Chapter 24
Phosphate Mobilisation by Soil Microorganisms

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Abstract Microorganisms are fundamental to the cycling of phosphorus (P) in soil-plant systems as they are involved in a range of processes that govern P transformations and availability. Soil microorganisms in particular are able to release plant available P from otherwise sparingly available forms of soil P, through solubilisation and mineralisation reactions of inorganic and organic P, respectively. The potential of phosphate solubilising microorganisms (PSM) to improve plant P nutrition is widely recognised, and the mechanisms involved are being investigated. The feasibility of developing efficient management systems based on PSM as biofertilisers is of current interest in rhizosphere biotechnology. Mycorrhizosphere interactions involving PSM and their interaction with AM fungi is of further relevance for the acquisition, transport and supply of P to plant roots, and therefore to soil P cycling and plant P nutrition. Managing these interactions (mycorrhizosphere tailoring) provides an environmentally-acceptable agro-technological practice to improve agricultural sustainability.

24.1 Phosphorus in the Soil-Plant System

Phosphorus (P) is a vital element for life on earth. In particular, P is essential for plant growth and development, as it is a component of fundamental macromolecules involved in genetic, regulatory, structural, signal transduction and other metabolic processes. In addition to the orthophosphate anion, other plant P-integrating molecules include nucleic acids and ADP/ATP, indispensable for photosynthesis,

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respiration and other biochemical processes involved in energy storage and transfer reactions. Plant P also occurs in storage compounds such as phytate and related compounds, pyrophosphate and as a component of membrane phospholipids and phosphoproteins (White and Hammond 2008).

Forms of Phosphorus in Soil Soil P occurs as either inorganic phosphates or organic phosphate derivatives. The primary mineral form of P in soil is apatite. The weathering of apatite results in the release of orthophosphate anions, primarily as HPO_4^{2-} and $H_2PO_4^{1-}$ to soil solution, but only in small quantities. Soil solution orthophosphate content typically ranges from 0.1 to 1 mg P kg^{-1} which represents about 1 % of the total soil P. Most orthophosphate in soil undergoes reactions which makes it only sparingly available to plants. Orthophosphate is rapidly adsorbed on clay mineral surfaces and other soil particles and colloids or precipitated as inorganic salts (e.g., with calcium in alkaline soils or with aluminum and iron in acidic soils), which are of low solubility. A significant amount of orthophosphate is also integrated in complex organic molecules (soil organic P), which can account for 30–60 % of the total soil P. Major identifiable fractions of organic P in soil include inositol phosphates, such as phytate (salts of *myo*-inositol hexakisphosphate), nucleic acids, phospholipids and phosphonates. Inositol phosphates are considered to be the dominant form of organic P in many soils. Phosphorus immobilised within the living soil microbial biomass is also significant, and typically represents about 5 % of the total soil P (Plante 2007; White and Hammond 2008).

The Soil Phosphorus Cycle From a functional point of view the various forms of P in soil are interconnected and integrated through the so called soil P cycle. As outlined by Plante (2007) the soil *solution P* pool is central to the P cycle and is the primary source of labile orthophosphate for biological uptake by microorganisms and plants. Soil *solution P* also provides the interconnection between the *biological subsystem* (including plant residues, soil microbial P, labile and stable organic P) and the *geochemical subsystem* (i.e., primary minerals, secondary minerals and adsorbed P, that includes P occluded with soil constituents). Whilst the availability of orthophosphate in the *geochemical subsystem* is mediated largely by physical-chemical reactions such as dissolution, precipitation, sorption-desorption and oxidation-reduction, these processes are also influenced strongly by biological activities. Soil microorganisms are able to interact across both *subsystems* through either solubilisation of inorganic P or mineralisation of organic P and thus play a key role in the cycling of soil P. Furthermore, soil microorganisms interact directly with soil *solution P* and may thus directly influence the availability of orthophosphate to plants through mobilisation or, conversely, in the short term, by competition with plants for available nutrient through P immobilisation.

