activity and in P_o and P_i solubilization activity in soil (Takeda et al. 2009; Hu et al. 2009). However, longer-term trials have shown that organic residues may in some cases reduce biological P solubilization (Martens et al. 1992; Garcia-Gil et al. 2000). Similarly, crop types could be used that are known to promote PSM activity in soil. For example, Oliveira et al. (2009) provided evidence to suggest that maize cultivar varieties may differentially stimulate PSM in soil. Similarly, Souchie and Abboud (2007) have shown a soil type × genotype interaction regulating the abundance and type of PSM in pigeonpea. This opens the potential for influencing PSM activity in soil; however, translating this information into a reliable means of enhancing crop P acquisition remains a long-term goal.

7.6 Conclusions and Future Research Directions

This chapter has highlighted the wide range of non-mycorrhizal microorganisms that possess an innate capacity to enhance P cycling in soil. Presumably, this functional group of microorganisms use their capacity to mobilize P to gain a competitive advantage in an environment where resources can be growth limiting. There appears to be two main strategies used by PSM for enhancing P availability in soil, namely (1) the enhanced dissolution of P-containing minerals through a combination of soil acidification and the release of metal complexing agents (predominantly organic acid anions and siderophores), and (2) the enzymatic breakdown and subsequent release of P from organic P. In terms of P cycling in natural environments, it is likely that strategy (2) is most important in terms of the annual flux of P through the plant–soil system. However, in highly P-limiting environments it is likely that strategy (1) becomes more important for mobilizing highly insoluble mineral-bound P. Furthermore, P temporarily immobilized in the microbial biomass may leave a significant proportion of P_o in a potentially bioavailable form. Due to the in vitro procedures used to select PSM from soil (e.g. Petri-dish culture), most research has focussed on the organisms that can accelerate the dissolution of phosphate rock. Rarely are PSM isolated that have the capacity to mobilize both organic and inorganic P (including Al- and Fe-P) in soil. To a large extent, this limits their ability to work across a wide range of soil types with vastly different properties. In terms of sustainable agriculture there is an urgent need to find new ways to make soil P more available to crop plants. Consequently, PSM isolated in the laboratory have been multiplied ex situ and then inoculated back into soil, mostly in greenhouse studies and often at very high dose rates. Typically, inoculation trials in pots show higher foliar P concentrations and a positive growth response, especially when conditions are optimized to show an effect. However, the results from field application of PSM are much more erratic. This is because many PSM are not selected for their rhizosphere competence or for their ability to survive extreme conditions, which are typical in many P-limiting soils. One major problem when interpreting the results of PSM field trials is the lack of consideration or quantification of P dynamics in the soil. Therefore, it remains difficult to differentiate between a direct P effect and an indirect effect induced by the addition of large amounts of PSM into soil (e.g. suppression of pathogens, stimulation of SOM cycling upon the death of the PSM inoculum). In addition, the indirect effects of PSM on plant growth (e.g. a hormone-induced stimulation of root growth or suppression of root pathogens that are not linked to any P-solubilization mechanism) also deserve more attention (Richardson et al. 2009b). If PSM are to be adopted by industry and farmers, a greater mechanistic understanding of PSM behaviour in soil is required. Specifically, a thorough understanding is required of their rhizosphere ecology, genetic stability and the mechanisms associated with enhancing P availability in soils and with promoting plant growth .

References

Abdulla H (2009) Bioweathering and biotransformation of granitic rock minerals by actinomycetes. Microb Ecol 58:753–761

Achat DL, Bakker MR, Morel C (2009) Process-based assessment of phosphorus availability in a low phosphorus sorbing forest soil using isotopic dilution methods. Soil Sci Soc Am J 73:2131–2142

Ajiboye B, Hu Y, Flaten DN (2007) Phosphorus speciation of sequential extracts of organic amendments using nuclear magnetic resonance and X-ray absorption near-edge structure spectroscopies. J Environ Qual 36:1563–1576

Alexander M (1977) Introduction to soil microbiology, 2nd edn. Wiley, New York, p 467

Ali MA, Louche J, Legname E, Duchemin M, Plassard C (2009) *Pinus pinaster* seedlings and their fungal symbionts show high plasticity in phosphorus acquisition in acidic soils. Tree Physiol 29:1587–1597

Alphei J, Bonkowski M, Scheu S (1996) Protozoa, Nematoda and Lumbricidae in the rhizosphere of *Hordelymus europaeus* (Poaceae): faunal interactions, response of microorganisms and effects on plant growth. Oecologia 106:111–126

Anderson G (1961) Estimation of purines and pymiridines in soil humic acid. Soil Sci 91:156–161

Anderson G, Malcolm RE (1974) The nature alkali-soluble soil organic phosphates. J Soil Sci 13:216–224

Arcand MM, Schneider KM (2006) Plant- and microbial-based mechanisms to improve the agronomic effectiveness of phosphate rock: a review. Ann Braz Acad Sci 78:791–807

