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REVIEW ARTICLE

Acquisition of phosphorus and nitrogen in the rhizosphere and plant growth promotion by microorganisms

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Abstract The rhizosphere is a complex environment where roots interact with physical, chemical and biological properties of soil. Structural and functional characteristics of roots contribute to rhizosphere processes and both have significant influence on the capacity of roots to acquire nutrients. Roots also interact extensively with soil microorganisms which further impact on plant nutrition either directly, by influencing nutrient availability and uptake, or indirectly through plant (root) growth promotion. In this paper, features of the rhizosphere that are important for nutrient acquisition from soil are reviewed, with specific emphasis on the characteristics of roots that influence the availability and uptake of phosphorus and nitrogen. The interaction of roots with soil microorganisms, in particular with mycorrhizal fungi and non-symbiotic plant growth promoting rhizobacteria, is also considered in relation to nutrient availability and through the mechanisms that are associated with plant growth promotion.

Keywords Soil microorganisms · PGPR · Mycorrhizal fungi · Exudate · Phosphorus · Nitrogen · Uptake · Mineralization

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Introduction

The rhizosphere can be defined as the zone of soil around plant roots whereby soil properties are influenced by the presence and activity of the root. Changes to the physical, chemical and biological properties of rhizosphere soil has significant influence on the subsequent growth and health of plants. In terms of nutrient acquisition, both the structural and

functional characteristics of roots have long been recognized as being important in determining the capacity for plants to access and mediate the availability of essential nutrients in soil and to alleviate against those that are toxic (Darrah 1993; Hinsinger 1998; Marschner 1995). Furthermore, roots interact with diverse populations of soil microorganisms which have significant implication for growth and nutrition (Curl and Truelove 1986; Bowen and Rovira 1999; Mukerji et al. 2006; Brimecombe et al. 2007). Soil nutrients are transferred towards the root surface through the rhizosphere or, in the case of roots associated with mycorrhizal fungi, through the mycorrhizosphere, prior to acquisition.

Plants modify the physico-chemical properties and biological composition of the rhizosphere through a range of mechanisms, which include acidification through proton extrusion and the release of root exudates. Along with changes to soil pH, root exudates directly influence nutrient availability or have indirect effects through interaction with soil microorganisms. An outstanding feature of the rhizosphere is that rhizodeposition and root turnover account for up to 40% of the carbon input into soil and clearly is the major driver for soil microbiological processes (Grayston et al. 1996; Jones et al. 2009). Interactions between plant roots and soil microorganisms are ubiquitous across various trophic levels and are an essential component of ecosystem function. It has become increasingly evident that root interactions with soil microorganisms are intricate and involve highly complex communities that function in very heterogeneous environments (Giri et al. 2005). Microbial interactions with roots may involve either endophytic or free living microorganisms and can be symbiotic, associative or casual in nature. Beneficial symbionts include N_2-fixing bacteria (e.g. rhizobia) in association with legumes and interaction of roots with mycorrhizal fungi, with the later being particularly important in relation to plant P uptake. Associative and free-living microorganisms may also contribute to the nutrition of plants through a variety of mechanisms including direct effects on nutrient availability (e.g. N_2-fixation by diazotrophs and P-mobilization by many microorganisms), enhancement of root growth (i.e. through plant growth promoting rhizobacteria, or PGPR), as antagonists of root pathogens (Raaijmakers et al. 2009) or as saphrophytes that decompose soil detritus and subsequently increase nutrient availability through mineralization and microbial turnover. Such processes are likely to be of greater significance for nutrient availability in the rhizosphere where there is increased supply of readily metabolizable carbon and where mobilized nutrients can be more easily captured by roots.

In this review we address the acquisition of nutrients from soil by plants with specific emphasis on the structural and functional characteristics of roots that influence the availability and uptake of P and N. In particular, the importance of soil microorganisms and their interactions with roots in relation to nutrient availability is considered, along with their associated mechanisms of plant growth promotion. The review complements previous reviews that have specifically focused on either plant-based traits or mechanistic processes associated with P and N uptake (Raghothama 1999; Vance et al. 2003; Bucher 2007, Miller and Cramer 2004; Jackson et al. 2008). Although the rhizosphere is important for the efficient uptake of a wider range of macro and micronutrients (including Fe; Lemanceau et al. 2009), the review specifically focuses on N and P which are key nutrients that limit sustainable agricultural production across much of the globe (Tilman et al. 2002).

Mechanisms of nutrient acquisition by plant roots

Efficient capture of nutrients from soil by roots is a critical issue for plants given that in many environments nutrients have poor availability and may be deficient for optimal growth. Whilst nutrient supply in soil is often augmented by the application of fertilizers, the availability of nutrients is governed by a wide range of physico-chemical parameters, environmental and seasonal factors and biological interactions. Competition for nutrient uptake across different plant species, between different roots and with microorganisms is also significant (Hodge 2004). The rate of root growth and the plasticity of root architecture along with development of the rhizosphere, through either root growth or extension of root hairs, are clearly important for effective exploration of soil and interception of nutrients (Lynch 1995). Biochemical changes in the rhizosphere and interaction with microorganisms are also significant. However, the importance of different root traits and rhizosphere-mediated processes is dependent on the nutrient in question and other factors

that include plant species and soil type (Tinker and Nye 2000). For example, for nutrients present at low concentrations in soil solution and/or with poor diffusivity (e.g. P as either HPO_4^{2-} or $H_2PO_4^-$, and micronutrients, such as Fe and Zn), root growth and proliferation into new regions of soil and release of root exudates are of particular importance (Barber 1995; Darrah 1993). In contrast, nutrients present in either higher concentrations (e.g. K^+, NH_4^+), or with greater diffusion coefficients (e.g. NO_3^-, SO_4^- and Ca^{2+}), are able to move more freely toward the root through mass flow, where root distribution and architectural characteristics that facilitate water uptake are of greater relative significance (Barber 1995; Tinker and Nye, 2000; Lynch 2005). The relative significance of such factors in the acquisition and uptake of P and N is therefore considered in more detail below.

Acquisition of phosphorus by plants

Phosphorus availability and uptake

Although soils generally contain a large amount of total P only a small proportion is immediately available for plant uptake. Plants obtain P as orthophosphate anions (predominantly as HPO_4^{2-} and $H_2PO_4^{1-}$) from the soil solution. In most soils the concentration of orthophosphate in solution is low (typically 1 to 5 μM; Bieleski 1973) and must therefore be replenished from other pools of soil P to satisfy plant requirements. Orthophosphate is rapidly depleted in the immediate vicinity of plant roots, and as such a large concentration gradient occurs across the rhizosphere between bulk soil and the root surface (Gahoonia and Nielsen 1997; Tinker and Nye 2000; Fig. 1). However, for most soils the rate of diffusion of orthophosphate is insufficient to overcome 'localized' gradients, which in most cases limits the uptake of sufficient P. Evidence from both modelling and empirical studies also suggests that actual P uptake capacity at the root surface is unlikely to be limiting for plant growth (Barber 1995). This is supported by more recent studies on the expression of genes that encode for transport proteins with high affinity for uptake of orthophosphate (e.g. K_m ~3 μM), which are predominantly expressed in root hair cells on the epidermis (Mitsukawa et al. 1997; Mudge et al. 2002; Schünmann et al, 2004). Whilst expression of these genes has been shown to facilitate the P uptake capacity of cells in suspension culture (Mitsukawa et al. 1997), their over-expression in transgenic plants did not result in increased P uptake by barley (*Hordeum vulgare* L.) when grown at a range of P concentrations in either solution or soil (Rae et al. 2004). This is consistent with the view that plants are well adapted for uptake of P from the low concentrations that are

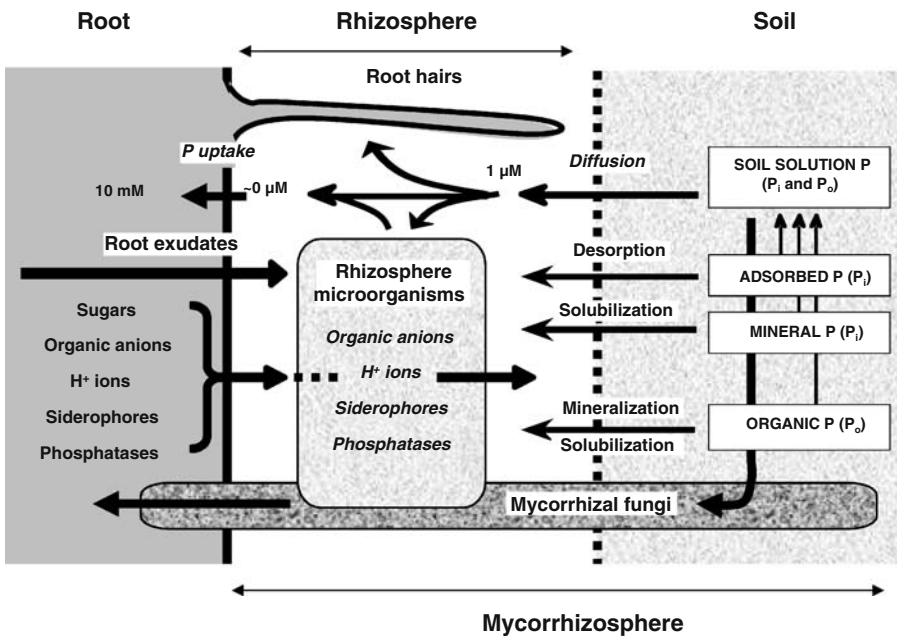

Fig. 1 Physiological and chemical processes that influence the availability and transformation of phosphorus in the rhizosphere (adapted from Richardson 1994; Richardson 2001)

typical of soil solutions as indicated by minimum uptake concentrations (C_{lim} values) of 0.01 to 0.1 μM for different species (Jungk 2001). On this basis it is suggested that the supply of P to the root surface, and its availability as influenced by root and microbial processes (as outlined below), or the capacity of roots to exploit new regions of soil are of greater importance for P acquisition than the kinetics associated with its uptake.