Availability of Phosphorus for Plant Nutrition Plant roots acquire orthophosphate from soil solution via their associated volume of soil through either the rhizosphere (Chap. 3) or mycorrhizosphere (Chap. 25) (Fig. 24.1) However, because of the high reactivity of P in soil and the rapid uptake of orthophosphate by roots, the concentration of orthophosphate around roots is often low. This low concentration is further

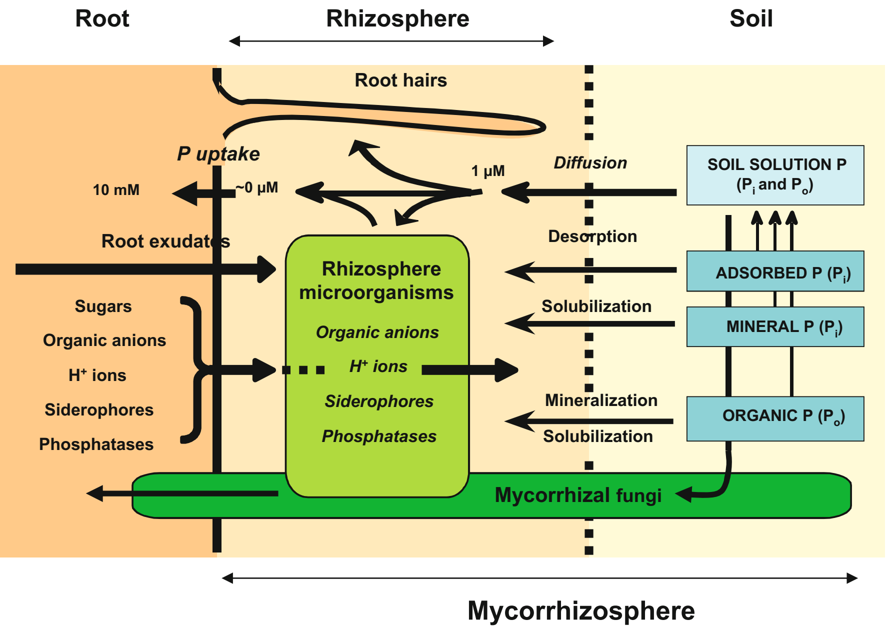

Fig. 24.1 Root-soil microbiome processes governing transformation and availability of phosphorus in soil-plant systems highlighting the importance of the rhizosphere and mycorrhizosphere. (Reproduced from Richardson et al. 2009 by permission of the publisher)

compounded by slow diffusion of orthophosphate anions in solution which results in a distinct zone of depletion in soil immediately surrounding the root system. The low rate of replenishment of orthophosphate in the rhizosphere/mycorrhizosphere soil solution from the bulk soil is therefore a major factor that regulates P availability to plants (White and Hammond 2008). Consequently, P-based fertilisers are routinely used in agricultural production systems to either maintain the P status of fertile soils or to increase P availability in deficient soils. The efficiency of P fertiliser use in most systems, however, is low, whereby only 10–50 % of applied P is recovered by crops in the year of application. The remainder of the P accumulates in soil in either inorganic or organic P fractions and, subject to efficient mobilisation, can provide a P benefit in subsequent years. Rock phosphates (RP), which are used for the production of water soluble P-fertilisers, are also widely used as a direct source of P albeit with relatively low agronomic efficiency. Development of strategies to increase the mobilisation of P from accumulated forms in soil or to enhance the utilisation of RP are thus promoted as being important to increase the efficiency of P fertiliser use. As microorganisms are a key component of the soil P cycle they are widely considered as the basis of some of these alternative strategies to improve the sustainability of P use in agriculture systems (Zapata and Roy 2004).

24.2 Microbial Mobilisation of Phosphorus in Soil

Microorganisms are known to drive plant nutrient cycling and many other fundamental processes resulting in plant growth promotion (Barea et al. 2007; Lugtenberg et al. 2013). In particular, specific soil microorganisms (i.e., plant growth promoting rhizobacteria; PGPR) change the capacity of plants to acquire P from soil solution via mechanisms that include; (i) modifying soil sorption equilibria to facilitate P diffusion, (ii) enhancing mobilisation of poorly available sources of P, (iii) increasing the extension of root surface area, (iv) by stimulating root branching and/or root hair development and (v) altering root surface properties to enhance P uptake (Richardson et al. 2009). Here we focus on mechanisms under (ii), whereby microbial activities result in increased release of available P from sparingly available forms of either inorganic (solubilisation) or organic (mineralisation) P in soil. This has particular relevance from a sustainability point of view because P mobilisation activities have broad significance in the maintenance and productivity of both agricultural and natural ecosystems (Richardson 2007).