Aria MM, Lakzian A, Haghnia GH, Berenji AR, Besharati H, Fotovat A (2010) Effect of *Thiobacillus*, sulfur, and vermicompost on the water-soluble phosphorus of hard rock phosphate. Bioresour Technol 101:551–554

Arvieu JC, Leprince F, Plassard C (2003) Release of oxalate and protons by ectomycorrhizal fungi in response to P-deficiency and calcium carbonate in nutrient solution. Ann For Sci 60: 815–821

Asea PEA, Kucey RMN, Stewart JWB (1988) Inorganic phosphate solubilization by two *Penicillium* species in solution culture and soil. Soil Biol Biochem 20:459–464

Aspiras RB, Allen ON, Harris RF, Chesters G (1971) The role of microorganisms in the stabilization of soil aggregates. Soil Biol Biochem 3:347–353

Babana AH, Antoun H (2006) Effect of Tilemsi phosphate rock-solubilizing microorganisms on phosphorus uptake and yield of field-grown wheat (*Triticum aestivum* L.) in Mali. Plant Soil 287:51–58

Banik S, Dey BK (1982) Available phosphate content of an alluvial soil as influenced by inoculation of some isolated phosphate solubilizing bacteria. Plant Soil 69:353–364

Barreto TR, da Silva ACM, Soares ACF, de Souza JT (2008) Population densities and genetic diversity of Actinomycetes associated to the rhizosphere of *Theobroma cacao*. Braz J Microbiol 39:464–470

Ben Farhat M, Farhat A, Bejar W, Kammoun R, Bouchaala K, Fourati A, Antoun H, Bejar S, Chouayekh H (2009) Characterization of the mineral phosphate solubilizing activity of *Serratia marcescens* CTM 50650 isolated from the phosphate mine of Gafsa. Arch Microbiol 191:815–824

Benmore RA, Coleman ML, McArthur JM (1983) Origin of sedimentary francolite from its sulphur and carbon composition. Nature 302:516–518

Blake L, Mercik S, Koerschens M, Moskal S, Poulton PR, Goulding KWT, Weigel A, Powlson DS (2000) Phosphorus content in soil, uptake by plants and balance in three European long-term field experiments. Nutr Cycl Agroecosys 56:263–275

Bolton H, Elliott LF, Papendick RI, Bezdicek DF (1985) Soil microbial biomass and selected soil enzyme-activities – effect of fertilization and cropping practices. Soil Biol Biochem 17: 297–302

Browne P, Rice O, Miller SH, Burke J, Dowling DN, Morrissey JP, O'Gara F (2009) Superior inorganic phosphate solubilization is linked to phylogeny within the *Pseudomonas fluorescens* complex. Appl Soil Ecol 43:131–138

Bünemann E, Bossio DA, Smithson PC, Frossard E, Oberson A (2004) Microbial community composition and substrate use in a highly weathered soil as affected by crop rotation and P fertilization. Soil Biol Biochem 36:889–901

Bünemann EK, Prusisz B, Ehlers K (2011) Characterization of phosphorus forms in soil microorganisms. In: Bünemann E, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_2

Butterly CR, Bünemann EK, McNeill AM, Baldock JA, Marschner P (2009) Carbon pulses but not phosphorus pulses are related to decrease in microbial biomass during repeated drying and rewetting of soils. Soil Biol Biochem 41:1406–1416

Caballero-Mellado J, Onofre-Lemus J, Estrada-de los Santos P, Martinez-Aguilar L (2007) The tomato rhizosphere, an environment rich in nitrogen-fixing *Burkholderia* species with capabilities of interest for agriculture and bioremediation. Appl Environ Microbiol 73:5308–5319

Casarin V, Plassard C, Souche G, Arvieu JC (2003) Quantification of oxalate ions and protons released by ectomycorrhizal fungi in rhizosphere soil. Agronomie 23:461–469

Celi L, Barberis E (2005) Abiotic stabilization of organic phosphorus in the environment. In: Turner BL, Frossard E, Baldwin DS (eds) Organic phosphorus in the environment. CABI, Wallingford, pp 113–132

Chang CH, Yang SS (2009) Thermo-tolerant phosphate-solubilizing microbes for multi-functional biofertilizer preparation. Bioresour Technol 100:1648–1658

Chapuis-Lardy L, Le Bayon R-C, Brossard M, López-Hernández D, Blanchart E (2011) Role of soil macrofauna in phosphorus cycling. In: Bünemann E, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_8

Chauhan BS, Stewart JWB, Paul EA (1979) Effect of carbon additions on soil labile inorganic, organic and microbially held phosphate. Can J Soil Sci 59:387–396

Chauhan BS, Stewart JWB, Paul EA (1981) Effect of labile inorganic-phosphate status and organic-carbon additions on the microbial uptake of phosphorus in soils. Can J Soil Sci 61:373–385

Chen CR, Condron LM, Davis MR, Sherlock RR (2003) Seasonal changes in soil phosphorus and associated microbial properties under adjacent grassland and forest in New Zealand. For Ecol Manage 117:539–557

