Soil Microorganisms Mediating Phosphorus Availability

Alan E. Richardson* and Richard J. Simpson

CSIRO Sustainable Agriculture National Research Flagship/CSIRO Plant Industry, Canberra, Australian Capital Territory 2601, Australia

Microorganisms are integral to the soil phosphorus (P) cycle and as such play an important role in mediating the availability of P to plants. Understanding the microbial contribution to plant P nutrition and opportunities for manipulating specific microorganisms to enhance P availability in soil has therefore been of considerable interest over many decades. This interest is accentuated by P deficiency being common in weathered and tropical soils throughout the world, by rising costs of P fertilizer, and because the efficiency of P use by plants from soil and fertilizer sources is often poor despite many soils containing a relatively large amount of total P that is only sparingly available to plants. The world's high-quality sources of rock phosphate are finite and this itself justifies the need to develop plants and/or agricultural systems that are more P efficient. Utilization of microorganisms to increase the availability of P in soil therefore is an attractive proposition for developing a more sustainable agriculture. This is relevant to the high-input production systems of the developed world, and also to developing countries where access to mineral fertilizers is restricted (Sánchez, 2010).

The concept of microbial enhancement of P availability to plants is not new. Gerretsen (1948) showed that pure cultures of soil bacteria could increase the P nutrition of plants under controlled conditions through solubilization of precipitated forms of calcium (Ca) phosphates. Since this study, many examples of microbially mediated P mobilization and characterization of different microorganisms have been reported (for review, see Richardson, 2001; Gyaneshwar et al., 2002; Khan et al., 2007, 2010; Harvey et al., 2009; Richardson et al., 2009a; Zaidi et al., 2009). However, despite considerable promise microbial products for P mobilization have not had major application to broad-acre farming systems. An exception to this is the commercialization of fungal-based inoculants in North America and more recently in Australia and Europe. Clearly, interactions between microorganisms and plants in soil environments are complex and with a few exceptions only (such as rhizobia, and to a much lesser extent mycorrhizal fungi), have proven difficult to manage and as a consequence responses to inoculants have been highly variable. In addition, P in soil is subject to extensive physicochemical and biological reactions with only a small component of total soil P being in a form directly available for plant or microbial uptake (Fig. 1). Uptake of P from soil solution occurs as orthophosphate via high-affinity transporters that in plants are localized to the root epidermis and are coordinately expressed in response to P deficiency and through interaction with mycorrhizal fungi (Bucher, 2007). P in soil exists predominantly in inorganic fractions that are either adsorbed to soil mineral surfaces or occur as sparingly available precipitates, and in organic forms that are either adsorbed, incorporated within biomass, or associated with soil organic matter. It is the dissolution (or mobilization) of orthophosphate from these forms, and rates of P diffusion within soil solution that represents the major limitation to adequate supply of P required for plant growth. In this Update we summarize current evidence concerning the role of free-living nonsymbiotic microorganisms in increasing the availability of P to plants. Critical issues that impede our understanding of microbially mediated P dynamics in the rhizosphere are outlined and opportunities for enhancing P mobilization are discussed.

MECHANISMS OF P MOBILIZATION BY SOIL MICROORGANISMS

Microorganisms can enhance the capacity of plants to acquire P from soil through various mechanisms that can be summarized as: (1) increased root growth through either an extension of existing root systems (e.g. mycorrhizal associations) or by hormonal stimulation of root growth, branching, or root hair development (phytostimulation; e.g. production of indole-3-acetic acid, GAs, or enzymes that alter plant ethylene precursors, such as 1-aminocyclopropane-1-carboxylate deaminase; Richardson et al., 2009a; Hayat et al., 2010); (2) alteration of sorption equilibria that may result in increased net transfer of orthophosphate ions into soil solution or facilitate the mobility of organic P either directly or indirectly through microbial turnover (Seeling and Zasoski, 1993); and (3) through induction of metabolic processes that are effective in directly solubilizing and mineralizing P from sparingly available forms of soil inorganic and organic P (Fig. 1; Richardson et al., 2009a). This includes the efflux of protons and organic anions, production of siderophores, and release of phosphatase and cellulolytic enzymes required for the hydrolysis of

* Corresponding author; e-mail alan.richardson@csiro.au.
www.plantphysiol.org/cgi/doi/10.1104/pp.111.175448

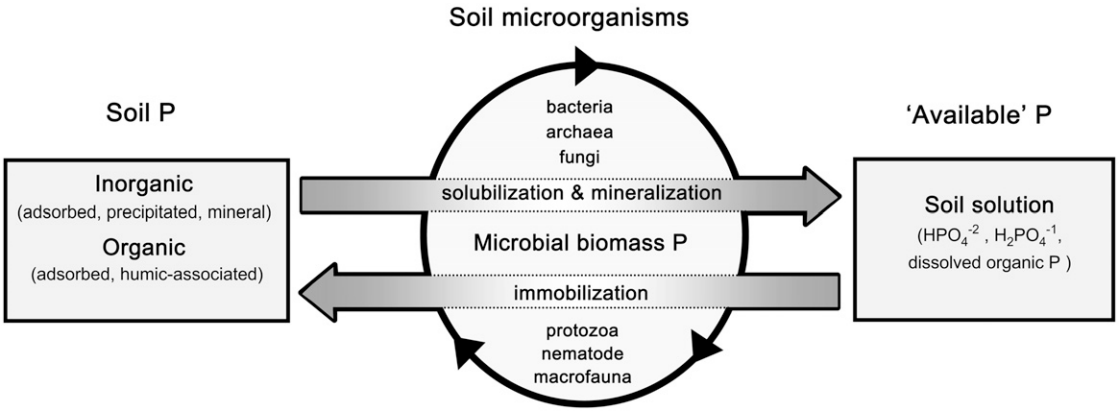

Figure 1. Schematic representation of the importance of microorganisms to P availability in soil. Microorganisms and their interactions in soil play a critical role in mediating the distribution of P between the available pool in soil solution and the total soil P through solubilization and mineralization reactions, and through immobilization of P into microbial biomass and/or formation of sparingly available forms of inorganic and organic soil P.

