Chapter 8
THE ROLE OF RHIZOSPHERE MICROORGANISMS IN RELATION TO P UPTAKE BY PLANTS

Petra Marschner

INTRODUCTION

The rhizosphere is defined as the soil around the roots that is influenced by the root (Hiltner 1904). Due to the release of easily decomposable compounds by the roots (root exudates), the rhizosphere is characterized by high microbial density. Rhizosphere microorganisms strongly influence nutrient uptake by plants by either enhancing or decreasing nutrient availability.

Rhizosphere microbial communities are a subset of the soil microbial community, but are often quite distinct from those in the bulk soil (Foster 1986; Marilley and Aragno 1999; Gomes *et al*. 2001; Berg *et al*. 2002). Rhizosphere communities are influenced by soil and plant factors. Soils can have distinct microbial communities (Gelsomino *et al*. 1999; Carelli *et al*. 2000), as a result of the soil physical and chemical characteristics (e.g. soil texture, nutrient and organic matter content and pH) and environmental factors such as climate and vegetation. Plants contribute to these physical and chemical properties by depositing between 1% and 25% of their net photosynthetic production, which includes dead roots, sloughed-off cells and soluble compounds (Merbach *et al*. 1999). A large proportion of the root exudates such as sugars, organic acid anions or amino acids are easily degradable by microorganisms in the rhizosphere resulting in high microbial density and activity in the rhizosphere (Foster 1986; Kandeler *et al*. 2001).

The main driver of rhizosphere community composition is the plant species; different plant species growing in the same soil often have distinct rhizosphere communities (Ibekwe and Kennedy 1998; Marschner *et al*. 2001b); a given plant species may have a similar community structure when grown in different soils (Grayston *et al*. 1998; Miethling *et al*. 2000). The effects of plant species on rhizosphere community composition often become more pronounced during plant development (Gomes *et al*. 2003; Marschner *et al*. 2001b). It is generally accepted that plant species-specific rhizosphere communities are the result of differential rhizodeposition and, in particular, root exudate amount and composition.

In agreement with the view that a large proportion of root exudates are easily degradable, microbial species with high growth rates and relatively high nutrient requirements, such as Pseudomonas spp., are often found to dominate in the

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rhizosphere (De Leij *et al*. 1993; Marilley and Aragno 1999). Although the rhizosphere is a habitat with large amounts of readily-available C sources, it is however, also the site of intense competition between microorganisms (Whipps and Lynch 1983). Indeed, as an increasing number of rhizosphere microbial species are identified, it becomes clear that they have a wide range of growth strategies (Gomes *et al*. 2001; Smalla *et al*. 2001; Mansfeld-Giese *et al*. 2002).

Root exudation, and consequently microbial density and community structure, vary along the root axis. Root exudates are primarily released in the zone of elongation behind the root tip (Hoffland *et al*. 1989; Römheld 1991; Marschner *et al*. 1997). In the older root parts, the main substrates for microbial growth are cellulose and other recalcitrant cell wall materials from sloughed-off root cortex tissues. The differences in the type and quantity of carbon available in different root zones influence microbial growth and result in distinct rhizosphere community structures (Yang and Crowley 2000; Marschner *et al*. 2001a). Certain components of root exudates have a selective influence on rhizosphere microorganisms by repelling some species and attracting others (Geurts and Franssen 1996). Examples for the latter are flavonoids released by legume roots that specifically attract Rhizobium. In contrast, microorganisms can influence the conditions in the rhizosphere by enhancing root exudation (Meharg and Killham 1995) or producing growth factors that influence root growth (Frankenberger and Poth 1987).

From this brief overview it is evident that microbial community composition and activity in the rhizosphere are temporarily and spatially highly variable and affected by plant species, soil and environmental factors. These not only make studying rhizosphere microorganisms challenging, but are also important considerations when the role of rhizosphere microorganisms in P uptake by plants is discussed.

Rhizosphere microorganisms may increase or decrease the availability of phosphate (Pi) to plants (Figure 8.1). Solubilization and mineralization of soil P or stimulation of root and root hair growth by rhizosphere microorganisms will lead to increased plant Pi uptake. Alternatively, plant Pi uptake may be decreased by competition for Pi or inhibition of root and root hair growth. The amount of P in the microbial biomass available for plant P uptake is variable and influenced by the carbon supply. Phosphorus uptake into the microbial biomass (net immobilization) may reduce plant P availability, whereas turnover of the biomass may release P.