Chen ZX, Ma S, Liu L (2008) Studies on phosphorus solubilizing activity of a strain of phosphobacteria isolated from chestnut type soil in China. Bioresour Technol 99:6702–6707

Clarholm M (1993) Microbial biomass P, labile P and acid-phosphatase-activity in the humus layer of a spruce forest, after repeated additions of fertilizers. Biol Fertil Soils 16:287–292

Cole CV, Elliot ET, Hunt HW, Coleman DC (1978) Trophic interactions in soil as they affect energy and nutrient dynamics. V. Phosphorus transformations. Microb Ecol 4:381–387

Cordell D, Drangert JO, White S (2009) The story of phosphorus: global food security and food for thought. Glob Environ Change 19:292–305

Criquet S, Tagger S, Vogt G, Le Petit J (2002) Endoglucanase and β-glycosidase activities in an evergreen oak litter: annual variation and regulating factors. Soil Biol Biochem 34:1111–1120

Criquet S, Ferre E, Farner EM, Le Petit J (2004) Annual dynamics of phosphatase activities in an evergreen oak litter – influence of biotic and abiotic factors. Soil Biol Biochem 36:1111–1118

Crowley DE (2007) Microbial siderophores in the plant rhizosphere. In: Barton LL, Abadia J (eds) Iron nutrition in plants and rhizospheric microorganisms. Springer, Dordrecht, pp 169–198

Dadhich SK, Somani LL, Verma A (2006) Improved soybean yield, nutrient uptake and P enrichment in soil due to co-inoculation of phosphate solubilizing bacteria and VAM fungi in a clay loam soil. Indian J Microbiol 46:405–407

Dalal RC (1977) Soil organic phosphorus. Adv Agron 29:83–117

Danhorn T, Fuqua C (2003) The effect of phosphorus concentration on the adherence of *Agrobacterium tumefaciens* to surfaces. In: Abstracts of the general meeting of the American Society for Microbiology 103. pp I–100

Das AC, Debnath A (2006) Effect of systemic herbicides on N_2-fixing and phosphate solubilizing microorganisms in relation to availability of nitrogen and phosphorus in paddy soils of West Bengal. Chemosphere 65:1082–1086

deFreitas JR, Banerjee MR, Germida JJ (1997) Phosphate-solubilizing rhizobacteria enhance the growth and yield but not phosphorus uptake of canola (*Brassica napus* L). Biol Fertil Soils 24:358–364

Denton MD, Reeve WG, Howieson JG, Coventry DR (2003) Competitive abilities of common field isolates and a commercial strain of *Rhizobium leguminosarum* bv. *trifolii* for clover nodule occupancy. Soil Biol Biochem 35:1039–1048

Dephilippis R, Sili C, Tassinato G, Vincenzini M, Materassi R (1991) Effects of growth-conditions on exopolysaccharide production by *Cyanospira capsulata*. Bioresour Technol 38:101–104

Dephilippis R, Margheri MC, Pelosi E, Ventura S (1993) Exopolysaccharide production by a unicellular cyanobacterium isolated from a hypersaline habitat. J Appl Phycol 5:387–394

Dwivedi BS, Singh VK, Dwivedi V (2004) Application of phosphate rock, with or without *Aspergillus awamori* inoculation, to meet phosphorus demands of rice-wheat systems in the Indo-Gangetic plains of India. Aust J Exp Agric 44:1041–1050

Eivazi F, Tabatabai MA (1977) Phosphatases in soils. Soil Biol Biochem 9:167–172

Elkoca E, Kantar F, Sahin F (2008) Influence of nitrogen fixing and phosphorus solubilizing bacteria on the nodulation, plant growth, and yield of chickpea. J Plant Nutr 31:157–171

El-Tarabily KA, Nassar AH, Sivasithamparam K (2008) Promotion of growth of bean (*Phaseolus vulgaris* L.) in a calcareous soil by a phosphate-solubilizing, rhizosphere-competent isolate of *Micromonospora endolithica*. Appl Soil Ecol 39:161–171

Fabre B, Armau E, Etienne G, Legendre F, Tiraby G (1988) A simple screening method for insecticidal substances from actinomycetes. J Antibiot 41:212–219

Fernández LA, Zalba P, Gomez MA, Sagardoy MA (2007) Phosphate-solubilization activity of bacterial strains in soil and their effect on soybean growth under greenhouse conditions. Biol Fertil Soils 43:805–809

Filius JD, Hiemstra T, Van Riemsdijk WH (1997) Adsorption of small weak organic acids on goethite: modeling of mechanisms. J Colloid Interface Sci 195:368–380

Foster RC, Dormaar JF (1991) Bacteria-grazing amebas in situ in the rhizosphere. Biol Fertil Soils 11:83–87

Foth HD, Ellis BG (1997) Soil fertility. CRC, Boca Raton

Frossard E, Skrabal P, Sinaj S, Bangerter F, Traore O (2002) Forms and exchangeability of inorganic phosphate in composted solid organic wastes. Nutr Cycl Agroecosys 62:103–113