The importance of root growth and architecture for the efficient capture of P is well documented and in many cases is a specific response of plants to P deficiency (reviewed by Hodge 2004; Lynch 2005; Raghothama 1999; Richardson et al. 2009; Vance et al. 2003). Characteristics of roots that facilitate soil exploration and hence P uptake include; rapid rate of root elongation and high root to shoot biomass ratio (Hill et al. 2006), increased root branching and root angle particularly in surface soils and nutrient rich regions (Lynch and Brown 2001; Manske et al. 2000; Rubio et al. 2003), high specific root length (i.e. length per unit mass or root fineness; Silberbush and Barber, 1983), the presence of root hairs (Föhse et al. 1991; Gahoonia and Nielsen 1997; Gahoonia and Nielsen 2003) and, in some species, the formation of specialized root structures such as aerenchyma (Fan et al. 2003), dauciform roots in the Cyperaceae (Shane et al. 2006) and proteoid roots (or cluster roots) in the Proteaceae and certain *Lupinus* spp. (Dinkelaker et al. 1995; Gardner et al. 1981; Roelof et al. 2001; Lambers et al. 2006).

Depletion of phosphorus in the rhizosphere

The extent of P depletion in both the rhizosphere and mycorrhizosphere has been highlighted in a number of studies. Root hairs in particular contribute to increased root volume and can constitute up to 70% of the total root surface area (Itoh and Barber 1983; Jungk 2001; Fig. 1). As such they are the major site for nutrient acquisition and can account for up to 80% of total P uptake in non-mycorrhizal plants (Föhse et al. 1991). Variation in length and density of root hairs is important particularly under conditions of low P and their contribution to P uptake has been verified through modelling studies and the use of root-hairless mutants (Gahoonia and Nielsen 2003; Ma et al. 2001). Mycorrhizal colonization of roots (as discussed below) similarly provides a significant increase in the effective volume of soil explored with associated depletion of soil P (Tarafdar and Marschner 1994 and as modelled by Schnepf et al. 2008). Interestingly, the benefit derived from mycorrhizal fungi has been shown to be inversely associated with root hair length across a range of plant species, suggesting a complementary function of these traits (Baon et al. 1994; Schweiger et al. 1995). Reduced P acquisition by a root-hairless mutant of barley at low soil P was similarly compensated for by the presence of mycorrhiza (Jakobsen et al. 2005a).

Depletion of P in the rhizosphere occurs from both inorganic and organic P which includes soluble orthophosphate and various forms of extractable P (both inorganic and organic) that are widely considered to be labile. In addition, it is evident that pools of P that are more recalcitrant to extraction (e.g. NaOH-extractable P; Fig. 2), and thus previously considered to be only of poor availability to plants, can also be depleted in the rhizosphere. Such studies have used a range of different plants species and soil types whereby roots, root hairs and mycorrhizas are separated from bulk soil using meshed-compartments in rhizobox systems (e.g. Chen et al. 2002; Gahoonia and Nielsen 1997; George et al. 2002; Morel and Hinsinger 1999; Nuruzzaman et al. 2006; Tarafdar and Jungk 1987). Such approaches are useful in identifying different processes that contribute to P depletion even if they may exaggerate rhizosphere effects. For example, Chen et al. (2002) investigated P dynamics around the roots of ryegrass (*Lolium perenne* L.) and radiata pine (*Pinus radiata* D. Don) and showed a significant depletion of various pools of P at distances of up to 2 and 5 mm from the root surface of the two species respectively, which was related to different rhizosphere properties (Fig. 2). Both species also showed a significant increase in microbial biomass around the roots and associated increases in bicarbonate-extractable organic P may be a consequence of microbial-mediated immobilization of orthophosphate within the rhizosphere (Richardson et al. 2005). Further work to elucidate the role of microorganisms in influencing P availability within the rhizosphere and the extent to which they either complement or compete with plant processes in P acquisition is required (Jakobsen et al. 2005b).

Role of root exudates in phosphorus mobilization

The availability of P in the rhizosphere is influenced significantly by changes in pH and root exudates which

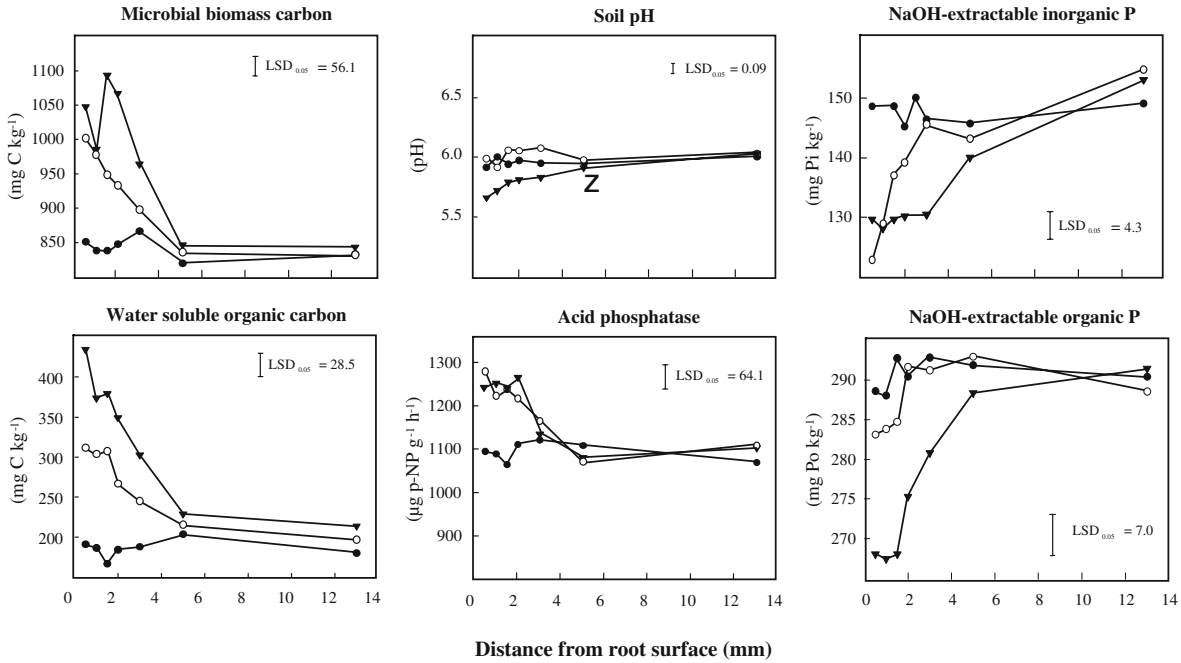

Fig. 2 Features of rhizosphere soil from perennial ryegrass (*Lolium perenne* L.; ○·····○) and radiata pine (*Pinus radiata* D. Don; ▼- -▼) when grown in a rhizobox system and compared to an unplanted (control; ●—●). Shown are changes in microbial biomass C, water-soluble C, pH, acid phosphatase activity and NaOH-extractable inorganic and organic P contents of the soil at various distances from the root surface. The soil (orthic brown soil; Dystrochrept; Hurunui, New Zealand) had a total P content of 958 mg P kg^{-1} soil. For each panel the error bar (LSD P=0.05) shows least significant difference (data taken from Chen *et al*. 2002)

can either directly or indirectly affect nutrient availability and/or microbial activity (Fig. 1; Richardson 1994). Acidification of the rhizosphere in response to P deficiency has been demonstrated for a number of species (see review by Hinsinger et al. 2003) and can alter the solubility of sparingly-soluble inorganic P compounds (particularly Ca-phosphates in alkaline soils), or affect the kinetics of orthophosphate adsorption-desorption reactions in soil and the subsequent availability of orthophosphate and various micronutrients in soil solution (Hinsinger and Gilkes 1996; Gahoonia and Nielsen 1992; Hinsinger 2001; Neumann and Römheld 2007).

Organic anions are released into the rhizosphere in response to various nutritional stresses including P, Fe and micronutrient deficiency and Al toxicity (see reviews by Hocking 2001; Neumann and Römheld 2007; Ryan et al. 2001). The concentration of different organic anions is typically greater in the rhizosphere (around 10-fold) compared with that in bulk soil (Jones et al. 2003). Organic anions are commonly released from roots in association with protons which results in an acidification of the rhizosphere (Dinkelaker et al. 1989; Hoffland et al. 1989; Neumann and Römheld 2002). In addition to this change in rhizosphere pH, organic anions can also directly facilitate the mobilization of P through reduced sorption of P by alteration of the surface characteristics of soil particles, desorption of orthophosphate from adsorption sites (ligand exchange and ligand-promoted dissolution reactions), and through chelation of cations (e.g. Al and Fe in acidic soils or Ca in alkaline soils) that are commonly associated with orthophosphate in soil (Bar-Yosef 1991; Jones 1998; Jones and Darrah 1994b). Organic anions also mobilise P bound in humic-metal complexes (Gerke 1993) and have been shown to increase both the availability of organic P and its amenability to dephosphorylation by phosphatases (Hayes et al. 2000). However, the effectiveness of different organic anions in nutrient mobilization depends on various factors including; the form and amount of the

particular anion released, with citrate and oxalate being more effective relative to others (e.g. malate, malonate and tartrate followed by succinate, fumarate, acetate and lactate; Bar-Yosef 1991) and interactions of the anion within the soil environment, including its effective concentration in soil solution and relative turnover rate (Jones 1998). The presence of micro-organisms is of further importance because of their capacity to either rapidly metabolize different organic anions within the rhizosphere or through their own ability to release anions (Jones et al. 2003). For example, in a calcareous soil, Ström et al. (2001) showed greater stability and resistance to microbial degradation of oxalate compared with citrate and malate which resulted in greater mobilization of P within localized regions of soil with a subsequent increase in P uptake by maize (*Zea mays* L.) roots (Ström et al. 2002).