ROLE OF RHIZOSPHERE MICROORGANISMS IN INCREASING PLANT AVAILABLE P

As a result of the low P availability in most soils, the capacity to mobilize P is widespread among soil microorganisms. Mechanisms by which P availability can be increased include (i) solubilization of poorly soluble inorganic P forms by releasing organic acid anions or protons to modify soil pH (Illmer *et al*. 1995; Illmer and Schinner 1995) and (ii) mineralization of organic P by release of phosphatases.

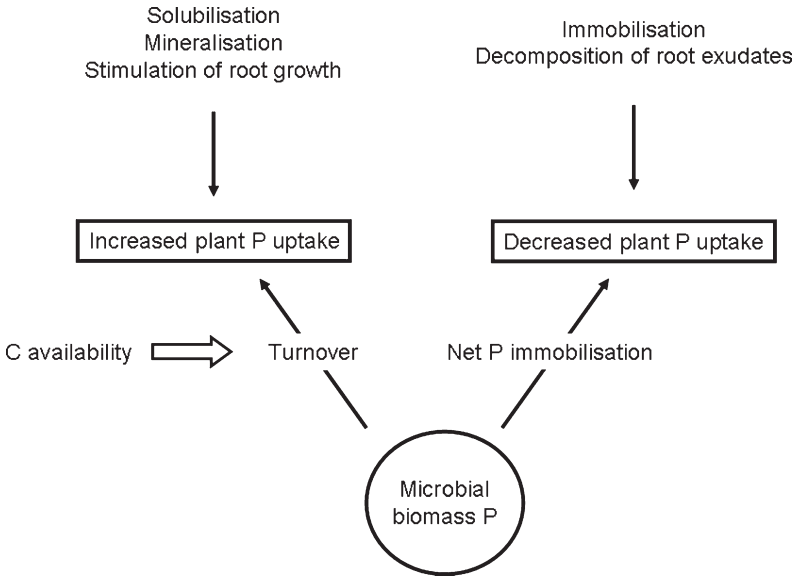

Fig. 8.1 Mechanisms by which rhizosphere microorganisms can increase or decrease plant P uptake

The effectiveness of these mechanisms will depend on a number of factors, namely the pH buffering capacity of the soil, decomposition rate and/or sorption of organic acid anions and phosphatases to soil particles.

P solubilization

A large number of microorganisms have been isolated that show high P solubilization *in vitro* (Table 8.1; Banik and Dey 1983; Whitelaw *et al*. 1999). However, these *in vitro* tests should be viewed with caution. On nutrient-rich media, a large number of soil microorganisms can solubilize poorly soluble Ca-phosphates (Louw 1969), because high growth rates are often associated with proton release and hence dissolution of Ca-phosphates. Proton release is not effective in mobilizing P from Fe or Al phosphates or Pi adsorbed to Fe or Al oxides. For these forms of P, mobilization requires the release of organic acid anions, which release Pi via ligand exchange or chelation of Fe or Al. Hence, the capacity to mobilize Pi from Fe- or Al-phosphates is less common, and Pi mobilization rates are often lower than for Ca-phosphates (Barthakur 1978; Banik and Dey 1983).

Under nutrient-poor conditions, and hence lower microbial growth rates, P solubilization is often strongly reduced. As mentioned above, the rhizosphere may not be as nutrient-rich as previously thought. Therefore isolates selected as strong P solubilizers *in vitro* may not be effective in the rhizosphere due to lack of carbon

Table 8.1 Examples of microbial genera that have been shown to be P solubilizers or phytase producers

Genus	Reference
P solubilizers	
Aspergillus, Penicillium, Trichoderma	Barthakur 1978
Bradyrhizobium, *Rhizobium*	Antoun *et al*. 1998
Enterobacter	Kim *et al*. 1997b
Gordonia	Hoberg *et al*. 2005
Panthoea	Deubel *et al*. 2000
Pseudomonas	Deubel *et al*. 2000; Hoberg *et al*. 2005
Rahella	Kim *et al*. 1997a
Phytase producers	
Aspergillus, Emmericella, Penicillum	Yadav and Tarafdar 2003
Peniophora	George *et al*. 2007
Pseudomonas	Richardson and Hadobas 1997
Telephora, Suillus (ectomycorrhizal fungi)	Colpaert *et al*. 1997

and other nutrients. Additionally, P mobilization may be transient because of the re-formation of poorly soluble P forms (Delvasto *et al*. 2006) and the uptake of Pi by microorganisms (Hoberg *et al*. 2005).