Frossard E, Achat DL, Bernasconi SM, Bünemann EK, Fardeau J-C, Jansa J, Morel C, Rabeharisoa L, Randriamanantsoa L, Sinaj S, Tamburini F, Oberson A (2011) The use of tracers to investigate phosphate cycling in soil–plant systems. In: Bünemann E, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_3

Gächter R, Meyer JS (1993) The role of microorganisms in mobilization and fixation in sediments. Hydrobiologia 253:103–121

Garcia-Gil JC, Plaza C, Soler-Rovira P, Polo A (2000) Long-term effects of municipal solid waste compost application on soil enzyme activities and microbial biomass. Soil Biol Biochem 32:1907–1913

Gaume A, Weidler PG, Frossard E (2000) Effect of maize root mucilage on phosphate adsorption and exchangeability on a synthetic ferrihydrite. Biol Fertil Soils 31:525–532

George TS, Gregory PJ, Robinson JS, Buresh RJ (2002) Changes in phosphorus concentrations and pH in the rhizosphere of some agroforestry and crop species. Plant Soil 246:65–73

Gerke J, Beißner L, Römer W (2000) The quantitative effect of chemical phosphate mobilization by carboxylate anions on P uptake by a single root. I. The basic concept and determination of soil parameters. J Plant Nutr Soil Sci 163:207–212

Giller KE, Witter E, McGrath SP (1998) Toxicity of heavy metals to microorganisms and microbial processes in agricultural soils: a review. Soil Biol Biochem 30:1389–1414

Gonzalez-Chavez MDA, Newsam R, Linderman R, Dodd J, Valdez-Carrasco JM (2008) Bacteria associated with the extraradical mycelium of an arbuscular mycorrhizal fungus in an As/Cu polluted soil. Agrociencia 42:1–10

Govindan K, Thirumurugan V (2005) Synergistic association of *Rhizobium* with phosphate-solubilizing bacteria under different sources of nutrient supply on productivity and soil fertility in soybean (*Glycine max*). Indian J Agron 50:214–217

Grierson PF, Comerford NB, Jokela EJ (1998) Phosphorus mineralization kinetics and response of microbial phosphorus to drying and rewetting in a Florida Spododol. Soil Biol Biochem 30:1323–1331

Gunes A, Ataoglu N, Turan M, Esitken A, Ketterings QM (2009) Effects of phosphate-solubilizing microorganisms on strawberry yield and nutrient concentrations. J Plant Nutr Soil Sci 172:385–392

Gyaneshwar P, Parekh LJ, Archana G, Poole PS, Collins MD, Huston RA, Naresh Kumar G (1999) Involvement of a phosphate starvation inducible glucose dehydrogenase in soil phosphate solubilization by *Enterobacter asburiae*. FEMS Microbiol Lett 171:223–229

Gyaneshwar P, Naresh Kumar G, Parekh LJ, Poole PS (2002) Role of soil microorganisms in improving P nutrition of plants. Plant Soil 245:83–93

Hamdali H, Hafidi M, Virolle MJ, Ouhdouch Y (2008a) Growth promotion and protection against damping-off of wheat by two rock phosphate solubilizing actinomycetes in a P-deficient soil under greenhouse conditions. Appl Soil Ecol 40:510–517

Hamdali H, Hafidi M, Virolle MJ, Ouhdouch Y (2008b) Rock phosphate-solubilizing Actinomycetes: screening for plant growth-promoting activities. World J Microbiol Biotechnol 24:2565–2575

Hamdali H, Bouizgarne B, Hafidi M, Lebrihi A, Virolle MJ, Ouhdouch Y (2008c) Screening for rock phosphate solubilizing Actinomycetes from Moroccan phosphate mines. Appl Soil Ecol 38:12–19

Hamdali H, Smirnov A, Esnault C, Ouhdouch Y, Virolle MJ (2010) Physiological studies and comparative analysis of rock phosphate solubilization abilities of Actinomycetales originating from Moroccan phosphate mines and of *Streptomyces lividans*. Appl Soil Ecol 44:24–31

Hariprasad P, Navya HM, Nayaka SC, Niranjana SR (2009) Advantage of using PSIRB over PSRB and IRB to improve plant health of tomato. Biol Control 50:307–316

Harris WG (2002) Phosphate minerals. In: Dixon JB, Schulze DG (eds) Soil mineralogy with environmental applications, SSSA book series 7. SSSA, Madison, pp 637–665

Harrison AF (1987) Soil organic phosphorus: a review of world literature. CABI, Wallingford

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

Hoberg E, Marschner P, Lieberei R (2005) Organic acid exudation and pH changes by *Gordonia* sp and *Pseudomonas fluorescens* grown with P adsorbed to goethite. Microbiol Res 160:177–187