The effectiveness of organic anions in mobilizing P from soil is highlighted by studies with white lupin (*Lupinus albus* L.) which exudes significant amounts of citrate (and to some extent malate) from cluster roots that are formed in response to P deficiency (Dinlelaker et al. 1989; Gardner et al. 1983; Keerthisinghe et al. 1998; Neumann and Martinoia 2002; Vance et al. 2003). Citrate is effective in mobilizing orthophosphate from pools of soil P that are otherwise not available to plants that either do not exude, or show limited release of organic anions, such as soybean (*Glycine max* (L.) Merr.) and wheat (*Triticum aestivum* L.) (Braum and Helmke 1995; Hocking et al. 1997). In addition, and analogous to the role of root hairs, cluster roots have a relatively short life span and form on lateral roots as closely packed tertiary roots with a dense covering of root hairs. This provides a zone for both concentrated release of organic anions and high surface area for the uptake of mobilized P (Dinkelaker et al. 1995, Neumann and Martinoia 2002). Interestingly, cluster roots form on plant species that are essentially non-mycorrhizal and therefore appear to provide an important alternative strategy for plant acquisition of soil P (Shane and Lambers 2005). Indeed, the formation of cluster roots and high rates of organic anion release are reported for various native Australian species (e.g. the Proteaceae and Casuarinaceae families) which have evolved on low P soils (Roelofs et al. 2001; Shane and Lambers 2005). Increased organic anion efflux from roots in response to P-deficiency also occurs in other species including chickpea (*Cicer arietinum* L.) and pigeon pea (*Cajanus cajan* L.) and to a lesser extent in lucerne (alfalfa; *Medicago sativa* L.), canola (oil seed rape; *Brassica napus* L.) and rice (*Oryza sativa* L.) (Ae et al. 1991; Hedley et al. 1982; Hoffland et al. 1989; Lipton et al. 1987; Otani et al. 1996; Pearse et al. 2006a; Veneklaas et al. 2003; Wouterlood et al. 2004). The increase in organic anion efflux by these species in response to P deficiency however, is considerably less than for the Proteaceae or *Lupinus* spp, and in many cases the agronomic significance of organic anion release remains to be verified in soil environments, as does the role of various organic anions in mobilizing P from different forms of soil P (Pearse et al. 2006b).

Activity of phosphatases is significantly greater in the rhizosphere and is considered to be a general response of plants to mobilize P from organic forms in response to P deficiency (Richardson et al. 2005). Phosphatases are required for the hydrolysis (mineralization) of organic P, and in bulk soil microbial-mediated mineralization of organic P contributes significantly to plant availability (Frossard et al. 2000; Oehl et al. 2004). Depending on soil type and land management, organic forms of P commonly constitute around 50% of the total P in soil and is the predominant form of P found in soil solutions (Ron Vaz et al. 1993; Shand et al. 1994). Dissolved organic P is derived largely from the turnover of soil micro-organisms and, relative to orthophosphate, has greater mobility in solution (Helal and Dressler 1989; Seeling and Zasoski 1993) and is therefore of critical importance to the dynamics and subsequent availability of P within the rhizosphere (Jakobsen et al. 2005a; Richardson et al. 2005).

Extracellular phosphatases released from roots have been characterized for a wide range of plant species and been shown to be effective for the *in vitro* hydrolysis of various organic P substrates (George et al. 2008; Hayes et al. 1999; Tadano et al. 1993; Tarafdar and Claassen 1988). Products of microbial turnover also contain high amounts of dissolved organic P (>80%) (primarily as nucleic acids and phospholipids), and are rapidly mineralized in soil and as such are of high availability to plants (Macklon et al. 1997). Direct hydrolysis of organic P and subsequent utilization of released orthophosphate by roots has been demonstrated in soil using both whole plant systems (e.g. McLaughlin et al. 1988) and in rhizobox studies. In the later case, depletion of

various pools of extractable organic P from the rhizosphere is associated with higher activities of phosphatases around plant roots (Chen et al. 2002; Tarafdar and Claassen 1988; Fig. 2). In the study by Chen et al. (2002), greater net depletion of organic P by radiata pine (compared to ryegrass) occurred despite similar increase in phosphatase activity for both species and the development of a lesser 'root mat' at the soil interface for pine roots, which suggests the possible involvement of other mechanisms. Indeed pine roots acidified the rhizosphere to a greater extent and had higher water soluble carbon and microbial biomass (Chen et al. 2002). Higher water soluble C suggests either greater root exudation or higher turnover of microbial biomass which could result in increased P mobilization. Alternatively, greater radial depletion of P by pine roots maybe associated with the presence of longer root hairs or more likely by association with ectomycorrhizal fungi. This latter possibility is suggested by the authors and is supported by observations from more recent studies where mycorrhizal fungi have been shown to be particular effective for the capture of P by pine roots (Liu et al. 2005; Scott and Condron 2004). Casarin et al. (2004) similarly showed the importance of ectomycorrhizas for mobilization of poorly available soil P around roots of maritime pine (*Pinus piaster* Ait.) and that this benefit was from both increased soil exploration and, depending on the species of mycorrhizal fungi, due to the release of oxalate and protons. However, the relative importance of such microbial processes as compared to direct plant mechanisms and other processes remains to be fully established. In the study by Chen et al. (2002), numbers and activities of free-living and root-associated microorganisms were also enhanced significantly within the rhizosphere (e.g. as shown by increased microbial biomass; Fig. 2) and these may also contribute substantially to the mechanisms of P depletion and solubilization.

Acquisition of nitrogen by plants

Nitrogen availability and uptake

Nitrogen occurs in soil in both organic and inorganic forms and in addition to marked seasonal changes is characterised by a heterogeneous distribution within the soil. Nitrogen inputs through fixation reactions (by either symbiotic microorganisms or potentially through free-living diazotrophs, as discussed below) and transformations of N between different pools have important implications for plant growth and for the loss of N from soil systems (Jackson et al. 2008). Microbial-mediated mineralization of organic forms of N to ammonium (NH_4^+) and its subsequent nitrification to nitrate (NO_3^-) is of major significance to N availability (Fig. 3) and has influence on root behaviour and rhizosphere dynamics. Although mineral forms of N have classically been considered to dominate plant uptake (see review by Miller and Cramer 2004), there is evidence that soluble organic forms of N (e.g. low molecular weight compounds such as amino acids) may also play a significant role (Chapin et al. 1993), but few studies have quantified the relative importance of each (Leadley et al. 1997; Schimel and Bennett 2004). Of particular significance in the rhizosphere is the effect that uptake of different N forms has on soil pH in the immediate vicinity of the root and subsequent influence of this on nutrient acquisition, especially in relation to the availability of P and various micronutrients (e.g. Zn, Mn and Fe) (Marschner 1995). Changes in rhizosphere pH, caused by the influx of protons that occurs with uptake of NO_3^-, or the net release of protons for NH_4^+ uptake, can also bring about changes in the nature of substrates exuded from roots or the quantities of exudates released, and consequently may have major impact on the structure of microbial communities around the root (Bowen and Rovira 1991; Meharg and Killham 1990; Smiley and Cook 1983).

Both NO_3^- and NH_4^+ reach the root surface via a combination of mass flow and diffusion (De Willigen 1986). Nitrate is typically present in soil solution at mM concentrations and, relative to orthophosphate, is more mobile (Tinker and Nye 2000) and thus, is potentially able to move in soil by up to several mm per day (Gregory 2006). Ammonium is less mobile since it readily adsorbs to the cation exchange sites in soil and has lower rates for both mass flow and diffusion. Nevertheless, diffusion and mass flow is the major pathway for inorganic N uptake and, although it is difficult to differentiate diffusion from root interception, it is generally considered that interception of N in soil solution following root extension accounts for a small percentage only of N taken up by plants (Barber 1995; Miller and Cramer 2004).