organic P or mineralization of organic residues and organic matter, respectively (Fig. 2). Organic anions and protons are particularly effective in solubilizing precipitated forms of P (e.g. Ca phosphates under alkaline conditions), chelating metal ions that are commonly associated with complexed forms of soil P (as is for the role of siderophores in mediating Fe availability), or by facilitating the release of adsorbed orthophosphate or organic P through ligand-exchange reactions (Ryan et al., 2001). However, while such mechanisms are widely demonstrable under laboratory and, in some cases, controlled glasshouse conditions, unequivocal evidence concerning their operation in field soils and quantification of their capacity to directly supply P to plants is more difficult to assess and hitherto remains poorly quantified. Indeed plants themselves display a wide range of root morphological and physiological changes in response to P deficiency (Vance et al., 2003; Richardson et al., 2009b) and delineation of the relative importance of microbial- versus plant-mediated processes for P mobilization are difficult to assess. Nonetheless microorganisms are integral to the cycling of soil P and localized enhancement of microbial activity in the rhizosphere has significant implication for the P nutrition of plants.

ACCUMULATION AND TURNOVER OF MICROBIAL BIOMASS P

The central role of the microbial biomass in the cycling of P in soil has received increased recognition in recent years (Oberson and Joner, 2005). P held within soil microorganisms constitutes a significant component of the total soil P and is generally equivalent to, or exceeds that held in plant biomass. Microbial P in bulk soil, while highly variable, is estimated to typically account for around 2% to 10% of total soil P, although at different stages of soil development and within litter layers (soil surface) this may be as much as 50% (Oberson and Joner, 2005; Achat et al., 2010). Importantly, microbial P is a highly dynamic pool of soil P and is subject to significant change in response to environmental factors such as soil temperature, moisture, and carbon (C) availability. Microorganisms decompose organic amendments added to soil (e.g. manures, plant residues) and mineralize organic P along with that of soil organic matter. Rapid incorporation of P from crop residues into microbial biomass occurs with high recovery of P over short time periods (e.g. 28% incorporation of P in microbial biomass from legume residues added to soil after 7 d; McLaughlin et al., 1988). More recent studies have shown that a severalfold increase in microbial P in response to added C (and nitrogen [N]) is associated with a significant decline in soil solution orthophosphate. This occurs in soils that are either P amended, or without added P and in soils that are considered to be P limited (Oehl et al., 2001; Bünemann et al., 2004; Ehlers et al., 2010). It is evident therefore that microorganisms effectively compete with plants for available orthophosphate from soil solution and also represent a significant pool of immobilized P that is temporarily unavailable to plants (Fig. 1). However, over the longer term, all microbial P is potentially available to plants and it is suggested that immobilization of P within the biomass is an important mechanism for regulating the supply of P in soil solution (Seeling and Zasoski, 1993) and for maintaining it in labile forms that are protected (in a temporal sense) from reactions with soil (Olander and Vitousek, 2004).

Significant amounts of P can be released from the microbial biomass in response to seasonal conditions when either C becomes limiting, soils undergo cycles of wetting and drying, or during processes of higher tropic-level predation (Turner and Haygarth, 2001;