Hu J, Lin X, Wang J, Chu H, Yin R, Zhang J (2009) Population size and specific potential of P-mineralizing and -solubilizing bacteria under long-term P-deficiency fertilization in a sandy loam soil. Pedobiologia 53:49–58

Huang Q, Liang W, Cai P (2005) Adsorption, desorption and activities of acid phosphatase on various colloidal particles from an Ultisol. Colloid Surface B 45:209–241

Huang XL, Chen Y, Shenker M (2008) Chemical fractionation of phosphorus in stabilized biosolids. J Environ Qual 37:1949–1958

Illmer P, Schinner F (1992) Solubilization of inorganic phosphates by microorganisms isolated from forest soils. Soil Biol Biochem 24:389–395

Illmer P, Barbato A, Schinner F (1995) Solubilization of hardly-soluble $AlPO_4$ with P-solubilizing microorganisms. Soil Biol Biochem 27:265–270

Intorne AC, de Oliveira MVV, Lima ML, da Silva JF, Olivares FL, de Souza GA (2009) Identification and characterization of *Gluconacetobacter diazotrophicus* mutants defective in the solubilization of phosphorus and zinc. Arch Microbiol 191:477–483

Ionescu M, Belkin S (2009) Overproduction of exopolysaccharides by an *Escherichia coli* K-12 rpoS mutant in response to osmotic stress. Appl Environ Microbiol 75:483–492

Jansa J, Finlay R, Wallander H, Smith FA, Smith SE (2011) Role of mycorrhizal symbioses in phosphorus cycling. In: Bünemann E, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_6

Jilani G, Akram A, Ali RM, Hafeez FY, Shamsi IH, Chaudhry AN, Chaudhry AG (2007) Enhancing crop growth, nutrients availability, economics and beneficial rhizosphere microflora through organic and biofertilizers. Ann Microbiol 57:177–184

Joergensen RG, Scheu S (1999) Response of soil microorganisms to the addition of carbon, nitrogen and phosphorus in a forest Rendzina. Soil Biol Biochem 31:859–866

Jones DL (1998) Organic acids in the rhizosphere – a critical review. Plant Soil 205:25–44

Jones DL, Dennis PG, Owen AG, van Hees PAW (2003) Organic acid behaviour in soils misconceptions and knowledge gaps. Plant Soil 248:31–41

Jorquera MA, Hernandez MT, Rengel Z, Marschner P, Mora MD (2008) Isolation of culturable phosphobacteria with both phytate-mineralization and phosphate-solubilization activity from the rhizosphere of plants grown in a volcanic soil. Biol Fertil Soils 44:1025–1034

Juma NG, Tabatabai MA (1977) Effects of trace-elements on phosphatase-activity in soils. Soil Sci Soc Am J 41:343–346

Juma NG, Tabatabai MA (1988) Hydrolysis of organic phosphates by corn and soybean roots. Plant Soil 107:31–38

Kao PH, Huang CC, Hseu ZY (2006) Response of microbial activities to heavy metals in a neutral loamy soil treated with biosolid. Chemosphere 64:63–70

Khan MR, Khan SM (2001) Biomanagement of Fusarium wilt of tomato by the soil application of certain phosphate-solubilizing microorganisms. Int J Pest Manage 47:227–231

Khan MS, Zaidi A (2007) Synergistic effects of the inoculation with plant growth-promoting rhizobacteria and an arbuscular mycorrhizal fungus on the performance of wheat. Turk J Agric For 31:355–362

Kim KY, Jordan D, McDonald GA (1998) *Enterobacter agglomerans*, phosphate solubilizing bacteria, and microbial activity in soil: effect of carbon sources. Soil Biol Biochem 30: 995–1003

Kucey RMN, Jenzen HH, Leggett ME (1989) Microbially mediated increases in plant available phosphorus. Adv Agron 42:199–228

Lopez-Hernandez D, Lavelle P, Fardeau JC, Nino M (1993) Phosphorus transformations in two P-sorption contrasting tropical soils during transit through *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta). Soil Biol Biochem 25:789–792

Lopez-Hernandez D, Bossard M, Frossard E (1998) P-isotopic exchange values in relation to Po mineralization in soils with very low P-sorbing capacities. Soil Biol Biochem 30:1663–1670

Lugtenberg B, Kamilova F (2009) Plant-growth-promoting rhizobacteria. Annu Rev Microbiol 63:541–556

Maguire RO, Hesterberg D, Gernat A, Anderson K, Wineland M, Grimes J (2006) Liming poultry manures to decrease soluble phosphorus and suppress the bacteria population. J Environ Qual 35:849–857

Malboobi MA, Behbahani M, Madani H, Owlia P, Deljou A, Yakhchali B, Moradi M, Hassanabadi H (2009) Performance evaluation of potent phosphate solubilizing bacteria in potato rhizosphere. World J Microbiol Biotechnol 25:1479–1484

Mansfeld-Giese K, Larsen J, Bodker L (2002) Bacterial populations associated with mycelium of the arbuscular mycorrhizal fungus *Glomus intraradices*. FEMS Microbiol Ecol 41:133–140