Phosphate Solubilisation Bacteria and fungi isolated from plant rhizospheres have been shown to solubilise *in vitro* various inorganic phosphates, such as calcium, aluminum or iron salts. These microorganisms are collectively termed "phosphate solubilising microorganisms" (PSM). They include *Bacillus*, *Enterobacter, Rhizobium, Bradyrhizobium*, *Enterobacter, Panthoea, Erwinia*, and *Pseudomonas* as common bacterial genera, and *Aspergillus, Trichoderma* and *Penicillium* as fungal representatives (Marschner 2008). In the case with sparingly soluble forms of calcium phosphates, the mechanism of soloublisation is most commonly associated with proton release and media acidification. For iron or aluminum phosphates, solubilisation due to acidification appears to be less effective and production of organic acids is of greater importance. Organic anions are effective in chelation processes that result in the sequestration of calcium, iron or aluminum which is associated with a release of orthophosphate to solution. Commonly reported organic anions include citrate, oxalate, lactate, succinate, gluconate and 2-ketogluconic acid. Siderophore production likewise has been reported to be effective for solubilisation of Fe phosphates (Marschner 2008). The amount of orthophosphate released from sparingly soluble forms is dependent on the microorganisms involved, culture conditions and the degree of solubility of the P substrate (Whitelaw 2000). Solubilisation of P is further dependent on the presence of readily metabolisable carbon sources. As such, isolates selected as being effective for P solubilistion under laboratory conditions may not be effective in soil due to either carbon limitation or other unfavorable microhabitat conditions (Richardson 2007).

Molecular-based approaches have recently been used to investigate the mechanisms involved in P solubilisation by specific microorganisms. For example, one mechanism is based on the ability of *Pseudomonas* spp. to produce gluconic acid from glucose by the oxidation reaction catalysed by glucose dehydrogenase which uses pyrroloquinoline quinone (PQQ) as a redox cofactor. Finally, 2-ketogluconate is produced which facilitates both the chelation of calcium and release of protons. A genomic library of *Pseudomonas* spp. has recently been analysed for PQQ biosynthetic genes to determine their involvement in P solubilisation (Browne et al. 2013).

Phosphate Mineralisation The mineralisation of organic P in soil and release of orthophosphate to soil solution is largely mediated by microbial activities (Richardson et al. 2009). Bacteria and fungi isolated from plant rhizospheres have been shown to have capacity to hydrolyse organic P substrates either *in vitro* or when added to soil. Common microorganisms include *Bacillus* and *Pseudomonas* as bacteria and *Aspergillus* and *Penicillium* as fungi (Marschner 2008). Mineralisation of organic P often first requires solublisation of substrates with subsequent hydrolysis by phosphatase enzymes, which in many cases is synonymous with the activities of PSM. Microorganisms produce diverse types of enzymes which include non-specific acid and alkaline phosphates, and specific enzymes, such as phytases which release orthophosphate from phytate and other inositol phosphates. The importance of microorganisms for phytate mineralisation has been demonstrated in various studies, whereby the availability and plant uptake of orthophosphate can be improved by inoculation with PSM with P mineralisation capability. Nevertheless, the effectiveness of phytases in many soil environments remains less clear since enzymes may also readily be absorbed to soil particles or degraded, and inositol phosphates adsorb strongly or precipitate readily with iron or aluminum oxides and other soils constituents (Marschner 2008). Nonetheless, microbial utilisation of organic P substrates in soil and its turnover has potential to supply a significant amount of P to meet plant requirements. This is of particular importance in the rhizosphere and mycorrhizosphere where metabolisable carbon is more available and there is greater capacity to capture mobilised P. However, further experimental evidence to quantify microbial mineralisation of P and the direct value of immobilised P in the microbial biomass to plant nutrition is required (Richardson et al. 2009).