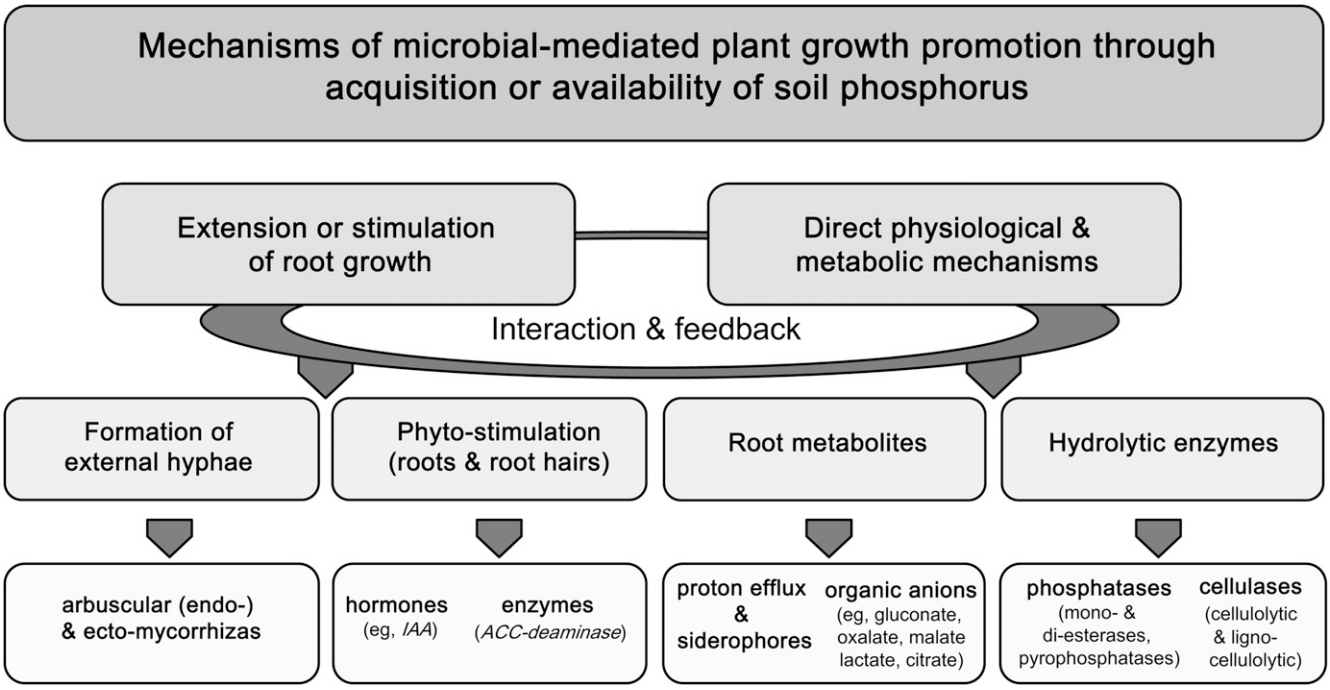

Figure 2. Key biological processes associated with microbially mediated plant growth promotion through mechanisms that may either directly or indirectly increase the availability of soil P or enhance a plant's capacity to acquire P from soil.

Bonkowski, 2004). Release of P from the biomass occurs as orthophosphate and in organic forms that are rapidly mineralized in soil (Macklon et al., 1997). In soils with low adsorption capacity this can be associated with a measurable increase in soil solution P (Oehl et al., 2001). Significant amounts of P can also be released from soil microorganisms without net change in the size of the microbial biomass pool due to recycling and turnover. Radioactive tracer studies indicate that orthophosphate released through microbial turnover contributes significantly to basal rates of mineralization in soil that are significant for supply of orthophosphate to plants. Estimates suggest a turnover time of the total microbial biomass in bulk soil of between 42 and 160 d depending on the farming system, with faster rates of turnover occurring in C-amended soils (Oehl et al., 2004; Bünemann et al., 2007). More recently, Achat et al. (2010) has reported a faster cycling of a major component of the soil microbial P pool, or fast pool (accounting for 80% of the total microbial P), with a turnover time of less than 10 d in an organic-P-dominated forest soil. Across these various studies it is evident that a significant amount of P is cycled through the microbial biomass on an annual basis (i.e. with estimates of up to 100 mg P kg^{-1} soil $year^{-1}$). Given that turnover of microbial P is largely driven by the availability of C this is therefore of particular significance in the rhizosphere. To be available to plants, orthophosphate (or dissolved organic P) must diffuse through the rhizosphere (or mycorrhizosphere; Jakobsen et al., 2005) and as such will be subject to direct competition for uptake and immobilization by microorganisms. Subsequently, the rate of release of P from microorganisms or the turnover time for the microbial biomass within the rhizosphere will have major implications for P availability to plants.

RHIZOSPHERE INTERACTIONS AND SOIL P DYNAMICS

The rhizosphere is characterized by a significant increase in the number and activity of soil microorganisms due to exudation of photosynthetic C from roots. Various estimates indicate that some 5% to 20% of photosynthetic C is typically released into the rhizosphere, primarily as high M_r mucilages, simple hexose sugars, and organic anions, along with more complex C derived from root turnover and sloughed cells (Jones et al., 2009). This C is available to soil microorganisms and results in a significant increase in microbial biomass C (and microbial P) within the rhizosphere, as shown in the study by Chen et al. (2002) using a rhizobox system to investigate P dynamics in the rhizosphere of perennial ryegrass (*Lolium perenne*) and radiata pine (*Pinus radiata*; Fig. 3). Following early studies, which used autoradiography to demonstrate depletion of radioactive ^{32}P and ^{33}P orthophosphate around roots, numerous studies have since quantified P depletion in the rhizosphere and demonstrated a significant concentration gradient that is largely coincident with the root hair/hyphal zone.

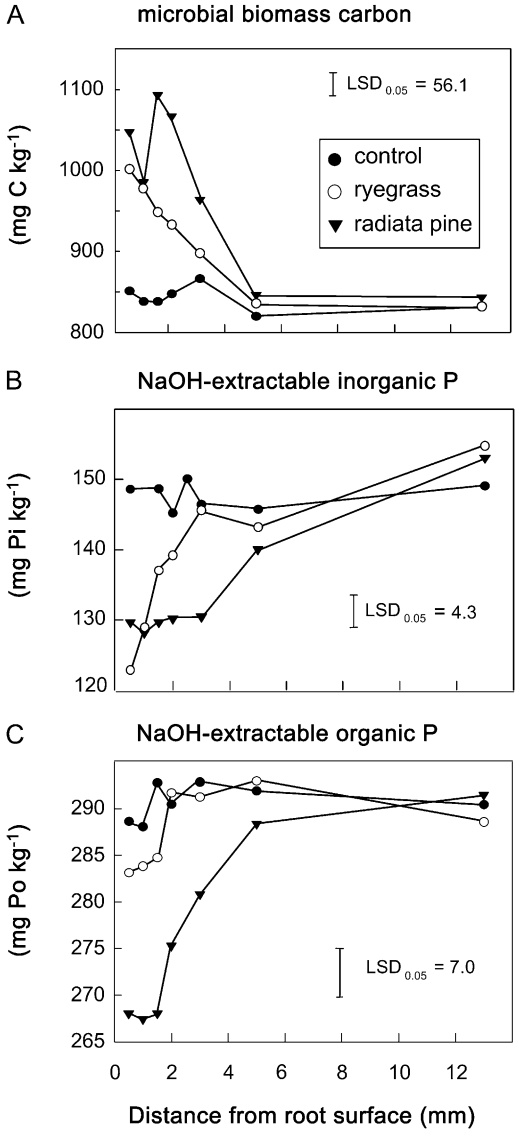

Figure 3. Microbial biomass and depletion of soil P in the rhizosphere of perennial ryegrass (white circles) and radiata pine (black triangles), as compared to control (unplanted; black circles) soil. Shown are: microbial biomass C (A) and NaOH-extractable inorganic P (B) and organic P (C) following a sequential extraction procedure. Plants were grown in a rhizobox system using an Orthic brown soil (Dystrochrept) from Hurunui in New Zealand (pH 5.6; soil-water extract) and analyzed as reported by Chen et al. (2002). For each panel the error bar (LSD) shows LSD ($P = 0.05$).