Martell AE, Smith RM (1977) Critical stability constants. Other organic ligands, vol 3. Plenum, New York

Martens DA, Johanson JB, Frankenberger WT (1992) Production and persistence of soil enzymes with repeated addition of organic residues. Soil Sci 153:53–61

Mba CC (1994) Field studies on two rock phosphate solubilizing Actinomycete isolates as biofertilizer sources. Environ Manage 18:263–269

Mba CC (1997) Rock phosphate solubilizing *Streptosporangium* isolates from casts of tropical earthworms. Soil Biol Biochem 29:381–385

McGill WB, Cole CV (1981) Comparative aspects of cycling of organic C, N, S and P through soil organic matter. Geoderma 26:267–268

Nannipieri P, Giagnoni L, Landi L, Renella G (2011) Role of phosphatase enzymes in soil. In: Bünemann E, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_9

Oberson A, Joner EJ (2005) Microbial turnover of phosphorus in soil. In: Turner BL, Frossard E, Baldwin DS (eds) Organic phosphorus in the environment. CABI, Wallingford, pp 133–164

Oberson A, Pypers P, Bünemann EK, Frossard E (2011) Management impacts on biological phosphorus cycling in cropped soils. In: Bünemann E, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_17

Oburger E, Jones DL (2009) Substrate mineralization studies in the laboratory show different microbial C partitioning dynamics than in the field. Soil Biol Biochem 41:1951–1956

Oburger E, Kirk GJD, Wenzel WW, Puschenreiter M, Jones DL (2009) Interactive effects of organic acids in the rhizosphere. Soil Biol Biochem 41:449–457

Ochoa-Loza FJ, Artiola JF, Maier RM (2001) Stability constants for the complexation of various metals with a rhamnolipid biosurfactant. J Environ Qual 30:479–485

Odongo NE, Hyoung-Ho K, Choi HC, van Straaten P, McBride BW, Romney DL (2007) Improving rock phosphate availability through feeding, mixing and processing with composting manure. Bioresour Technol 98:2911–2918

Oehl F, Oberson A, Probst M, Fliessbach A, Roth HR, Frossard E (2001a) Kinetics of microbial phosphorus uptake in cultivated soils. Biol Fertil Soils 34:31–41

Oehl F, Oberson A, Sinaj S, Frossard E (2001b) Organic phosphorus mineralization studies using isotopic dilution techniques. Soil Sci Soc Am J 65:780–787

Okon Y, Labandera-Gonzalez CA (1994) (1994) Agronomic applications of *Azospirillum* – an evaluation of 20 years worldwide field inoculation. Soil Biol Biochem 26:1591–1601

Olander LP, Vitousek PM (2000) Regulation of soil phosphatase and chitinase activity by N and P availability. Biogeochemistry 49:175–190

Oliveira CA, Alves VMC, Marriel IE, Gomes EA, Scotti MR, Carneiro NP, Guimaraes CT, Schaffert RE, Sa NMH (2009) Phosphate solubilizing microorganisms isolated from rhizosphere of maize cultivated in an oxisol of the Brazilian Cerrado Biome. Soil Biol Biochem 41:1782–1787

Otani T, Ae N (1999) Extraction of organic phosphorus in Andosols by various methods. Soil Sci Plant Nutr 45:151–161

Park KH, Lee CY, Son HJ (2009) Mechanism of insoluble phosphate solubilization by *Pseudomonas fluorescens* RAF15 isolated from ginseng rhizosphere and its plant growth-promoting activities. Lett Appl Microbiol 49:222–228

Parker DR, Reichmann SM, Crowley DE (2005) Metal chelation in the rhizosphere. In: Zobel RW (ed) Roots and soil management: interactions between roots and the soil. Agronomy monograph no. 48. American Society of Agronomy, Madison, pp 57–93

Patel DK, Archana G, Naresh Kumar G (2008) Variation in the nature of organic acid secretion and mineral phosphate solubilization by *Citrobacter* sp. DHRSS in the presence of different sugars. Curr Microbiol 65:168–174

Pedersen AL, Nybroe O, Winding A, Ekelund F, Bjornlund L (2009) Bacterial feeders, the nematode *Caenorhabditis elegans* and the flagellate *Cercomonas longicauda*, have different effects on outcome of competition among the *Pseudomonas* biocontrol strains CHA0 and DSS73. Microb Ecol 57:501–509

Quiquampoix H, Mousain D (2005) Enzymatic hydrolysis of organic phosphorus. In: Turner BL, Frossard E, Baldwin DS (eds) Organic phosphorus in the environment. CABI, Wallingford, pp 89–112

Reid RK, Reid CPP, Szaniszlo PJ (1985) Effects of synthetic and microbially produced chelates on the diffusion of iron and phosphorus to a simulated root in soil. Biol Fertil Soils 1:45–52

Renella G, Egamberdiyeva D, Landi L, Mench M, Nannipieri P (2006) Microbial activity and hydrolase activities during decomposition of root exudates released by an artificial root surface in Cd-contaminated soils. Soil Biol Biochem 38:702–708