It is important to note that to date much of the work on P solubilisation and mineralisation has involved soil microorganisms that have been isolated and grown in culture media. More recent culture-independent molecular-based studies have shown that a high percentage (i.e., greater that 90 %, and possibly as high as 99 %) of soil microorganisms are unculturable, and that this includes therefore likely microorganisms that are involved in phosphate-solubilisation and P cycling (Barret et al. 2013). As culture-independent approaches are being used to further dissect plant-microbial interactions it is evident that plants play a significant role in shaping microbial communities in the rhizosphere and mycorrhizosphere. As such there is new opportunity for linking the structure and function of the root-soil microbiome to orthophosphate availability and P-solubilising capacity (Browne et al. 2013).

Significance of PSM in Improving Plant Nutrition While it is clear that soil microorganisms are integral to the operation of the soil P cycle, the extent to which P released by soil microorganisms actually benefits plant P acquisition remains to be more fully elucidated. Indeed because orthophosphate release from sparingly available soil P sources by microbiological-driven activities may be highly transient in nature, this has implications for its efficacy in promoting plant growth.

In addition, mobilised orthophosphates are also subject to further reaction in soil, for example through either ‘re-fixation’ reactions or immobilistion into microbial biomass, and may thus not be considered to be immediately available to plants. Spatial interactions may likewise impede the availability of orthophosphate within the plant rhizosphere and/or mycorrhizosphere and thereby limit any potential agricultural benefit (Richardson 2007). However, if orthophosphate made available by PSB can be taken up more efficiently by plant roots or through an effective mycorrhizal mycelium (Chap. 25), then the resultant microbial interaction could synergistically act to improve P supply to the host plant (Richardson et al. 2009).

Managing PSM to Improve Plant Phosphorus Nutrition Given the potential of PSM to contribute to the development of more sustainable agricultural systems, a number of approaches have been proposed for their management and opportunity for capture of benefits. These are based on either the manipulation of naturally existing microbial populations, or by the development of microbial inoculants that contain specific microorganisms with recognised potential for P mobilisation. Management of naturally existing populations, whilst attractive, is a relatively untargeted approach, where it is often difficult to predict the response of microbial populations as a consequence of different agricultural practices (Richardson 2007). For example, crop rotation and amendment of soils with organic wastes (e.g., manure crops) is known to enhance P cycling or to increase the biological activity in soils, although specific effects on either solubilisation or mineralisation processes remain to be more fully investigated. Likewise, because of its distinct physical, chemical and biological properties, biochar (produced by pyrolitic transformations of organic materials) is also being used widely as a soil amendment that may also facilitate the efficacy of phosphate solubilising or mineralisation activities in soil (Lehmann et al. 2011).

A range of biofertiliser-based products using selected PSM (both bacteria and fungi) have been developed as commercial products for use in various agricultural systems across the world. These products, using specific microorganisms either individually or as part of a microbial consortium, have in many cases shown positive effects in various field trials (Antoun 2012). However, inconsistent results are commonly observed indicating the complexity of interactions in the soil-plant systems, where diverse ecological variables need to be considered. In some instances it seems that benefits of plant growth promotion derived from microbial inoculants occurs by stimulation of root growth, allowing a greater exploration of soil P, rather than by direct increase in P-mobilisation (Richardson et al. 2009).

Successful development of PSM requires that appropriate inoculant formulations and delivery systems be developed for specific microorganisms (Antoun 2012). Furthermore, selected microorganisms must be able to maintain their ability to solubilise P after repeated sub-culturing under laboratory conditions or following re-isolation from soil, and exhibit sufficient saphrophytic competence for persistence in soil environments. To be effective in soil it is critical that selected PSM are able to establish themselves either on the root surface or within in the root-soil habitat. *Rhizosphere competence* is a key trait involved in microbial establishment in the rhizosphere (Chap. 3) and there is need to develop non-disruptive visualisation techniques for assessing microbial colonisation of the rhizosphere and/or mycorrhizosphere (Barea et al. 2013).