This depletion occurs not only as orthophosphate, but also to some extent from various fractions of extractable-soil P including those previously considered to be poorly available to plants, such as NaOH-extractable inorganic and organic P. In the study by Chen et al. (2002) depletion of approximately 20% and of 5% to 10% depletion of extractable inorganic and organic P was observed at the root surface, respectively (Fig. 3). While this represents only a small portion of the total extractable P, it demonstrates increased mobilization of soil P within the rhizosphere. However, it also remains to be determined whether specific forms of soil P (for both inorganic and organic P fractions) are preferentially mobilized. For soil organic P in particular, there is need to better link chemical characterization of forms of organic P (i.e. as determined by spectroscopy-based studies; Turner et al., 2003) with their biological availability. There is also a need to better understand the relative importance of plant mechanisms compared to microbial processes for P mobilization in the rhizosphere and whether either can be manipulated to improve P use efficiency in agricultural systems.

MINERALIZATION OF ORGANIC P

Utilization of organic P by plants and microorganisms requires mineralization (hydrolysis) of substrates by phosphatase enzymes that may be of either plant or microbial origin. Increased activity of phosphatases occurs in response to P deficiency as part of P starvation responses. In plants, this includes the release from roots of extracellular phosphatases that are considered to be important for capture and recycling of organic P lost from roots, or to allow greater access to soil organic P (Richardson et al., 2005). Enhanced phosphatase activity in the rhizosphere in response to P deficiency has been observed across a wide range of plant species and is commonly reported to be higher in P-deficient soils. In the study by Chen et al. (2002) depletion of soil organic P (Fig. 3) was associated with a significant increase in the activity of both mono- and diester phosphatases.

Soil microorganisms similarly produce a range of phosphatases and when cultured in laboratory media have the capacity to utilize P from various forms of organic P that occur in soil. This includes inositol phosphates (phytate; myoinositol hexakisphosphate along with other isomers and lower-order derivatives), a predominant form of organic P identified in many soils (Lim et al., 2007; Turner, 2007). When added to soils organic P substrates (both mono- and diester) are rapidly hydrolyzed (Macklon et al., 1997). Conversely, when soil suspensions or soil extracts are treated with an excess of phosphatase activity appreciable amounts of orthophosphate can be released (George et al., 2007b). Bünemann (2008) reported that up 60% of the total organic P may typically be hydrolyzed by phosphatases with highest amounts being released by phytases (monoester phosphatases active against phytate). Both plant and microbial phosphatases are effective in releasing orthophosphate from soil organic P, with some evidence that microbial enzymes show higher efficiency for P release (Tarafdar et al., 2001). Collectively these studies highlight the potential importance of enzyme-labile soil organic P for plant availability.

Increased mineralization of soil organic matter associated with higher microbial activity also occurs in

the rhizosphere as a result of a microbial priming effect due to utilization of exudate C with subsequent mineralization of nutrients from soil organic matter (Cheng, 2009). However, the direct coupling of C mineralization with amounts of N (and P) released requires more detailed investigation. While C:N ratios are reasonably constant across different soils and for various fractions of soil organic matter, wider variation in C:P or C:organic P ratios are often observed (Kirkby et al., 2011). Presently it is unknown to what extent P mineralization may occur independently of organic matter turnover. This has implications for competition between plants and microorganisms for nutrient uptake within the rhizosphere, resulting in either a net mineralization or immobilization of P (Fig. 1) and, subject to microbial turnover times (estimated to be 2–3 times faster in the rhizosphere; Cheng, 2009), the temporal availability of P for plant uptake.

Controlled experiments using plants inoculated with P-mineralizing microorganisms provide further evidence for microbially mediated P availability to plants. Studies by Richardson et al. (2001) showed that when grown in defined media, utilization of phytate P by grass and legume pasture species was improved by inoculation with soil microorganisms. More specifically this was demonstrated using a bacterial isolate with high phytase activity. Plants genetically modified to release an extracellular fungal phytase (from *Aspergillus niger*) from roots showed similar novel ability to acquire P directly from phytate (Richardson et al., 2005). However, when evaluated in soil, these plants show significant improvement in P nutrition only in soils with higher substrate levels (as measured by enzyme lability assays), or in soils that were artificially amended with phytate (George et al., 2005a, 2005b). In addition to the importance of substrate availability, rapid adsorption of phytase to the soil solid phase was observed with loss of activity being dependent both on enzyme characteristics and soil properties (George et al., 2007a; Giaveno et al., 2010). Assessment of rhizosphere soils after plant growth indicated a depletion of phytase-labile P that, although soil-type dependent, did not differ substantially between control and transgenic lines or to control soils without plants (Richardson et al., 2009b). This suggests that microorganisms are in fact a key driver in regulating the mineralization of phytate in soil and their presence within the rhizosphere may compensate for a plants inability to otherwise acquire P directly from phytate. Bacteria with ability to mineralize phytate have been isolated from the rhizosphere and further work to assess the ecology and in situ function of such microorganisms in soil environments is warranted along with further assessment of their potential for development as inoculants (Unno et al., 2005; Jorquera et al., 2011).