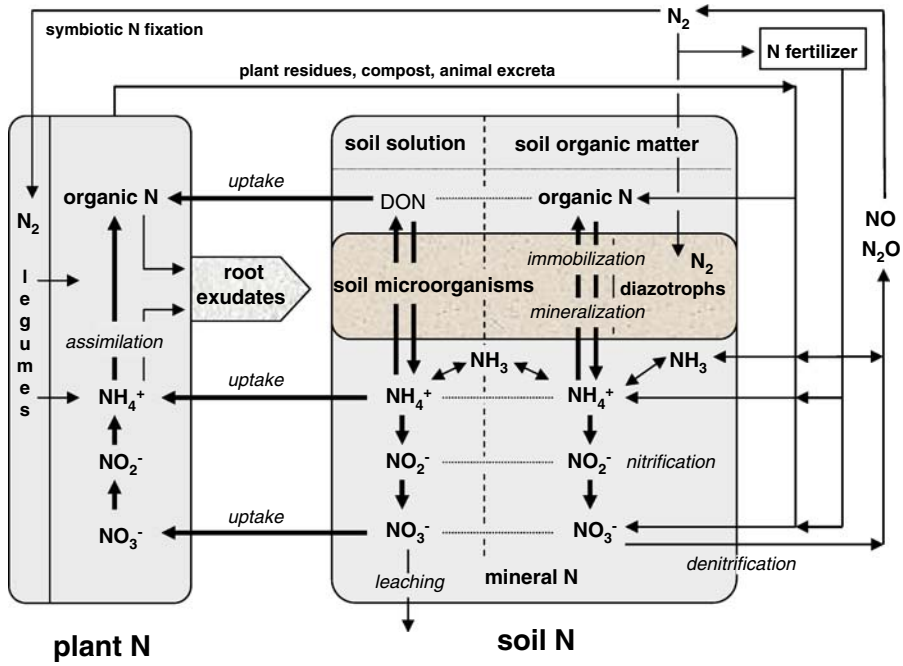

Fig. 3 The plant-soil N cycle and pathways for N transformation mediated by physiological processes (DON = dissolved organic nitrogen; redrawn from McNeill and Unkovich, 2007)

Plant uptake of NH_4^+ and NO_3^- is a function of their concentrations in soil and soil solution, root distribution, soil water content and plant growth rate. The latter is most important under conditions of liberal N supply, whereas mineral N concentration and root distribution are more critical under N limiting conditions. Whilst some plant species show a preference for either NH_4^+ or NO_3^- uptake, the significance of this for N uptake at the field level is usually less than the abovementioned factors, especially in agro-ecosystems (McNeill and Unkovich 2007). Indeed, NH_4^+ tends to dominate in many natural ecosystems for reasons which may include a suppression of microbial-mediated nitrification (reviewed by Subbarao et al. 2006). In addition and depending on soil type, non-exchangeable forms of NH_4^+ may contribute significantly to crop nutrition (Scherer and Ahrens 1996; Mengel et al. 1990), especially for lowland rice grown under flooded conditions (Keerthisinghe et al. 1985). Although many crop plants differ in their sensitivity to toxic effects of NH_4^+, the crucial factor seems to be the relative concentration of the two ions, with the optimal mix being dependent on factors such as plant species, age and soil pH (Britto and Kronzucker 2002; Badalucco and Nannipieri 2007). Furthermore, uptake of NO_3^- across the plasma membrane is more costly in terms of energy expenditure but nonetheless occurs effectively over almost the entire range of NO_3^- concentrations found in soil solutions (Forde and Clarkson 1999). However, for crop production systems the regulation of whole plant N uptake remains relatively poorly understood (Gastal and Lemaire 2002; Jackson et al. 2008), although there is evidence that the concentrations of both NO_3^- and NH_4^+ in soil solution, as well as plant N status are involved (Aslam et al. 1996; Devienne-Barret et al. 2000).

The significance of soluble organic N for plant nutrition was first highlighted in solution culture studies and has since been demonstrated for soils in a range of different ecosystems (Jones and Darrah 1994a; Schimel and Bennett 2004). Amino acids typically constitute up to half of the total soluble N in soil solution (concentrations ranging from 0.1 to 50 mM) and thus comprise a significant part of the potentially plant available N pool (Christou et al. 2005; Jones et al. 2002). Amino acids in soil solution occur as a result of either direct exudation by roots or from the breakdown of proteins and peptides from soil organic matter and microbial biomass turnover as a result of microbial-derived proteases (Jaeger et al. 1999; Owen and Jones 2001). In addition the involvement of plant-exuded proteases in digestion of proteins at the root surface has been reported along

with the possibility of direct uptake of proteins by roots through endocytosis (Paungfoo-Lonhienne et al. 2008). Uptake of organic N compounds by plants may also be facilitated by association with ectomycorrhizal fungi (Chalot and Brun 1998; Nasholm et al. 1998). However, the relative importance of such mechanisms in many ecosystems remains debatable since the diffusion rates of amino acids and proteins are typically orders of magnitude lower than for NO_3^- (Kuzyakov et al. 2003), and thus mycorrhizas may offer distinct advantages, whereas microorganisms in the rhizosphere are likely to compete more strongly for these compounds (Hodge et al. 2000a). Although direct evidence that plant roots can out-compete microorganisms for N is limited to a few studies (Hu et al. 2001; Jingguo and Bakken 1997), there is some evidence from ^{15}N time-course studies where plants accumulate ^{15}N and thus benefit over the longer term which may be associated with microbial turnover (Hodge et al. 2000b; Kaye and Hart 1997; Yevdokimov and Blagodatsky 1994).

Given the heterogeneous distribution of N in soil in terms of chemical form, temporal dynamics and spatial distribution, plants adopt one or more of three main strategies to optimize their acquisition of N. Broadly these are; (i) to explore greater volume of soil and/or soil solution by extending root length and branching or increasing root surface area via changes in root diameter or root hair morphology, (ii) specific adaptive response mechanisms in order to exploit spatial and temporal 'niches' such as N-rich patches or due to the presence of particular forms of N (amino acids, NH_4^+ or NO_3^-), and (iii) influences on plant available N in the rhizosphere through plant-microbial interactions.

Root growth and morphological responses to nitrogen

The size and architecture of the root system is an important feature for ensuring adequate access to soil N, and root system size (relative to shoot growth) has generally been shown to increase when N is limiting (Chapin 1980; Ericsson 1995). However, changes to biomass alone are not necessarily indicative of the total absorptive area of a root system and morphological changes can occur without change in biomass. Although the architecture of root systems is intrinsically determined by genotype and the pattern of root branching, species specific attributes related to size and architecture are also strongly determined by external physical, chemical and biological factors (Miller and Cramer 2004). Whilst primary root growth is generally less sensitive to nutritional effects than is the growth of secondary or higher root orders (Forde and Lorenzo 2001), the diameter of first and second order laterals were significantly thicker in cereals grown at high concentrations of NO_3^- (Drew et al. 1973). Thicker roots may be more costly to produce but have greater capacity for the transport of water and nutrients and are less vulnerable to adverse edaphic conditions (Fitter 1987). Conversely, fine roots allow greater exploration of soil and plants appear to accommodate trade-off between the two by exhibiting plasticity in root diameter (and morphology) according to the environmental conditions (Forde and Lorenzo 2001). Root angle, an important component of root architecture in soil in relation to P deficiency (Rubio et al. 2003), appears to be unaffected by N deficiency.

Apart from the size and depth of root systems other attributes may also influence the capacity for efficient capture of N. Only a limited portion of the root may actually be effective in the uptake of N (Robinson 2001) and thus the spatial localization of roots is important when nutrient is distributed heterogeneously (Ho et al. 2005). Electrophysiological and molecular evidence supports a role for root hairs in the uptake and transport of both NO_3^- and NH_4^+ (Gilroy and Jones 2002) and proliferation of fine roots and root hairs in response to localized patches of N has been demonstrated (Jackson et al., 2008).

Rooting depth, which varies greatly between species, influences the capture of N by plants, particularly of NO_3^- during periods of leaching, and is clearly an important characteristic for many perennial agricultural species and tree crops (Gastal and Lemaire 2002). However, a dimorphic root system, having both shallow and deep roots to enable acquisition of mineralized N in the topsoil as well as leached N at depth, is considered to be important (Ho et al. 2005). Indeed, vigorous wheat lines with faster vertical root growth and more extensive horizontal root development have been shown to take up significantly more N (Liao et al. 2006).

Roots exhibit high plasticity as a physiological response to localized patches of organic and inorganic nutrients in soil, including proliferation in N-rich zones (Hodge et al. 1999a; Robinson and van Vuuren

1998). This proliferation essentially involves the initiation of new laterals, but may also include increases in the elongation rate of individual roots and expansion of the rhizosphere through root hairs. Roots can also enhance their physiological ion-uptake capacities in localized nutrient-rich zones. This root 'foraging' capability is considered to be an important plant response to optimize resource allocation in regard to N capture and is of particular ecological importance in situations where there is competition with neighbouring roots for limited resources (Hodge et al. 1999b; Robinson et al. 1999). However, foraging is not a fixed property but varies within species in response to different environmental conditions (Wijesinghe et al. 2001), indicating that the environmental context in which the root response is expressed is as important as the response itself. However, most studies investigating root growth in response to patches of N have largely ignored the attributes of the patch itself despite the fact that the dynamics of nutrient transformation within the patch and microbial interactions are of major importance. There is need for research to follow both together, including consideration of the complexity of interactions with other root systems, soil microorganisms and fauna, and physical/chemical interactions in the soil (Hodge 2004).

Association with microorganisms and plant growth promotion

Microbial associations with roots are complex in soil and can enhance the ability of plants to acquire nutrients from soil through a number of mechanisms. These include; i) an increase in the surface area of roots by either a direct extension of existing root systems (e.g. mycorrhizal associations) or ii) by enhancement of root growth, branching and/or root hair development (e.g. through plant growth promoting rhizobacteria), (iii) a direct contribution to nutrient availability though either N fixation (e.g. rhizobia and diazotrophs) or by stimulation and/or contribution to metabolic processes that mobilize nutrients from poorly available sources (e.g. organic anions) or, an indirect effect on nutrient availability by (iv) displacement of sorption equilibrium that results in increased net transfer of nutrients into solution and/or as the mediators of transformation of nutrients between different pools (e.g. nitrification inhibitors and microbial-mediated processes that alter the distribution of nutrients between inorganic and organic forms) or v) through the turnover of microbial biomass within rhizosphere (Gyaneshwar et al. 2002; Jakobsen et al. 2005a; Kucey et al. 1989; Richardson 2007; Tinker 1980).