PSM Interactions to Improve Key Rhizosphere Processes Interaction of PSM with other PGPR has been shown in several cases to be beneficial for plant growth. For example, PSM have been used in conjunction with N_2-fixing bacteria and mycorrhizal fungi to improve N_2-fixation by legumes though a greater P supply (Zaidi et al. 2010). Inoculation of lucerne (alfalfa) with phosphate-solubilising bacteria (PSB) enhanced both nodulation and N_2-fixation, as estimated by using ^{15}N and ^{32}P isotopic methods. Using the ^{32}P dilution approach, Barea et al. (2013) showed that inoculation with PSB increased the mobilisation of sparingly available P from either endogenous soil P or from P supplied as rock phosphate.

24.3 Mycorrhizosphere Interactions to Improve Plant Phosphorus Nutrition

The colonisation of roots by mycorrhiza affects diverse aspects of plant physiology resulting in quantitative and qualitative changes in root structure and composition of root exudates. This has a significant effect on the compositional structure and function of microbial communities in the rhizosphere. In addition, mycorrhizal mycelium directly modifies the physical characteristics of surrounding soil and interacts further with soil microorganisms. These mycorrhiza-induced interactions, has led to the development of the so-called mycorrhizosphere (Barea et al. 2013). Other rhizobacteria that favor the formation of mycorrhiza on roots have also been recognised (Frey-Klett et al. 2007), and are commonly referred to as "mycorrhiza-helper-bacteria" (MHB).

Mycorrhizosphere interactions involving PGPR can be managed (mycorrhizosphere tailoring) to benefit plant growth and health, and soil quality (Barea et al. 2013). Interactions between mycorrhizas and PSB in particular are relevant to P cycling and plant P nutrition (Richardson et al. 2009). PSB interactions with arbuscular mycorrhizal (AM) associations are considered in more detail below, as association with AM fungi is common with some 80 % of terrestrial plant species being able to be colonized, including those of agronomic interest (Chap. 25).

Biological and Ecological Basis of Mycorrhizosphere Interactions The extensive and highly branched external mycelium of AM fungi characteristically increases the zone of soil exploration and potential for plant nutrient uptake beyond the rhizosphere (Chap. 25). External AM mycelium are able to extend several cm (up to 25 cm) from the root and thus provide for the uptake and transport of P in soil that is independent of the diffusive rate of orthophosphate in soil solution. In addition, 1 cm of root length can harbour as much as 1 m of fungal hyphae, with densities of up to 40 m of mycelia per gram of mycorrhizosphere soil (Smith and Smith 2012). These properties of AM mycelium are especially relevant for acquisition of P from soil as has been widely demonstrated using compartmented devices and ^{32}P isotopic labelling studies. Importantly, orthophosphate made available by PSM has potential to be taken up and transported more effectively by roots that are colonised with AM fungi.