Due to the ease of isolating microorganisms with apparently high P solubilization capacity, many studies have been conducted to investigate the effect of inoculation with P solubilizers on plant growth and Pi uptake. In several pot and field experiments, inoculation with P-solubilizing microorganisms resulted in increased plant growth and Pi uptake (Gerretsen 1948; Kundu and Gaur 1980; Kumar and Narula 1999; see also Table 8.1). Compared to plants grown in sterile media, Pi uptake by oat plants inoculated with a soil microbial community increased by 120% and 320% when grown with Fe-phosphate and Ca-phosphate (rock-P), respectively (Gerretsen 1948). But there are also reports in which inoculation did not increase plant growth and Pi uptake (Azcon-Aguilar *et al*. 1986; Badr el-Din *et al*. 1986). It is likely that there are a large number of similar 'disappointing' results that have not been published. The poor effectiveness of inoculated strains to increase the plant available Pi, may be the result of poor growth and survival due to lack of nutrients and/or low competitiveness compared to the indigenous microflora. Successful inoculants must be 'rhizosphere-competent.' A number of traits have been shown to be important for rhizosphere competence, including motility, high growth rate, ability to synthesize amino acids and vitamin B1, ability to utilize organic acids, presence of certain cell surface proteins as well as rapid adjustment to changing conditions (Lugtenberg and Dekkers 1999).

Often, a combination of microorganisms with different characteristics, such as P solubilizers combined with N_2 fixers or with AM fungi, is superior to inoculation with the P solubilizers alone (Kundu and Gaur 1980; Toro *et al*. 1997; Sahin *et al*. 2004).

P mineralization

Up to 80% of soil P can be in organic form (Richardson 2001). Hence, the ability to access organic P can contribute substantially to increasing plant available Pi. Phosphatases hydrolyze organic P and release Pi. The activity of phosphatases decreases with increasing distance from the root surface (Tarafdar and Jungk 1987; Kandeler *et al*. 2001). Phosphomonoesterases and phosphodiesterases can be released by plant roots, rhizosphere microorganisms and also mycorrhizal fungi (Joner and Johansen 2000; Koide and Kabir 2000). Therefore, it is difficult to quantify the contribution of rhizosphere microorganisms to phosphatase activity in the rhizosphere.

Phytate, which is considered to be the dominant form of organic P in soils (Turner *et al*. 2003), is a poor P source for plants grown under sterile conditions, because plant roots have low extracellular phytase activity (Hayes *et al*. 2000; Richardson *et al*. 2001). However, microorganisms can excrete phytase (Table 8.1; Richardson and Hadobas 1997; George *et al*. 2007). Indeed, compared with plants grown under sterile conditions, inoculation with a soil suspension strongly increased plant Pi uptake from phytate, suggesting that microorganisms play an important role in mobilizing P from phytate (Richardson *et al*. 2001). However, the effectiveness of phytase in the soil is unclear because (i) phytate is adsorbed to Fe or Al oxides, which strongly reduces its availability, and (ii) phytase is rapidly adsorbed to soil particles, leading to decreased activity (George *et al*. 2005, 2007). Moreover, phytate may not be the dominant form of organic P in soils (Smernik and Dougherty 2007). It appears that some of the compounds in NMR spectra may have been falsely identified as phytate. In a range of different Australian pasture soils, phytate comprised <5% of organic P and <3% of total P (Smernik and Dougherty 2007).

Indirect stimulation of plant P uptake

Rhizosphere microorganisms can also enhance plant Pi uptake indirectly by releasing plant growth regulators or stimulating mycorrhizal colonization. Release of plant growth regulators such as IAA by rhizosphere microorganisms can enhance root hair formation (Schmidt *et al*. 1988). Mycorrhiza helper bacteria (MHB), which can be readily isolated from AM and ectomycorrhiza, have been shown to stimulate mycorrhizal colonization even in non-sterile soil and when present at low numbers (Garbaye 1994; Frey-Klett *et al*. 1997). In bulk soil it has been shown that organic acids produced during microbial decomposition of plant residues can increase P availability by competition for sorption sites and complexation of Al and Fe (Iyamuremye *et al*. 1996). Decomposition of root exudates or sloughed-off root cells could therefore also increase P availability in the rhizosphere.

ROLE OF RHIZOSPHERE MICROORGANISMS IN DECREASING PLANT AVAILABLE P

Rhizosphere microorganisms can also reduce the availability of Pi to plants by taking up P into the microbial biomass, decomposing Pi-mobilizing root exudates or by inhibiting root growth.