SOLUBILIZATION OF INORGANIC P

A wide range of microorganisms able to solubilize inorganic P have been cultured from soil, including bacteria (e.g. *Actinomycetes*, *Pseudomonas*, and *Bacillus* spp.) and fungi (e.g. *Aspergillus* and *Penicillium* spp.). Such microorganisms are commonly isolated from the rhizosphere and their capacity to solubilize P is generally reported to be associated with ability in culture to acidify growth media (particularly when evaluated on Ca phosphates) and release organic anions, with citrate, gluconate, oxalate, and succinate being predominant (Khan et al., 2007). The amount of P solubilized in culture is dependent on the composition of the media, form of inorganic P precipitate used (including Ca, iron, and aluminum phosphates and various sources of rock phosphate), along with cultural and sampling procedures.

In many cases inoculation of plants with P-solubilizing microorganisms in controlled experiments results in improved growth and P nutrition, especially under glasshouse conditions and in fewer cases in the field (e.g. for review, see Kucey et al., 1989; Rodríguez and Fraga, 1999; Whitelaw, 2000; Gyaneshwar et al., 2002; Jakobsen et al., 2005; Khan et al., 2007, 2010; Harvey et al., 2009; Zaidi et al., 2009). Inconsistent performance under field conditions is commonly observed (and lack of response is also likely to be less frequently reported) and has been attributed to various factors that include: lack of persistence and competiveness of introduced microorganisms in soil and poor understanding of actual mechanisms involved in growth promotion, where P mobilization may not necessarily be the primary mechanism (Richardson, 2001; Khan et al., 2007; Zaidi et al., 2009). Processes that appear to be effective in the laboratory may also not be operable in soil. Generally there is a lack of knowledge concerning reactions of P in different soils and, in many cases, experiments are designed inappropriately to allow a specific response to P mobilization to be confirmed (Jakobsen et al., 2005). Moreover, while microorganisms may have capacity to directly solubilize P to meet their own requirements, subsequent benefits to plants may only occur following turnover of the microbial biomass. There is also a need to demonstrate that microorganisms in the rhizosphere have ability to deplete inorganic forms of soil P (Fig. 3) over and above that by plants alone. A recent study by Esberg et al. (2010) showed correlation between microbial respiration and changes in NaOH-extractable P and suggested that microbial access to this fraction was greater. Likewise, Bünemann et al. (2004) and Ehlers et al. (2010) have suggested greater access to fixed pools of inorganic P may occur in Ferrosol soils in response to growth enhancement of microorganisms resulting from addition of C substrates under laboratory incubations. Further work to quantify the relative ability of microorganisms to access different fractions of soil P, as compared with plants, is warranted.

It is commonly proposed that microorganisms may therefore play an important role in the development of integrated and sustainable production systems to improve P use efficiency through use of specific inocu-

lants. For example, various commercial products (primarily based on bacterial isolates that reportedly solubilize P) are widely promoted as plant growth promoting and specific fungal-based products have been developed for extensive use in cropping systems for northern America and Australia. In particular, isolates of *Penicillium* spp. appear to have high potential for development as inoculants based on their capacity to solubilize P under various laboratory conditions, to be mass produced, and to readily and nonspecifically colonize the rhizosphere of a range of potential host plants (Kucey, 1987; Whitelaw, 2000; Wakelin et al., 2004; Harvey et al., 2009). However, while there is evidence that such inoculants can promote plant growth under different soil conditions (Kucey et al., 1989; Wakelin et al., 2007; Karamanos et al., 2010) whether this occurs as a direct consequence of P mobilization in soil environments remains to be confirmed. Stimulation of root growth or greater elongation of root hairs (e.g. Vessey and Heisinger, 2001; Fig. 2) by specific microorganisms may enhance plant P nutrition indirectly by allowing greater exploration of soil, rather than by direct increase in the availability of soil P. Indeed in a recent evaluation of the performance of *Penicillium bilaii* inoculant on wheat (*Triticum aestivum*) crops across a range of 47 field experiments, Karamanos et al. (2010) reported no consistent benefit in terms of plant P nutrition and found no relationship between growth responses and any soil or environmental parameters, despite the majority of trials being responsive to P addition. Such studies further highlight the need for better understanding of the potential mechanisms associated with microbially mediated P availability in soils and the complexity of managing biological interactions in such environments. A key requirement for successful deployment of inoculants is the development of appropriate formulation and delivery systems to ensure survival and effective establishment of target microorganisms within the rhizosphere. Poor competitive ability and lack of persistence of inoculants in soils is commonly considered to be an important factor that may restrict their effectiveness (Richardson, 2001). In addition, there is need to better understand how soil properties and/or environmental factors may influence the efficacy or potential for P mobilization or to improve the predictability of likely response.

ECOLOGICAL CONSIDERATIONS AND FUTURE PROSPECTS

Opportunities for enhancing microbially mediated P availability in soils appear feasible and might be achieved by either management of existing populations of microorganisms to optimize their capacity to mobilize P or through the use of specific microbial inoculants. However, limited success has been achieved to date and future opportunity with either approach requires more detailed understanding of microbial interactions in soil across the Bacterial, Archaeal, and Eukaryal (e.g. fungi and protozoa) domains. This includes ecological consideration of single microorganisms (as inoculants) or different groups of soil microorganisms (as communities), how they interact in the rhizosphere or within roots (endophytes), their ability to mobilize P from different soil fractions, and how soil and farm management practices influence these processes. Microbial communities in soil are highly diverse; for example, bacteria alone may be represented by as many as 10^4 species per gram of soil with indications of more than one million distinct soil bacterial genomes (Torsvik et al., 2002; Gans et al., 2005). With molecular tools and metagenomic approaches we are only now starting to unravel the structure and function of soil microbial communities. Molecular-based techniques combined with high-resolution image analysis (Sørensen et al., 2009) and ability to integrate these with respect to biogeochemical interactions using nanoSIMS and other spectroscopic methods, provides new possibilities for investigating spatial and temporal aspects of microbial communities in the rhizosphere along with their associated functions.