Reyes I, Bernier L, Simard RR, Antoun H (1999) Effect of nitrogen source on the solubilization of different inorganic phosphates by an isolate of *Penicillium rugulosum* and two UV-induced mutants. FEMS Microbiol Ecol 28:281–290

Richardson AE, Hocking PJ, Simpson RJ, George TS (2009a) Plant mechanisms to optimise access to soil phosphorus. Crop Pasture Sci 60:124–143

Richardson AE, Barea JM, McNeill AM, Prigent-Combaret C (2009b) Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms. Plant Soil 321:305–339

Rodriguez H, Fraga R (1999) Phosphate solubilizing bacteria and their role in plant growth promotion. Biotechnol Adv 17:319–339

Rojo MJ, Carcedo SG, Mateos MP (1990) Distribution and characterization of phosphatase and organic phosphorus in soil fractions. Soil Biol Biochem 22:169–174

Roos W, Luckner M (1984) Relationships between proton extrusion and fluxes of ammonium ions and organic acids in *Penicillium cyclopium*. J Gen Microbiol 130:1007–1014

Rosenberg K, Bertaux J, Krome K, Hartmann A, Scheu S, Bonkowski M (2009) Soil amoebae rapidly change bacterial community composition in the rhizosphere of *Arabidopsis thaliana*. ISME J 3:675–684

Rudresh DL, Shivaprakash MK, Prasad RD (2005) Tricalcium phosphate solubilizing abilities of *Trichoderma* spp. in relation to P uptake and growth and yield parameters of chickpea (*Cicer arietinum* L.). Can J Microbiol 51:217–222

Rugheim AME, Abdelgani ME (2009) Substituting chemical fertilizers with microbial fertilizers for increasing productivity of Faba bean (*Vicia faba* L.) in arid lands. International Symposium on Environmental Science and Technology, June 2005, Shanghai, China

Saha S, Prakash V, Kundu S, Kumar N, Mina BL (2008) Soil enzymatic activity as affected by long term application of farm yard manure and mineral fertilizer under a rainfed soybean-wheat system in N-W Himalaya. Eur J Soil Biol 44:309–315

Sahin F, Cakmakci R, Kantar F (2004) Sugar beet and barley yields in relation to inoculation with N_2-fixing and phosphate solubilizing bacteria. Plant Soil 265:123–129

Sahu MK, Sivakumar K, Thangaradjou T, Kannan L (2007) Phosphate solubilizing Actinomycetes in the estuarine environment: an inventory. J Environ Biol 28:795–798

Sammauria R, Yadav RS, Nagar KC (2009) Performance of cluster bean (*Cyamopsis tetragonoloba*) as influenced by nitrogen and phosphorus fertilization and biofertilizers in Western Rajasthan. Indian J Agron 54:319–323

Sample EC, Soper RJ, Racz GJ (1980) Reaction of phosphate fertilizers in soils. In: Khasawneh FE, Sample AC, Kamprath EJ (eds) The role of phosphorus in agriculture. ASA–CSSA–SSSA, Madison, pp 263–310

Schwöppe C, Winkler HH, Neuhaus HE (2003) Connection of transport and sensing by UhpC, the sensor for external glucose-6-phosphate in *Escherichia coli*. Eur J Biochem 270:1450–1457

Sharan A, Shikha, Darmwal NS (2008) Efficient phosphorus solubilization by mutant strain of *Xanthomonas campestris* using different carbon, nitrogen and phosphorus sources. World J Microbiol Biotechnol 24:3087–3090

Sharma SN, Prasad R (2003) Yield and P uptake by rice and wheat grown in a sequence as influenced by phosphate fertilization with diammonium phosphate and Mussoorie rock phosphate with or without crop residues and phosphate solubilizing bacteria. J Agric Sci 141: 359–369

Sharma SN, Prasad R, Shivay YS, Dwivedi MK, Kumar S, Kumar D (2009) Effect of rates and sources of phosphorus on productivity and economics of rice (*Oryza sativa*) as influenced by crop-residue incorporation. Indian J Agron 54:42–46

Shober AL, Sims JT (2009) Evaluating phosphorus release from biosolids and manure-amended soils under anoxic conditions. J Environ Qual 38:309–318

Sims JT, Pierzynski GM (2005) Chemistry of phosphorus in soil. In: Tabatabai AM, Sparks DL (eds) Chemical processes in soil, SSSA book series 8. SSSA, Madison, pp 151–192

Souchie EL, Abboud ACD (2007) Phosphate solubilization by microorganisms from the rhizosphere of Pigeonpea genotypes grown in different soil classes. Semina Cienc Agrar 28:11–18

Sreenivas C, Narayanasamy G (2009) Role of earthworm (*Eisenia fetida*) and phosphate solubilising microorganism (*Aspergillus awamori*) in vermi-phosphocomposting. Res Crops 10:293–300