In this respect, mycorrhizal fungi, rhizobia and *Frankia* microsymbionts, and plant growth promoting (PGP) microorganisms are of particular importance and as such have been studied most widely. PGP microorganisms represent a wide diversity of bacteria and fungi that typically colonize the rhizosphere and are able to stimulate plant growth through either a 'biofertilizing' (direct) effect or through mechanisms of 'biocontrol' (indirect effect; Bashan and Holguin 1997; and see Raaijmakers et al. 2009; Harman et al. 2004; Fig. 4). Biofertilizing-PGPR (considered in more detail below) specifically refers to rhizobacteria that are able to promote growth by enhancing the supply of nutrients to plants (Vessey 2003). For rhizobia and *Frankia* this involves symbiotic relationships with host legume and actinorhizal plants, respectively (see review by Franche et al. 2009), and are therefore not considered here. Rhizobiaceae (rhizobia) can also develop non-specific associative interactions with roots and promote the growth of non-legumes, and as such are also commonly considered as PGPR (Sessitsch et al. 2002). However, PGP is a complex phenomenon that often cannot be attributed to a single mechanism and, as outlined below, PGPR may typically display a combination of mechanisms (Ahmad et al. 2008; Kuklinsky-Sobral et al. 2004). In addition, the effects of individual PGPR may not occur alone but through synergistic interactions between different microorganisms.

Association with mycorrhizal fungi

Mycorrhizal symbioses are found in almost all ecosystems and can enhance plant growth through a number of processes which include improvement of plant establishment, increased nutrient uptake (particularly P and essential micronutrients such as Zn and Cu, but also N and, depending on soil pH, may enhance the uptake of K, Ca and Mg; Clark and Zeto 2000), protection against biotic and abiotic stresses and improved soil structure (Buscot 2005; Smith and Read 2008). Mycorrhizal fungi typically

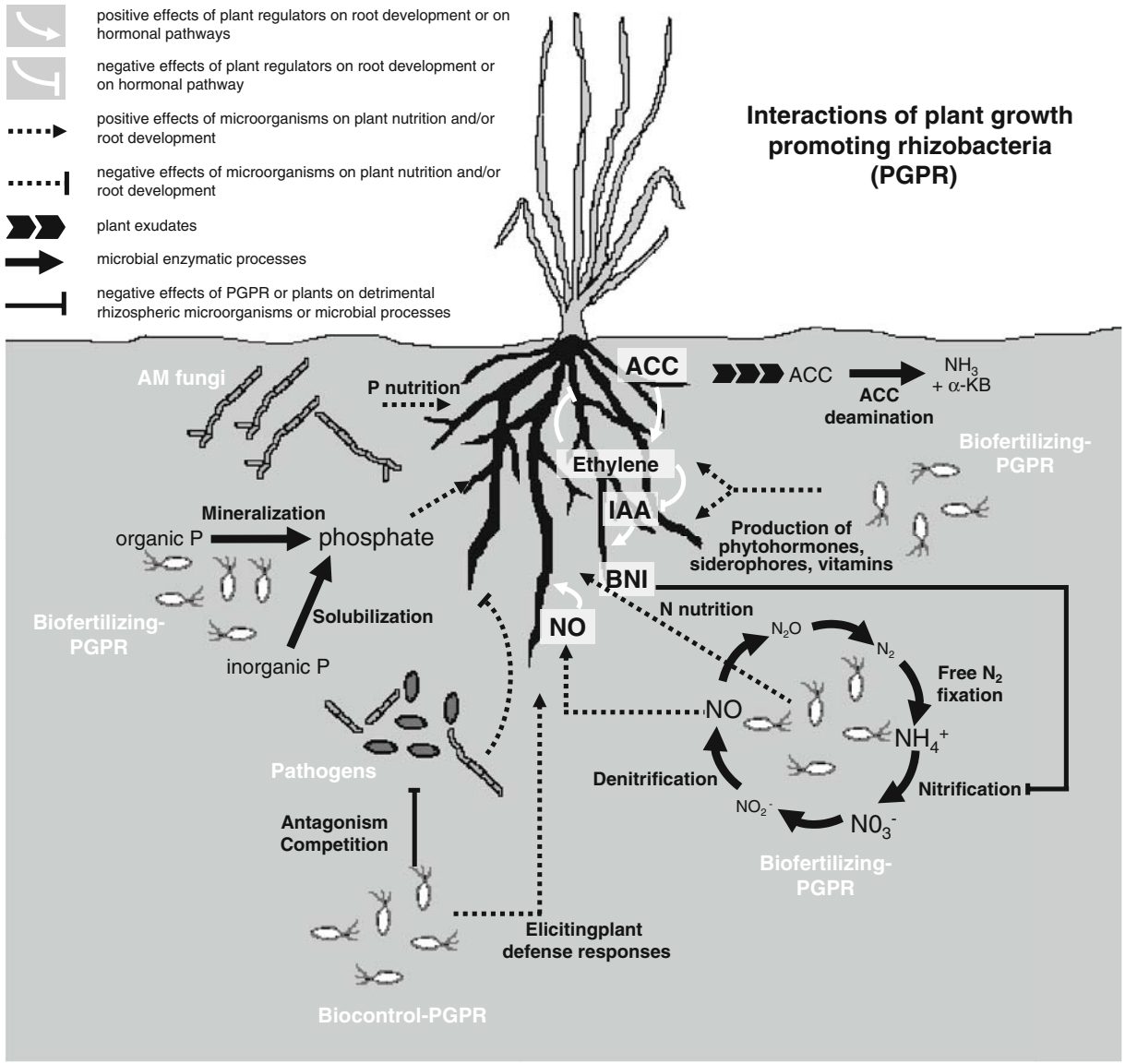

Fig. 4 Plant growth promotion mechanisms (positive and negative effects) associated with soil and rhizosphere (PGPR) microorganisms. Biofertilizing-PGPR and arbuscular mycorrhizal (AM) fungi stimulate plant nutrition by directly increasing the supply of nutrients to plants (e.g. through N fixation, P solubilization and/or mineralization, vitamin and siderophore production) or by increasing the plants access to nutrients due to enhancement of root volume. Promotion of root growth is linked to the ability of PGPR to produce phytohormones (e.g. IAA, ethylene, NO) or by direct influences on plant hormone levels (e.g. deamination of ACC precursor to plant ethylene). Biocontrol-PGPR improve plant heath by inhibiting the growth of plant pathogens or by eliciting plant defense responses

colonize the root cortex biotrophically and develop external hyphae (or extra-radical mycelia) which connect the root with the surrounding soil. All but few vascular plant species are able to associate with mycorrhizal fungi. The universality of this symbiosis implies a great diversity in the taxonomic features of the fungi and the plants involved. At least five types of mycorrhizas are recognized, the structural and functional features of which are reviewed in detail elsewhere (Smith and Read 2008; Brundrett, 2002) and are thus only considered briefly here.

Higher plants commonly form associations with ectomycorrhizas, mainly forest trees in the Fagaceae, Betulaceae, Pinaceae, *Eucalyptus,* and some woody

legumes. The fungi involved are usually Basidiomycetes and Ascomycetes which colonize cortical root tissues but without intracellular penetration (Smith and Read 2008). Three other types of mycorrhizas can be grouped as endomycorrhizas, in which the fungus colonizes the root cortex intercellularly. One of these is restricted to species within the Ericaceae (ericoid mycorrhizas), the second to the Orchidaceae (orchid mycorrhizas) and the third, which is by far the most widespread (and therefore considered in most detail here), are the arbuscular mycorrhizas (AM). A fifth group, the ectendomycorrhizas, are associated with plant species in families other than Ericaceae, including the Ericaless and the Monotropaceae (arbutoid and monotropoid mycorrhizas). The majority of plant families form arbuscular associations, with the AM fungi being an obligate symbiont that is unable to complete its life cycle without colonization of a host plant. The AM fungi were formerly included in the order Glomales, Zygomycota, but are now considered as new phylum, the Glomeromycota (Redecker 2002, Schübler et al. 2001).

The establishment of mycorrhizal fungi in roots changes key aspects of plant physiology, including mineral nutrient composition in tissues, plant hormonal balance and patterns of C allocation. The fungi may also alter the chemical composition of root exudates, whilst the development of mycelium in soil can act as a C source for microbial communities and introduce physical modifications to the soil environment (Gryndler 2000). Such changes in the rhizosphere can affect microbial populations both quantitatively and qualitatively such that the rhizosphere of mycorrhizal plants (known as the mycorrhizosphere) generally has features that differ substantially from those of non-mycorrhizal plants (Barea et al. 2002; Johansson et al. 2004; Offre et al. 2007). As discussed in more detail below, a wide range of bacteria (including actinomycetes and various PGPR) associate with mycorrhizas within the mycorrhizosphere (Rillig et al. 2006; Toljander et al. 2007).

Contribution of mycorrhizas to the phosphorus nutrition of plants

It is well established that mycorrhizal fungi contribute significantly to the P nutrition of plants, particularly under low P conditions (Barea et al. 2008). This is most evident for the ectomycorrhizal fungi which are largely associated with non-agricultural plants and appear to show greater functional diversity than the AM fungi (Brundrett 2002). Whilst it is generally accepted that mycorrhizal fungi have similar access to sources of P in soil solution that are also directly available to plants (reviewed by Bolan 1991) there is some evidence to suggest that both AM and ectomycorrhizal fungi have enhanced ability to use alternative sources of P (Bolan et al. 1984; Casarin et al. 2004). For example, for AM fungi, Tawaraya et al. (2006) showed that exudates from fungal hyphae solubilized more P than root exudates alone, suggesting that the mycorrhiza contribute to increased P uptake through solubilization. The extra-radical mycelium of AM fungi have also been shown to excrete phosphatases which could potentially enhance the mineralization and utilization of organic P (Koide and Kabir 2000; Joner and Johansen 2000). However, it is generally considered that this is unlikely to be of major significance to the overall contribution of AM fungi to plant P nutrition (Joner et al. 2000, Richardson et al. 2007). Alternatively, indirect effects of mycorrhizal fungi on P mobility may occur through changes in soil microbial communities within the mycorrhizosphere (Barea et al. 2005b).