P uptake into the microbial biomass (Immobilization)

In the rhizosphere, plant and microbial solubilization and mineralization processes occur simultaneously. For bulk soil it has been shown that mineralization/solubilization dominate at low soil C/P ratios, whereas immobilization (uptake of P by the microbial biomass) exceeds mineralization/solubilization at high C/P ratios (He *et al*. 1997). Root exudates consist predominantly of sugars, hence are C-rich. Therefore, it can be assumed that microbial immobilization of P dominates in the rhizosphere. Thus, plants and microorganisms compete for P. McLaughlin *et al*. (1988) investigated the distribution of P in the plant-soil system after addition of isotopically labeled residues or inorganic P fertilizer. Of the fertilizer P, 18% was taken up by the plants and 29% by the soil microbial biomass. The distribution of residue P showed a similar bias to the microbial biomass, with 65% being taken up by the microbial biomass and 16% being taken up by plants. This indicates that the microbial biomass is more competitive at acquiring P than plants (McLaughlin and Alston 1986). However, as explained below, microbial P demand is a function of C availability. Thus, microbial competition for P is mediated by the concentration of easily available C compounds.

Decomposition of root exudates

Organic acid anions released by plant roots, which could potentially mobilize P, are rapidly decomposed in the soil (Van Hees *et al*. 2002). Together with organic acid anion sorption (Ström *et al*. 2001), this explains the discrepancy between the often high exudation rates of P deficient plants, such as white lupin in solution culture, and the relatively low organic acid anion concentrations measured in the rhizosphere. Therefore, the importance of organic acid anions for Pi mobilization has been questioned by Jones (1998), who argued that the organic acid anion concentrations measured in the rhizosphere of most plants would not be high enough to mobilize sufficient amounts of Pi. Hence, by decomposing organic acid anions, rhizosphere microorganisms can reduce the availability of Pi for uptake by plants. However, organic acid anion exudation may not be as ineffective as the above discussion suggests. The main sites of organic acid anion exudation are the root tips

and, in some plant species, specialized root structures such as cluster roots. Microbial density at the root tip is lower than in the older root zones. Additionally, the low pH and release of phenolic compounds in cluster roots may inhibit microorganisms. Hence, in certain root zones, decomposition of organic acid anions may be lower than in the root system in general.

Finally, rhizosphere microorganisms and, particularly deleterious or pathogenic microorganisms, may reduce plant Pi uptake by inhibiting root growth or damaging roots. Similarly, inhibition of mycorrhizal colonization could reduce Pi uptake.

THE ROLE OF THE MICROBIAL BIOMASS IN P UPTAKE BY PLANTS

In the presence of a readily available carbon source, P is rapidly immobilized in the microbial biomass. However, upon C depletion microbial growth rates decrease and part of the microbial biomass may die off, releasing P. The rapid turnover of biomass P in response to addition of glucose to soil is shown in Figure 8.2. On day two, increasing the amount of glucose-C added to the soil resulted in increasing P in the microbial biomass and decreasing plant available P (resin P). Over time, microbial biomass P decreased due to depletion of C and, as a result of net P release from the microbial biomass, plant available P increased. This clearly shows (i) the importance of C supply for P immobilization in the microbial biomass, (ii) the rapid turnover of microbial biomass once C is depleted, and (iii) the direct and negative relationship between microbial P and plant available P. It should be noted that this study was carried out in a soil with low P fixation capacity. The relationship between microbial P and plant available P may be less clear in soils with high P fixation capacity, when P released from the biomass is fixed rather than becoming available. Interestingly, P addition did not increase microbial biomass P in the presence of glucose in this study, indicating that the microbial biomass in this soil was C and not P limited.

Hence, an active microbial biomass with a high turnover rate can rapidly take up P, but may also represent a slow and constant source of available P through decomposition of dead microbial cells (Seeling and Zasoski 1993; Oberson *et al*. 2001). Seeling and Zasoski (1993) suggested that P uptake by the microbial biomass could be beneficial for plants, because it would decrease P fixation by maintaining low inorganic P concentrations in the soil solution.

The importance of the microbial biomass for plant P uptake appears to vary among plant families. In an acidic soil with low P availability, microbial biomass P in the rhizosphere was positively correlated with P uptake of three Poaceae, but not with P uptake of three brassicas (Table 8.2; Marschner *et al*. 2007), although the concentration of microbial biomass P in the rhizosphere was similar in the two plant families. In the brassicas, plant P uptake was correlated with root length and P availability in the rhizosphere, suggesting that P uptake was mainly governed by plant-inherent properties.