To date research on P-mobilizing soil microorganisms has essentially focused on single microorganisms that can be cultured in isolation and we have little understanding of how they interact within the rhizosphere. Moreover, we have little appreciation of whether plants are able to host specific interactions with microorganisms to enhance P availability, other than by association with mycorrhizal fungi. Recent studies with *Pseudomonas* spp. isolated from soil suggests that capacity to solubilize P is associated with phylogenetic lineage and that it may be feasible therefore to select specific microorganisms or communities for enhanced capacity to mobilize P (Browne et al., 2009). Microbial activity and community composition in the rhizosphere is driven not only by availability of C, but also by interaction with various plant- and microbially derived signal molecules (Bais et al., 2006; Badri et al., 2009). These secondary metabolites include flavonoids, phytoalexins, and other antimicrobial compounds, various phytostimulants (e.g. strigolactones) shown to stimulate root colonization by mycorrhizal fungi (Xie and Yoneyama, 2010), and specific molecules that may mimic or interfere with microbial signaling mechanisms through quorum sensing (e.g. *N*-acyl homo-Ser lactones). Quorum sensing plays an important role in regulation of growth and function of various soil bacteria, including symbionts and some pathogens (including *Pseudomonas* spp.) that are known to inhabit the rhizosphere (Barriuso et al., 2008; Teplitski et al., 2011). However, research concerning how such factors might shape microbial communities and their functionality in processes like P mobilization are unknown. In a study by George et al. (2009), no differences in bacterial community structure were detected in the rhizosphere or on the root surface (rhizoplane) of tobacco (*Nicotiana*

tabacum) plants modified to release an extracellular fungal phytase as compared to control lines. By contrast, large differences in community structure occurred in response to soil treatments that were specifically implemented to modify P availability. Genetic manipulation of plants and microorganisms for key traits that are known to be associated with P mobilization or growth promotion (e.g. extracellular phytase and genes for synthesis and/or release of organic anions by plants and microorganisms; Gyaneshwar et al., 2002; George et al., 2005a; Rodriguez et al., 2006), along with generation of specific mutants in key target genes for particular traits (e.g. organic anion release in *Pseudomonas* spp., Miller et al., 2010), are useful for both elucidation of mechanisms and for quantifying their contribution to increased P availability in soil.

Molecular-based techniques also provide new opportunity to detect the presence and abundance of specific microorganisms or to quantify the expression of target genes directly in soil or in the rhizosphere with high levels of sensitivity. For example, specific primers based on conserved regions have been described for various microorganisms associated with P mobilization, including mycorrhizal fungi, *Penicillium* spp., and *Pseudomonas* spp. (e.g. Haugland et al., 2004; Costa et al., 2006; Oliveira et al., 2009), as have primers that are directed at traits such as bacterial phytases (Lim et al., 2007; Jorquera et al., 2011). Microarrays composed of suites of functional bacterial genes (He et al., 2007) and arrays for phylogenetic analysis of bacterial diversity based on 16S-RNA gene sequences (Brodie et al., 2006), along with next-generation sequencing and soil microbiome analyses, provide further application for assessment of diversity surrounding particular traits or functional groups of microorganisms. Collectively, these tools provide new opportunities to address key questions in microbial community ecology and to assess the survival and persistence of specific inoculants within the rhizosphere. It is evident that soil microorganisms play an important role in the cycling of P in soil-plant systems and it is expected that better understanding of their contribution to the mobilization of soil P and plant P nutrition will provide opportunity for development of more P-efficient and sustainable agricultural systems and improved knowledge of ecosystem function.

Received March 1, 2011; accepted May 20, 2011; published May 23, 2011.

LITERATURE CITED

Achat DL, Morel C, Bakker MR, Augusto L, Pellerin S, Gallet-Budynek A, Gonzalez M (2010) Assessing turnover of microbial biomass phosphorus: combination of an isotopic dilution method with a mass balance model. Soil Biol Biochem **42:** 2231–2240

Badri DV, Weir TL, van der Lelie D, Vivanco JM (2009) Rhizosphere chemical dialogues: plant-microbe interactions. Curr Opin Biotechnol **20:** 642–650

Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol **57:** 233–266

Barriuso J, Ramos Solano B, Fray RG, Cámara M, Hartmann A, Gutiérrez Mañero FJ (2008) Transgenic tomato plants alter quorum sensing in plant growth-promoting rhizobacteria. Plant Biotechnol J **6:** 442–452

Bonkowski M (2004) Protozoa and plant growth: the microbial loop in soil revisited. New Phytol **162:** 617–631

Brodie EL, Desantis TZ, Joyner DC, Baek SM, Larsen JT, Andersen GL, Hazen TC, Richardson PM, Herman DJ, Tokunaga TK, et al (2006) Application of a high-density oligonucleotide microarray approach to study bacterial population dynamics during uranium reduction and reoxidation. Appl Environ Microbiol **72:** 6288–6298

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

Bucher M (2007) Functional biology of plant phosphate uptake at root and mycorrhiza interfaces. New Phytol **173:** 11–26

Bünemann EK (2008) Enzyme additions as a tool to assess the potential bioavailability of organically bound nutrients. Soil Biol Biochem **40:** 2116–2129

Bünemann EK, Marschner P, McNeill AM, McLaughlin MJ (2007) Measuring rates of gross and net mineralisation of organic phosphorus in soils. Soil Biol Biochem **39:** 900–913