The increased efficiency of P acquisition by mycorrhizal plants is based mainly on the existence of the extra-radical mycelia which develop into soil and allow P to be accessed by the mycorrhiza from soil solution at distances up to several cm away from the root and then subsequently transferred to the plant (Jakobsen et al. 1992). High mycorrhizal hyphae density also provides considerably greater surface area for the absorption of orthophosphate by plants and, due to the smaller size of hyphae in relation to roots and root hairs and their greater length relative to root hairs, hyphae are also most effective in exploiting soil pores and nutrient patches that may not be directly accessible to roots (Jakobsen et al. 2005a). Thus, higher uptake of P by mycorrhizal plants (both ectomycorrhizas and AM) can generally be explained in term of increased hyphal exploitation of the soil as modelled by Schneph et al. (2008) and the competitive ability of the hyphae to absorb localized sources of orthophosphate and organic nutrient patches (Tibbett and Sanders 2002; Cavagnaro et al. 2005). In this context, numerous studies have shown positive correlations between fungal variables, such as hyphal

length or hyphal density, with growth response variables of colonized plants such as shoot biomass, P uptake and total P content (Avio et al. 2006; Jakobsen et al. 2001). However, this cannot be taken as a general conclusion since high hyphal development does not always correlate with plant growth responses (Smith et al. 2004) and in some situations, particularly under fertilized field conditions, the presence of AM mycorrhizal fungi appears to provide little or no benefit in terms of plant P nutrition (Ryan and Angus 2003, Ryan et al. 2005).

Apart from the physical extension of root systems, mycorrhizal fungi may also acquire orthophosphate from soil solution at lower concentrations than roots, but whether this contributes significant advantage to the P nutrition of plants remains uncertain. Some studies report higher affinity for orthophosphate uptake by mycorrhizal plants (i.e. lower K_m values than for non-mycorrhizal roots; Cardoso et al. 2006). Genes encoding for the high-affinity phosphate transport in AM fungi have been identified and shown to be preferentially expressed in the extraradical mycelium (Benedetto et al. 2005; Maldonado-Mendoza et al. 2001). Mycorrhizal plants therefore have 'two' pathways for P uptake, the 'direct' pathway via the plant-soil interface through root hairs, and the 'mycorrhizal' pathway via the fungal mycelium (Smith et al. 2003). Interestingly, several studies have shown that expression of plant epidermal P transporters is reduced in roots that are colonized by AM fungi, and that under these circumstances P uptake proceeds predominantly via fungal transporters with subsequent transfer of P to plants at the arbuscular-root interface (Burleigh et al. 2002; Chiou et al. 2001; Liu et al. 1998; Rausch et al. 2001). In some cases AM colonization results in a complete inactivation of the direct P uptake pathway via root hairs with essentially all of the P in plant tissues being provided through the mycorrhizal route (Smith et al. 2004).

Contribution of mycorrhizas to nitrogen nutrition

Several studies have also shown increased N uptake from soil by roots associated with mycorrhizal fungi (Barea et al. 2005a). For example, Ames et al. (1983) first showed that mycorrhizal hyphae were able to absorb, transport and utilize NH_4^+ and, using ^{15}N-based techniques, Barea et al. (1987) demonstrated that mycorrhizal plants under field conditions had increased N uptake. Further studies using ^{15}N and compartmented rhizobox systems verified that mycorrhizal hyphae in root-free compartments were able to access ^{15}N (Tobar et al. 1994b). To investigate whether the mycorrhizal contribution to N acquisition was from pools of N that were unavailable to non mycorrhizal plants, the apparent pool size of plant available N has been determined by isotopic dilution (i.e. the A_N value of the soil; Zapata 1990). Using this approach, higher A_N values for plants inoculated with AM fungi compared to non-inoculated controls were obtained, suggesting that the AM mycelium were able to access N from forms that were otherwise less available than that for non-mycorrhizal plants (Barea et al. 1991). Indeed the presence of a functional transporter for high-affinity uptake of NH_4^+ has recently been identified in the extraradical mycelium of *Glomus* sp. (López-Pedrosa et al. 2006).

Association with free-living microorganisms

Phosphate-mobilizing microorganisms

Free-living bacteria and fungi that are able to mobilize orthophosphate from different forms of organic and inorganic P have commonly been isolated from soil and in particular from the rhizosphere of plants (Kucey et al. 1989; Barea et al. 2005b). Phosphate-solubilizing microorganisms (PSM) are characterized by their capacity to solubilize precipitated forms of P when cultured in laboratory media and include a wide range of both symbiotic and non-symbiotic organisms, such as *Pseudomonas*, *Bacillus* and *Rhizobium* spp., actinomycetes and various fungi such as *Aspergillus* and *Penicillium* spp. (see reviews by Gyaneshwar et al. 2002; Kucey et al. 1989; Rodriguez and Frago 1999; Subba-Rao 1982; Whitelaw 2000). Selection of PSM is routinely based on the solubilization of sparingly soluble Ca phosphates (typically, tri-calcium phosphate [$Ca_3(PO_4)_2$] and rock phosphates containing hydroxy- and fluor-apatites [$Ca_5(PO_4)_3OH$ and $Ca_{10}(PO_4)_6F2$]) and Fe and Al phosphates such as strengite ($FePO_4.2H_2O$) and variscite ($AlPO_4.2H_2O$). The amount of P solubilized is highly dependent on the source (solubility) of the P and, for different microorganisms, is influenced to a large extent by the culture conditions. For example, fungi are commonly reported to be more effective at solubilization of Fe and Al

phosphates, whereas the ability of different organisms to solubilize Ca-phosphates is influenced by the source of carbon and nitrogen in the media, by the buffering capacity of the media and the stage at which cultures are sampled (Kucey 1983; Illmer and Schinner 1995; Nahas 2007; Whitelaw et al. 1999). From various studies it is evident that change in pH of the media is particularly important for solubilization of Ca-phosphates, whereby cultures supplied with NH_4^+ are more effective than those with NO_3^- due to associated proton release and acidification of the media. Acidification is also commonly associated with the release of organic anions which have been widely reported for various microorganisms (i.e. with citrate, oxalate, lactate, and gluconate being most common). Organic anions themselves may further increase the mobilization of particular forms of poorly soluble P (e.g. Al-P and Fe-P) through chelation reactions (Whitelaw 2000).

Under controlled growth conditions various studies have demonstrated enhanced growth and P nutrition of plants inoculated with PSM which is often attributed to the P-solubilizing activity of the microorganisms involved (see reviews by Gyaneshwar et al. 2002; Kucey et al. 1989; Rodriguez and Fraga 1999; Whitelaw 2000). However, clear effect of PSM in more complex soil environments and in field conditions, have proved more difficult to demonstrate and inconsistent response of plants and performance of different microorganisms have been observed. As discussed by Richardson (2001) this may be due to a range of factors that include, insufficient knowledge for introducing and understanding the dynamics of microorganisms and their interaction with complex microbial communities in soil, the apparent lack of any specific association between partners, and poor understanding of the actual mechanisms involved, both for the microorganisms and their interaction and efficacy within different soil environments. For example, whilst *Penicillium radicum* effectively solubilized P in laboratory media and was able to promote the growth of wheat, evidence for improved P uptake in response to inoculation was only evident in glasshouse trials particularly where fertilizer P was applied (Whitelaw et al. 1997). However, growth promotion may not necessarily be directly associated with P solubilization and production of phytohormones is likely to be involved (Wakelin et al. 2006). Similarly, promotion of root growth and enhanced P nutrition of plants inoculated with *P. bilaii* has been shown to be primarily associated with increased root growth, including greater specific root length and production of longer root hairs (Gulden and Vessey 2000). Such studies highlight the difficulties in determining the actual mechanism associated with growth promotion, as stimulation of root growth also contributes to greater potential for P acquisition. It is important therefore that experiments directed at demonstrating the benefits of PSM be conducted across a range of P supplies, whereby benefits of inoculation should be negated at higher levels of applied P, and that specific measures of P acquisition (e.g. by isotopic dilution) be made to confirm P mobilization from pools of soil that are otherwise poorly available to roots.

The mineralization of organic P in soil is largely mediated by microbial processes and as such microorganisms play a significant role in maintaining plant available P. Microorganisms are able to hydrolyze a wide range of organic P substrates when grown in culture and, when added to soil, different forms of organic P have been shown to be rapidly mineralized (Adams and Pate 1992; Macklon et al. 1997; and see review by Richardson et al. 2005). Indeed benefits of microbial inoculation for the utilization of organic P by plants under controlled growth conditions have been demonstrated (Richardson et al. 2001a). In addition, the microbial biomass is important for maintaining both inorganic and organic P in soil solution (Seeling and Zososki 1993) and turnover of the biomass represents an important potential supply of P to plants (Oberson and Joner 2005). This contribution is likely to be of greater significance in the rhizosphere where there is increased amount of readily metabolizable carbon and higher density of microorganisms (Brimecombe et al. 2007; Jakobsen et al. 2005b). However, the relative importance of microbial mineralization relative to the short-term immobilization of P by microorganisms in the rhizosphere and its impact on the availability of orthophosphate to plants requires more detailed investigation.