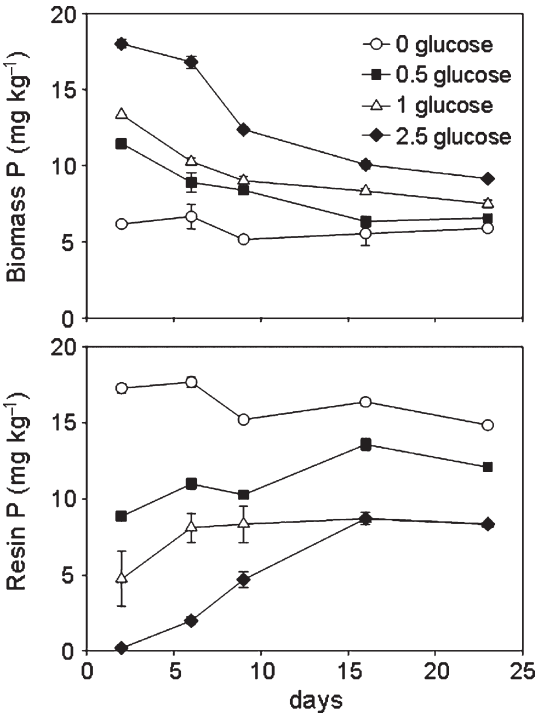

Fig. 8.2 Available P (resin P) and microbial P in soil after addition of C as glucose at 0, 0.5, 1 and 2.5 g C kg^{-1} soil

Table 8.2 Correlation coefficients between shoot P uptake (grams per plant) and rhizosphere properties (resin P, microbial P and acid phosphatase activity) or root length in Poaceae and brassicas at low and high P (across all growth stages) and at different growth stages (six-leaf, tillering/flowering and maturity; across P levels). (Data for Poaceae and brassicas are taken from Marschner *et al*. 2006 and Marschner *et al*. 2007, respectively. With permission from Elsevier.)

		Microbial P (mg kg^{-1})	Available P (mg kg^{-1})	Acid phosphatase activity (n Kat g^{-1})	Total root length (m)
Data set	Plant family	Correlation coefficient with plant P uptake			
Low P[a]	Poaceae	0.34	–	0.53	0.50
	brassicas	–	–0.57	0.53	0.77
High P[b]	Poaceae	0.68	–	–	0.61
	brassicas	–	–0.55	–	0.80
Six-leaf	Poaceae	0.97	0.77	0.81	0.85
	brassicas	0.45	0.88	0.46	0.79
Tillering/ flowering	Poaceae	0.78	0.96	0.73	0.67
	brassicas	–	0.75	0.48	0.47
Maturity	Poaceae	0.85	0.70	–	0.96
	brassicas	–	0.89	–	0.48

Only values with $P \leq 0.05$ are shown

[a]Low P: Poaceae 0; brassicas 25 mg P kg $soil^{-1}$ added as $FePO_4$

[b]High P: Poaceae 120; brassicas 100 mg P kg $soil^{-1}$ added as $FePO_4$

It can not be excluded that rhizosphere microorganisms contributed to P mobilization in the rhizosphere of the brassicas. However, differences in microbial community structure were not consistently related to differences in growth of Poaceae and brassicas (Marschner *et al*. 2006, 2007; Wang *et al*. 2007), indicating that presence or absence of certain microbial species or groups (e.g. P solubilizers) is not important for growth and P uptake.

CONCLUSIONS

We can conclude that rhizosphere microorganisms play an important role in the availability of Pi for plants. However, this is variable and affected by plant genotype, soil and environmental conditions. Moreover, the ratio of P mobilization to P immobilization and hence plant Pi availability are likely to vary along the root axis. The high rate of root exudation close to the root tip will lead to high growth rates of rhizosphere microorganisms accompanied by strong P mobilization. The mobilized P may be available to the plant, however exponentially growing microbial cells have a high P demand (low C/P ratio; Vrede *et al*. 2002). Thus, most of the mobilized P is likely to be taken up by the microorganisms. In the older root zones, the lower amount of carbon compounds results in lower microbial growth rates and hence P demand, as well as death of microorganisms (Vrede *et al*. 2002). Hence, microbial biomass P is likely to become available to the plant. Due to the widespread capacity among microorganisms to solubilize and/or mineralize poorly available P, the composition of the rhizosphere microbial community is probably less important than its activity.

To further elucidate the role of rhizosphere microorganisms it will be important to (i) quantify microbial biomass P turnover and the contribution of microbial biomass P to plant Pi uptake, e.g. by labeling the biomass with ^{32}P; (ii) measure the expression of genes involved in phosphatase and organic acid anion release by plant roots and rhizosphere microorganisms; and (iii) differentiate between plant and microbial phosphatases in the rhizosphere, for example using the techniques of proteomics.

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