Bünemann EK, Steinebrunner F, Smithson PC, Frossard E, Oberson A (2004) Phosphorus dynamics in a highly weathered soil as revealed by isotopic labelling techniques. Soil Sci Soc Am J **68:** 1645–1655

Chen CR, Condron LM, Davis MR, Sherlock RR (2002) Phosphorus dynamics in the rhizosphere of perennial ryegrass (*Lolium perenne* L.) and radiata pine (*Pinus radiata* D. Don.). Soil Biol Biochem **34:** 487–499

Cheng WX (2009) Rhizosphere priming effect: its functional relationships with microbial turnover, evapotranspiration, and C-N budgets. Soil Biol Biochem **41:** 1795–1801

Costa R, Salles JF, Berg G, Smalla K (2006) Cultivation-independent analysis of *Pseudomonas* species in soil and in the rhizosphere of field-grown *Verticillium dahliae* host plants. Environ Microbiol **8:** 2136–2149

Ehlers K, Bakken LR, Frostegard A, Frossard E, Bunemann EK (2010) Phosphorus limitation in a Ferralsol: impact on microbial activity and cell internal P pools. Soil Biol Biochem **42:** 558–566

Esberg C, du Toit B, Olsson R, Ilstedt U, Giesler R (2010) Microbial responses to P addition in six South African forest soils. Plant Soil **329:** 209–225

Gans J, Wolinsky M, Dunbar J (2005) Computational improvements reveal great bacterial diversity and high metal toxicity in soil. Science **309:** 1387–1390

George TS, Richardson AE, Li SS, Gregory PJ, Daniell TJ (2009) Extracellular release of a heterologous phytase from roots of transgenic plants: does manipulation of rhizosphere biochemistry impact microbial community structure? FEMS Microbiol Ecol **70:** 433–445

George TS, Richardson AE, Smith JB, Hadobas PA, Simpson RJ (2005a) Limitations to the potential of transgenic *Trifolium subterraneum* L. plants that exude phytase when grown in soils with a range of organic P content. Plant Soil **278:** 263–274

George TS, Simpson RJ, Gregory PJ, Richardson AE (2007a) Differential interaction of *Aspergillus niger* and *Peniophora lycii* phytases with soil particles affects the hydrolysis of inositol phosphates. Soil Biol Biochem **39:** 793–803

George TS, Simpson RJ, Hadobas PA, Marshall DJ, Richardson AE (2007b) Accumulation and phosphatase-lability of organic phosphorus in fertilised pasture soils. Aust J Agric Res **58:** 47–55

George TS, Simpson RJ, Hadobas PA, Richardson AE (2005b) Expression of a fungal phytase gene in *Nicotiana tabacum* improves phosphorus nutrition of plants grown in amended soils. Plant Biotechnol J **3:** 129–140

Gerretsen FC (1948) The influence of microorganisms on the phosphate intake by the plant. Plant Soil **1:** 51–81

Giaveno C, Celi L, Richardson AE, Simpson RJ, Barberis E (2010) Interaction of phytases with minerals and availability of substrate affect the hydrolysis of inositol phosphates. Soil Biol Biochem **42:** 491–498

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

Harvey PR, Warren RA, Wakelin S (2009) Potential to improve root access to phosphorus: the role of non-symbiotic microbial inoculants in the rhizosphere. Crop Pasture Sci **60:** 144–151

Haugland RA, Varma M, Wymer LJ, Vesper SJ (2004) Quantitative PCR

analysis of selected *Aspergillus*, *Penicillium* and *Paecilomyces* species. Syst Appl Microbiol **27:** 198–210

Hayat R, Ali S, Amara U, Khalid R, Ahmed I (2010) Soil beneficial bacteria and their role in plant growth promotion: a review. Ann Microbiol **60:** 579–598

He ZL, Gentry TJ, Schadt CW, Wu LY, Liebich J, Chong SC, Huang ZJ, Wu WM, Gu BH, Jardine P, et al (2007) GeoChip: a comprehensive microarray for investigating biogeochemical, ecological and environmental processes. ISME J **1:** 67–77

Jakobsen I, Leggett ME, Richardson AE (2005) Rhizosphere microorganisms and plant phosphorus uptake. *In* JT Sims, AN Sharpley, eds, Phosphorus: Agriculture and the Environment. American Society for Agronomy, Madison, WI, pp 437–494

Jones DL, Nguyen C, Finlay RD (2009) Carbon flow in the rhizosphere: carbon trading at the soil-root interface. Plant Soil **321:** 5–33

Jorquera MA, Crowley DE, Marschner P, Greiner R, Fernández MT, Romero D, Menezes-Blackburn D, De La Luz Mora M (2011) Identification of β-propeller phytase-encoding genes in culturable *Paenibacillus* and *Bacillus* spp. from the rhizosphere of pasture plants on volcanic soils. FEMS Microbiol Ecol **75:** 163–172

Karamanos RE, Flore NA, Harapiak JT (2010) Re-visiting use of *Penicillium bilaii* with phosphorus fertilization of hard red spring wheat. Can J Plant Sci **90:** 265–277

Khan MS, Zaidi A, Ahemad M, Oves M, Wani PA (2010) Plant growth promotion by phosphate solubilizing fungi—current perspective. Arch Agron Soil Sci **56:** 73–98

Khan MS, Zaidi A, Wani PA (2007) Role of phosphate-solubilizing microorganisms in sustainable agriculture—a review. Agron Sustain Develop **27:** 29–43

Kirkby CA, Kirkegaard JA, Richardson AE, Wade LJ, Blanchard C, Batten G (July 15, 2011) Stable soil organic matter: a comparison of C:N:P:S ratios in Australian and other world soils. http://dx.doi.org/10.1016/j.geoderma.2011.04.010