Whilst it is evident that microbial-mediated solubilization and mineralization of inorganic and organic P are important processes whereby microorganisms are able to acquire P from soil, it has been argued that they are unlikely to mobilize sufficient P above their own requirements to meet plant demand (Tinker

1980). Indeed, few studies have unequivocally demonstrated a direct release of P by microorganisms in soil and benefits to plant nutrition are therefore often inferred. Nevertheless, the cycling of P within the microbial biomass and its subsequent release is paramount to the P cycle in soil and represents an important pathway for movement of P from various soil pools into plant-available forms and may also serve to protect orthophosphate from becoming unavailable in soil due to various physicochemical reactions (Magid et al. 1996; Oberson et al. 2001). The significance of this in the rhizosphere warrants further research.

Microbial interactions and nitrogen availability

Root exudation also has important implications for N availability. Although the chemical composition of exudates varies widely for different species and root types and is primarily comprised of C compounds, exudates can also contain significant quantities of N, which is either available to microorganisms in the rhizosphere or can be recaptured by plants (Bertin et al. 2003; Uren 2007). In addition, root exudates are the major energy supply for the soil food web and play a significant role in the turnover of soil organic matter and associated nutrients. However, as suggested by Jones et al. (2004), although root exudates have been hypothesized to be involved in the enhanced mobilization and acquisition for many nutrients in soil, there is little mechanistic evidence from soil-based systems to verify this, which is further highlighted by a recent analysis of the literature concerning rhizodeposition by maize (Amos and Walters 2006). Despite this, some studies have demonstrated enhanced N cycling in the vicinity of plant roots (Jackson et al. 2008). For example, following the application of ^{15}N labelled fertilizer, the excess of ^{15}N in the microbial biomass increased significantly in both planted and control soils at up to 8 weeks after plant emergence, but then declined in control soils only (Qian et al. 1997). Retention of ^{15}N in the microbial biomass in planted soil was attributed to the release of root-derived C from maize as estimated using ^{13}C abundance methodology. This release of exudate was suggested to promote microbial immobilization of the N and is consistent with greater microbial biomass in the rhizosphere.

Increased rates of N mineralization have similarly been demonstrated in the rhizosphere of slender wild oats (*Avena barbata* Pott ex Link), where N mineralization was 10 times higher than in bulk soil, but this was highly dependent on location along the root (Herman et al. 2006). In addition, a rhizosphere 'priming effect' has been suggested to be involved in the decomposition of native soil organic matter around roots (Cheng et al. 2003; Kuzyakov 2002). However, stimulation of mineralization may be dependent on plant species and on the C:N ratio of substrates as highlighted in a study of peas (*Pisum sativum* L.) inoculated with *Pseudomonas fluorescens*, where increased uptake of N from ^{15}N enriched organic residues occurred, whereas decreased uptake was observed for wheat (Brimecombe et al. 1999). Additional work demonstrated that microbial-microfaunal interactions in the rhizosphere were also involved in this differential response, with lower numbers of nematodes and protozoa being present in the rhizosphere of uninoculated peas which appeared to exert a nematicidal effect (Brimecombe et al. 2000). On the contrary, higher numbers of nematodes and protozoa (e.g. up to 6-fold) have generally been reported in the rhizosphere where they specifically feed on bacteria, fungi and yeasts (Zwart et al. 1994). These interactions enhance N flows in the rhizosphere both directly, via the excretion of consumed nutrients and mineralization of nutrients on death (Griffiths 1989), and indirectly via changes to the composition and activity of the microbial community (Griffiths et al. 1999). For example, bacteriophagous nematodes mineralized up to six times more N than an equivalent biomass of protozoa grazing on bacteria (Griffiths 1990). Net mineralization is due to differences in C:N ratio between the protozoan (or nematode) predator and the bacterial prey and their relatively low assimilation efficiency, whereby ~60% of ingested nutrients are typically excreted and thus potentially available for plant or microbial uptake (Bonkowski 2004). Moreover, plants grown under controlled conditions have been observed to develop more highly branched root systems in the presence of protozoa which may partly be explained as a response to NO_3^- formed from mineralization of NH_4^+ excreted by protozoa (Forde 2002). However, other work has suggested that root responses are due to a direct phytohormone effect by the presence of either protozoa or a consequence of auxin producing bacteria stimulated by the presence of

the protozoa (Bonkowski 2004; Bonkowski and Brandt 2002). The consequences of soil organisms promoting a mutually beneficial relationship between plant roots and bacteria in the rhizosphere on root architecture, nutrient uptake and plant productivity is therefore of current research interest (Mantelin and Touraine 2004). For example, in an experiment using $^{15}N/^{13}C$ labelled organic nutrient sources combined with manipulation of the composition of microfaunal populations, Bonkowski et al. (2000) observed effects on ryegrass growth and concluded that microfaunal grazing increased the temporal coupling of nutrient release and plant uptake, whereas root foraging in organic nutrient-rich zones enhanced the spatial coupling of mineralization and plant uptake. More recent work has shown interaction at higher trophic levels where collembola that feed on bacteria, fungi, nematodes and protozoa further enhanced N mineralization without alteration to the microbial biomass C (Kaneda and Kaneko 2008).

At a larger scale there is increasing evidence from using *in situ* ^{15}N labelling of plant root systems of the importance of N rhizodeposition in sustaining the N cycle of agro-ecosystems (Hogh-Jensen 2006; Mayer et al. 2004; McNeill and Fillery 2008). A recent review (Wichern et al. 2008) highlights the wide variability in results and suggests there is need for more investigations on key environmental factors influencing the amounts of N released under field conditions from different species. Apart from a direct influence of the rhizosphere on N deposition, there is also need to more fully understand the role that plant roots have in interacting with soil microorganisms and influencing other parts of the soil N cycle. For example, the presence of plant-derived biological nitrification inhibitors (BNI) in the root zone can influence the conversion of NH_4^+ to NO_3^- (nitrification) and subsequently to the potential for gaseous losses of N through denitrification (Fig. 3). Indeed nitrification inhibitors have been recognized for some time in native plant ecosystems, but more recently have been shown to be effective as root exudates from brachiaria (*Brachiaria humidicola* (Rendle) Schweick) a tropical grass species (Subbarao et al. 2006). In these systems there is greater retention of NH_4^+ in soil which has important implication for improving N-use efficiency by reducing potential N losses through NO_3^- leaching and/or its conversion (denitrification) to N_2O gas (via NO), which contributes significantly to greenhouse-gas emissions (Fillery 2007; Subbarao et al. 2006). However, presently it appears that BNI is poorly expressed in many agricultural crop species, although activities has been reported for sorghum (*Sorghum bicolour* (L.) Moench.), pearl millet (*Pennisetum glaucum* (L.) R.Br.) and peanut (*Arachis hypogaea* L.) (Subbarao et al. 2007a) and more recently BNI has been shown to be effective in wild rye (*Leymus racemosus* (Lam.) Tzvelev), a wild relative of wheat (Subbarao et al. 2007b).

Nitrogen fixation by diazotrophs

Diazotrophs (i.e. N_2-fixing bacteria) are classified as being either symbiotic (rhizobia and *Frankia* species) or as free-living (associative) and/or root endophytic microorganisms (Cocking 2003). Rhizobia develop symbiotic relationships with host legumes and through atmospheric N_2 fixation within nodules can provide up to 90% of the N requirements of the plant (see Franche et al. 2009; Höflich et al. 1994). Free-living N_2-fixers also have the potential for providing N to host plants but so far, the direct contribution of N-fixation by diazotrophs to the N nutrition of plants and subsequent growth promotion remains in question. Free-living diazotrophs have been identified in several genera of common rhizosphere-inhabiting microorganisms such as *Acetobacter, Azoarcus, Azospirillum*, *Azotobacter*, *Burkholeria*, *Enterobacter*, *Herbaspirillum*, *Gluconobacter* and *Pseudomonas* (Baldani et al. 1997; Mirza et al. 2006; Vessey 2003), with some being recognized as endophytes. Endophytic diazotrophs may have advantage over root-surface associated organisms, as they can colonize the interior of plant roots and establish themselves within niches that are more conducive to effective N_2 fixation and subsequent transfer of the fixed N to host plants (Baldani et al. 1997; Reinhold-Hurek and Hurek 1998).

Mutants deficient in nitrogenase activity (i.e. Nif mutants) have been constructed in various PGPR, including *Azospirillum brasilense, Azoarcus* sp. and *Pseudomonas putida*, and importantly, have been shown in several cases to retain their ability to promote plant growth of certain crops (Hurek et al. 1994; Lifshitz et al. 1987). This questions the relative contribution of N_2 fixation to the growth promotion effect. On the contrary, Hurek et al. (2002) showed that an endophytic strain of *Azoarcus* sp. was able to fix

and transfer N when associated with kallar grass (*Leptochloa fusca* (L.) Kunth), as Nif⁻ mutants gave lower plant growth stimulation than the wild-type strain. Similar results were obtained in the case of the associative symbiosis between sugar-cane (*Saccharum officinarum* L.) and the endophytic diazotroph *Acetobacter diazotrophicus* (renamed *Gluconobacter diazotrophicus*) (Sevilla et al. 2001). Furthermore, N-balance, ^{15}N natural abundance and ^{15}N dilution studies, performed in either pot experiments or in the field, have provided clear evidence of the ability of endophytic N_2-fixing bacteria to supply significant inputs of nitrogen to some grasses and cereals (Boddey et al. 2001; Oliveira et al. 2002).