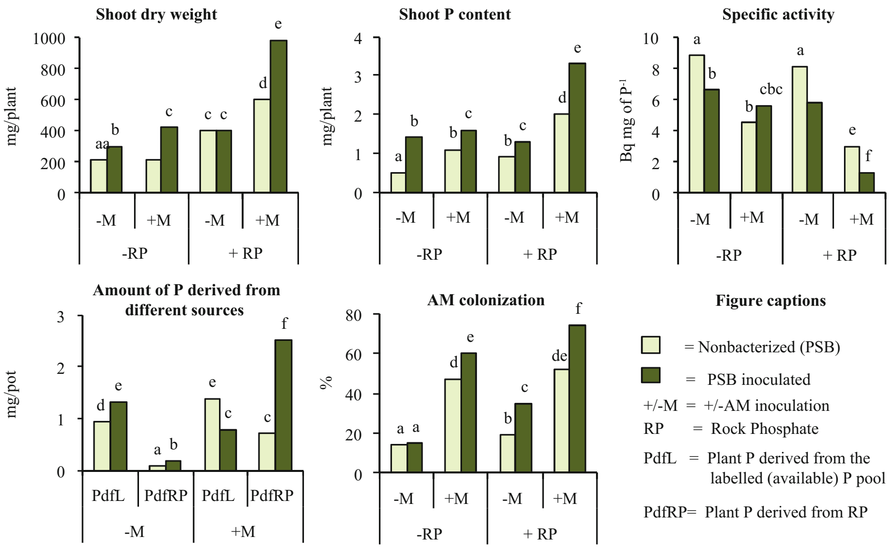

Fig. 24.2 Interactive effects of PSB and AM fungi in enhancing plant growth and phosphorus (P) uptake from endogenous soil P or P added as rock phosphate. Plants (*onions*) were grown in a soil microcosm system which integrated ^{32}P isotopic dilution approaches in an agricultural soil with indigenous microbiota either with or without inoculation. Plants inoculated with both PSB and AM fungi produced greater biomass, accumulated more shoot P and had a lower ^{32}P specific activity than non-inoculated or single-inoculated plants, thus indicating greater access to poorly-available sources of P. Up to 75 % of the P in dual-inoculated plants was derived from added RP and it was evident that inoculated PSB behaved as a mycorrhiza helper bacteria by promoting establishment of both indigenous and inoculated AM fungi. (Reproduced from Toro et al. 1997 by permission of the publisher)

Agronomical Application of PSB x AM Fungal Interactions The feasibility of capturing greater benefit for plant P nutrition through synergistic interactions between PSB and AM fungi has received wide interest since the pioneering work of Azcón et al. (1976). For example, various co-inoculation studies have shown significant increase in the mobilisation and plant uptake of P from sparingly available sources either directly from soil or when added as RP (Barea et al. 2013). In some studies the inoculated PSB behaved as MHB by promoting establishment of both indigenous and inoculated AM fungi (Fig. 24.2). Whilst consistent results have been reported for glasshouse studies, more variable response occurs under field conditions. Interestingly, in the study by Barea et al. (2007) the agronomic efficiency of P uptake by plants from RP was increased with dual inoculation, and was greatest when an organic matter amendment was applied. Whilst organic matter appeared to enhance the solubilisation activities of PSM, the underlying mechanisms involved and relative contribution of the various microbial partners in such interactions remains to be more fully investigated.

The Use of Isotopic Techniques to Assess Mycorrhizosphere Interactions Isotopic (^{32}P and ^{33}P) dilution approaches have commonly been used to investigate exchange rates in orthophosphate equilibrium between solution and solid phases of soil and to measure the availability of P from fertiliser sources (including RP) as influenced by management practices (Zapata and Roy 2004). Accordingly, ^{32}P-tracer methodologies have been used to determine the contribution of AM fungi and PSB to plant P uptake from different source of P (Toro et al. 1997). These techniques typically involve labelling of the exchangeable pool of soil P with ^{32}P-orthophosphate. Plants subject to different inoculation treatments are then grown in the soil amended either with or without RP. Difference in isotopic composition, or "specific activity" ($SA = {}^{32}P/{}^{31}P$ quotient) in plant tissues can then be used to assess P uptake, whereby lower SA of the plant (relative to control plants) is indicative of greater access to otherwise sparingly available forms of P (Toro et al. 1997).

Results from several isotopic-labeling experiments using different plant species (mainly legumes) have shown increased biomass and P content of plants co-inoculated with AM and PSB, along with lower SA of shoot tissues compared with non-inoculated or singularly-inoculated plants (Azcón and Barea 2010). This suggests that PSB are effective in releasing orthophosphate anions from soil or RP sources and, that in the presence of AM fungi, the P is more available for plant uptake (Fig. 24.2). By using isotope dilution concepts (Zapata and Roy 2004) the relative contribution of the different P sources to plant P content (i.e., from added RP) can also be determined. As such, it is evident that co-inoculated plants generally have significantly greater access to P from RP, while plants inoculated with PSB only showed greater reliance on the exchangeable soil P pool (Barea et al. 2007). Collectively, plants inoculated with both AM fungi and PSM therefore appear to be more P efficient compared to those that were non-inoculated or singly-inoculated. In conclusion this demonstrates that opportunity exists to gain benefit in plant P nutrition from interactive effects of PSB and AM-fungi through tailored management of the mycorrhizosphere (Azcón and Barea 2010).

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