Streeter JG (1994) Failure of inoculant rhizobia to overcome the dominance of indigenous strains for nodule formation. Can J Microbiol 40:513–522

Ström L, Owen AG, Godbold DL, Jones DL (2005) Organic acid behaviour in a calcareous soil implications for rhizosphere nutrient cycling. Soil Biol Biochem 37:2046–2054

Sud KC, Jatav MK (2007) Response of potato to phosphorus and phosphorus solubilizing bacteria in brown hill soils of Shimla. Potato J 34:109–110

Sutaliya R, Singh RN (2005) Effect of planting time, fertility level and phosphate-solubilizing bacteria on growth, yield and yield attributes of winter maize (*Zea mays*) under rice (*Oryza sativa*)-maize cropping system. Indian J Agron 50:173–175

Tabatabai MA (1994) Soil enzymes. In: Weaver RW (ed) Methods of soil analysis. Part 2. Microbial and biochemical properties. SSSA book series 5. SSSA, Madison

Takeda M, Nakamoto T, Miyazawa K, Murayama T, Okada H (2009) Phosphorus availability and soil biological activity in an Andosol under compost application and winter cover cropping. Appl Soil Ecol 42:86–95

Tang J, Leung A, Leung C, Lim BL (2006) Hydrolysis of precipitated phytate by three distinct families of phytases. Soil Biol Biochem 38:1316–1324

Tarafdar JC, Yadav RS, Meena SC (2001) Comparative efficiency of acid phosphatase originated from plant and fungal sources. J Plant Nutr Soil Sci 164:279–282

Tate KR, Salcedo I (1988) Phosphorus control of soil organic matter accumulation and cycling. Biogeochemistry 5:99–107

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D (2001) Forecasting agriculturally driven global environmental change. Science 292:281–284

Turner BL, McKelvie ID, Haygarth PM (2002) Characterisation of water-extractable soil organic phosphorus by phosphatase hydrolysis. Soil Biol Biochem 34:27–35

Turner B, Driessen J, Haygarth P, McKelvie I (2003) Potential contribution of lysed bacterial cells to phosphorous solubilisation in two rewetted Australian pasture soils. Soil Biol Biochem 35:187–189

Van Hees PAW, Vinogradoff SI, Edwards AC, Godbold DL, Jones DL (2003) Low molecular weight organic acid adsorption in forest soils: effects on solution concentration and biodegradation rates. Soil Biol Biochem 35:1025–1026

Vassilev N, Vassileva M, Niklaeva I (2006) Simultaneous P-solubilizing and biocontrol activity of microorganisms: potential and future trends. Appl Microbiol Biotechnol 71:137–144

Vessey JK (2003) Plant growth promoting rhizobacteria as biofertilizers. Plant Soil 255:571–586

Wakelin SA, Gupta VVSR, Harvey PR, Ryder MH (2007) The effect of Penicillium fungi on plant growth and phosphorus mobilization in neutral to alkaline soils from southern Australia. Can J Microbiol 53:106–115

Walker TW, Syers JK (1976) Fate of phosphorus during pedogenesis. Geoderma 15:1–19

Wan JHC, Wong MH (2004) Effects of earthworm activity and P-solubilizing bacteria on P availability in soil. J Plant Nutr Soil Sci 167:209–213

Whitelaw MA, Harden TJ, Bender GL (1997) Plant growth promotion of wheat inoculated with *Penicillium radicum* sp. Nov. Aust J Soil Res 35:291–300

Whitelaw MA, Harden TJ, Helyar KR (1999) Phosphate solubilization in solution culture by the soil fungus *Penicillium radicum*. Soil Biol Biochem 31:655–665

Wielbo J, Skorupska A (2008) Influence of phosphate and ammonia on the growth, exopolysaccharide production and symbiosis of *Rhizobium leguminosarum* bv. *trifolii* TA1 with clover (*Trifolium pratense*). Acta Biol Hung 59:115–127

Wu SC, Cao ZH, Li ZG, Cheung KC, Wong MH (2005) Effects of biofertilizer containing N-fixer, P and K solubilizers and AM fungi on maize growth: a greenhouse trial. Geoderma 125: 155–166

Xiao C, Chi R, He H, Qiu G, Wang D, Zhang W (2009) Isolation of phosphate-solubilizing fungi from phosphate mines and their effect on wheat seedling growth. Appl Biochem Biotechnol 159:330–342

Yadav BK, Tarafdar JC (2007) Ability of *Emericella rugulosa* to mobilize unavailable P compounds during Pearl millet [*Pennisetum glaucum* (L.) R. Br.] crop under arid condition. Indian J Microbiol 47:57–63

Yi YM, Huang WY, Ge Y (2008) Exopolysaccharide: a novel important factor in the microbial dissolution of tricalcium phosphate. World J Microbiol Biotechnol 24:1059–1065

Zhang X, Amelung WYY, Zech W (1998) Amino sugar signature of particle-size fractions in soils of the native prairie as affected by climate. Soil Sci 163:220–229