Kucey RMN (1987) Increased phosphorus uptake by wheat and field bean inoculated with phosphorus-solubilizing *Penicillium bilaji* strain and with vesicular arbuscular mycorrhizal fungi. Appl Environ Microbiol **53:** 2699–2703

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

Lim BL, Yeung P, Cheng C, Hill JE (2007) Distribution and diversity of phytate-mineralizing bacteria. ISME J **1:** 321–330

Macklon AES, Grayston SJ, Shand CA, Sim A, Sellars S, Ord BG (1997) Uptake and transport of phosphorus by *Agrostis capillaris* seedlings from rapidly hydrolysed organic sources extracted from P^{32}-labelled bacterial cultures. Plant Soil **190:** 163–167

McLaughlin MJ, Alston AM, Martin JK (1988) Phosphorus cycling in wheat-pasture rotations. II. The role of the microbial biomass in phosphorus cycling. Aust J Soil Res **26:** 333–342

Miller SH, Browne P, Prigent-Combaret C, Combes-Meynet E, Morrissey JP, O'Gara F (2010) Biochemical and genomic comparison of inorganic phosphate solubilization in *Pseudomonas* species. Environ Microbiol Reports **2:** 403–411

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

Oehl F, Frossard E, Fliessbach A, Dubois D, Oberson A (2004) Basal organic phosphorus mineralization in soils under different farming systems. Soil Biol Biochem **36:** 667–675

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

Olander LP, Vitousek PM (2004) Biological and geochemical sinks for phosphorus in soil from a wet tropical forest. Ecosyst **7:** 404–419

Oliveira CA, Sa NMH, Gomes EA, Marriel IE, Scotti MR, Guimaraes CT, Schaffert RE, Alves VMC (2009) Assessment of the mycorrhizal community in the rhizosphere of maize (*Zea mays* L.) genotypes contrasting for phosphorus efficiency in the acid savannas of Brazil using denaturing gradient gel electrophoresis (DGGE). Appl Soil Ecol **41:** 249–258

Richardson AE (2001) Prospects for using soil microorganisms to improve the acquisition of phosphorus by plants. Aust J Plant Physiol **28:** 897–906

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

Richardson AE, George TS, Hens M, Simpson RJ (2005) Utilization of soil organic phosphorus by higher plants. *In* BL Turner, E Frossard, DS Baldwin, eds, Organic Phosphorus in the Environment. CABI, Wallingford, UK, pp 165–184

Richardson AE, Hadobas PA, Hayes JE, O'Hara CP, Simpson RJ (2001) Utilization of phosphorus by pasture plants supplied with *myo*-inositol hexaphosphate is enhanced by the presence of soil microorganisms. Plant Soil **229:** 47–56

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

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

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

Ryan PR, Delhaize E, Jones DL (2001) Function and mechanism of organic anion exudation from plant roots. Annu Rev Plant Physiol Plant Mol Biol **52:** 527–560

Sánchez PA (2010) Tripling crop yields in tropical Africa. Nat Geosci **3:** 299–300

Seeling B, Zasoski RJ (1993) Microbial effects in maintaining organic and inorganic solution phosphorus concentrations in a grassland topsoil. Plant Soil **148:** 277–284

Sørensen J, Nicoliasen MH, Ron E, Simonet P (2009) Molecular tools in rhizosphere microbiology—from single-cell to whole-community analysis. Plant Soil **321:** 483–512

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

Teplitski M, Mathesius U, Rumbaugh KP (2011) Perception and degradation of N-acyl homoserine lactone quorum sensing signals by mammalian and plant cells. Chem Rev **111:** 100–116

Torsvik V, Øvreås L, Thingstad TF (2002) Prokaryotic diversity—magnitude, dynamics, and controlling factors. Science **296:** 1064–1066

Turner BL (2007) Inositol phosphates in soil: amounts, forms and significance of the phosphorylated inositol stereoisomers. *In* BL Tuner, AE Richardson, EJ Mullaney, eds, Inositol Phosphates; Linking Agriculture and the Environment. CABI, Wallingford, UK, pp 186–206

Turner BL, Haygarth PM (2001) Biogeochemistry: phosphorus solubilization in rewetted soils. Nature **411:** 258

Turner BL, Mahieu N, Condron LM (2003) The phosphorus composition of temperate pasture soils determined by NaOH-EDTA extraction and solution P^{-31} NMR spectroscopy. Org Geochem **34:** 1199–1210

Unno Y, Okubo K, Wasaki J, Shinano T, Osaki M (2005) Plant growth promotion abilities and microscale bacterial dynamics in the rhizosphere of Lupin analysed by phytate utilization ability. Environ Microbiol **7:** 396–404

Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. New Phytol **157:** 423–447

Vessey JK, Heisinger KG (2001) Effect of *Penicillium bilaii* inoculation and phosphorus fertilisation on root and shoot parameters of field-grown pea. Can J Plant Sci **81:** 361–366

Wakelin SA, Gupta VV, 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

Wakelin SA, Warren RA, Harvey PR, Ryder MH (2004) Phosphate solubilization by *Penicillium* spp. closely associated with wheat roots. Biol Fertil Soils **40:** 36–43

Whitelaw MA (2000) Growth promotion of plants inoculated with phosphate-solubilizing fungi. Adv Agron **69:** 99–151

Xie XN, Yoneyama K (2010) The strigolactone story. Annu Rev Phytopathol **48:** 93–117

Zaidi A, Khan MS, Ahemad M, Oves M (2009) Plant growth promotion by phosphate solubilizing bacteria. Acta Microbiol Immunol Hung **56:** 263–284