In contrast to symbiotic N_2 fixation, where there is direct transfer of N across the symbiotic interface, it is evident that root surface associated diazotrophs seem not able to readily release fixed N to the host plant and that this occurs only through microbial turnover (Lethbridge and Davidson 1983; Rao et al. 1998). This may account for inconsistent response of plants inoculated with diazotrophs and indicates that there is need for better understanding of the potential for free-living and endophytic diazotrophs to supply N to host plants. In addition to their potential for supplying plants with N, free-living diazotrophs may also promote plant growth and nutrition through various other mechanisms.

Other mechanisms of PGPR to enhance plant nutrition

Microbial production of phytohormones

Many PGPR produce phytohormones that are considered to enhance root growth and greater surface area (e.g. bigger roots, more lateral roots and root hairs) leading to an increase in explored soil volume and thus plant nutrition (Fig. 4). Such microorganisms, commonly termed 'phytostimulators', include a wide range of soil bacteria and fungi. The most common phytohormones produced by PGPR are auxins, cytokinins, giberellins and to a lesser extent ethylene, with auxins being the most well characterized (Khalid et al. 2004; Patten and Glick 1996; and see review by Arshad and Frankenberger 1998). Indeed in *Azospirillum*, auxin (IAA) production, rather than N_2 fixation, is generally considered to be the major factor responsible for the PGPR response through stimulation of root growth (Dobbelaere et al. 1999).

Indole-3-acetic acid (IAA) controls a wide variety of processes in plant development and plant growth and plays a key role in shaping plant root architecture such as regulation of lateral root initiation, root vascular tissue differentiation, polar root hair positioning, root meristem maintenance and root gravitrophism (Aloni et al. 2006; Fukaki et al. 2007). Production of IAA is widespread among rhizobacteria (Khalid et al 2004; Patten and Glick 1996; Spaepen et al. 2007), with increasing numbers of endophytic IAA-producing PGPR being reported (Tan and Zou 2001). For example, Kuklinsky-Sobral et al. (2004) screened a collection of root-associated bacteria from soybean for their ability to produce IAA and showed that it was present in 28% of isolates. More recently, the distribution of IAA biosynthetic pathways among annotated bacterial genomes suggests that 15% (from 369 analysed) contain genes necessary for synthesis of IAA (Spaepen et al. 2007). IAA production has also been observed in rhizobia and in phytopathogenic bacteria, although the amount of auxins produced by different rhizobacteria seems to differ according to their mode of interaction with plants (Kawaguchi and Syōno 1996). Several IAA biosynthetic pathways, classified according to their intermediates, exist in bacteria and for most, tryptophan has been identified as the precursor of IAA (Patten and Glick 1996; Spaepen et al. 2007). However, only few specific genes and proteins involved in IAA biosynthesis have been characterized to date, and only in a small number of PGPR (e.g. *Azospirillum brasilense*, *Enterobacter cloacae, Pantoea agglomerans* and *Pseudomonas putida*; Koga et al. 1991; Patten and Glick 2002; Zimmer et al. 1998). In phytopathogenic bacteria, IAA seems to be mainly produced from tryptophan via the intermediate indole-3-acetamide (IAM pathway), whilst in beneficial phytostimulatory bacteria, IAA appears to be synthesized predominantly via indole-3-pyruvic acid (IPyA pathway) (Manulis et al. 1998; Patten and Glick 1996; 2002; Zimmer et al. 1998).

In *A. brasilense*, inactivation of a key enzyme in the IPyA pathway (the *ipdC* gene, encoding an indole-3-pyruvate decarboxylase) resulted in up to 90% reduction of IAA production (Dobbelaere et al. 1999), but mutants were not completely abolished in IAA biosynthesis, suggesting some redundancy in pathways. Irrespective of this, various *ipdC* mutants

displayed altered phenotypes compared to the wild-type strains in their ability to alter wheat root morphology (i.e. either no increase in root hair and lateral root formation and no decrease in root length; Malhotra and Srivastava 2008; Dobbelaere et al 1999). The impact of exogenous auxin on plant development ranges from positive to negative effects, and occurs as a function of the amount of IAA produced, the cell number of auxin-producing rhizobacteria and on the sensitivity of the host plant to changes in IAA concentration (Dobbelaere et al 1999; Spaepen et al 2008; Xie et al. 1996). For example, Remans et al. (2008) highlighted cultivar specificity in the response of plants to auxin-producing bacterial strains. In many PGPR, genes involved in IAA production are fine-regulated by stress factors that commonly occur in soil and potentially within the rhizosphere (e.g. acidic pH and osmotic stress), and in some cases have been shown to be activated by plant extracts (e.g. amino acids such as tryptophan, tyrosine and phenylalanine, auxins and flavonoids; Ona et al. 2005; Prinsen et al. 1991; Vande Broek et al. 1999; Zimmer et al. 1998).

Cytokinins stimulate plant cell division, control root meristem differentiation, inhibit primary root elongation and lateral root formation but can promote root hair development (Riefler et al. 2006; Silverman et al. 1998). Cytokinin production has been reported in various PGPR including, *Arthrobacter* spp., *Azospirillum* spp., *Pseudomonas fluorescens*, and *Paenibacillus polymyxa* (Cacciari et al. 1989; de Salamone et al. 2001; Perrig et al. 2007; Timmusk et al. 1999). However, genes involved in the biosynthesis of bacterial cytokinins have not yet been characterized in PGPR and therefore their involvement in plant growth promotion largely remains speculative.

Gibberellins enhance the development of plant tissues particularly stem tissue and promote root elongation and lateral root extension (Barlow et al. 1991; Yaxley et al. 2001). Production of gibberellins have been documented in several PGPR such as *Azospirillum* spp., *Azotobacter* spp., *Bacillus pumilus*, *B. licheniformis, Herbaspirillum seropedica*e, *Gluconobacter diazotrophicus* and rhizobia (Bottini et al. 2004; Gutiérrez-Mañero et al. 2001). Some *Azospirillum* strains are also able to hydrolyze, both *in vitro* (Piccoli et al. 1997) and *in vivo* (Cassán et al. 2001), glucosyl-conjugates of gibberellic acid, which correspond to reserve or transport forms of gibberellic acid produced by plants (Schneider and Schliemann 1994). This activity leads to an increase in the release of active forms of the phytohormone into the rhizosphere. However, the bacterial genetic determinants involved in this mechanism remain to be identified as does the precise role of gibberellins in plant growth promotion by PGPR.

Ethylene is a key phytohormone that can inhibit root elongation, nodulation and auxin transport, and promotes seed germination, senescence and abscission of various organs and fruit ripening (Bleecker and Kende 2000; Glick et al. 2007b). Ethylene is required for the induction of systemic resistance in plants during associative and symbiotic plant-bacteria interactions and, at higher concentrations, is involved in plant defence pathways induced in response to pathogen infection (Broekaert et al. 2006; Glick et al. 2007a). Certain PGPR such as *A. brasilense* have been shown to produce small amounts of ethylene from methionine as a precursor (Perrig et al. 2007; Thuler et al. 2003), and this ability seems to promote root hair development in tomato plants (Ribaudo et al. 2006). However, a better knowledge (i.e. characterization of bacterial biosynthesis pathway and genetic determinants involved) has to be gained in order to determine the role of the production of this plant growth regulator in the growth promoting effect of PGPR.

Some plant-associated bacteria such as *A. brasilense* (strain Sp245) are able to produce nitric oxide (NO) due to the activity of nitrite reductases (Creus et al. 2005; Pothier et al. 2007). The formation of NO is an intermediate in the denitrification pathway, during which nitrate (or nitrite) is converted to nitrogen oxides (N_2O) and to N_2 (Zumft 1997; Fig. 3). This pathway is utilized by soil bacteria to gain energy under oxygen-limited conditions that may occur in the rhizosphere (Højberg et al. 1999). Although denitrification by rhizobacteria diminishes the amount of NO_3^- available for plant nutrition, it may have positive effects on root development by means of NO production, which is a key signal molecule that controls root growth and nodulation, stimulates seed germination and is involved in plant defence responses against pathogens (Lamattina et al. 2003; Pii et al. 2007). Furthermore, NO can interact with other plant hormone signalling networks including that for IAA (Lamattina et al 2003; Fig. 4). Bacterial denitrification and production of NO by *A. brasilense* has been demonstrated on wheat roots (Creus et al.

2005; Neuer et al. 1985; Pothier et al. 2007) and NO produced during tomato root colonization stimulated the formation of lateral roots (Creus et al. 2005). Nitrous oxide production therefore is potentially another plant-beneficial trait displayed by *Azospirillum* PGPR.

Microbial enzymatic activities influencing plant hormone levels

Certain PGPR are able to stimulate plant growth by directly lowering plant ethylene levels through the action of 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase (i.e. deamination of the plant ethylene precursor; Fig. 4). ACC deaminase (encoded by the *acdS* gene) catalyses the conversion of ACC, the immediate plant precursor for ethylene, into NH_3 and α-ketobutyrate and is widely distributed in soil fungi and bacteria, especially the Proteobacteria (Blaha et al. 2006; Prigent-Combaret et al. 2008). Whilst the ecological significance of ACC-deaminase in soil microorganisms is largely unknown, in plant-beneficial bacteria it may serve to diminish the amount of ACC available for production of ethylene (Glick et al. 2007a). Since ethylene inhibits growth and elongation of root, this may lead to enhanced root system development (Glick et al. 2007a). Indeed, this model has been validated by analysis of the root growth promoting effect of a *Pseudomonas putida* PGPR, where *acdS* was inactivated (Glick et al. 1994; Li et al. 2000). In the case of *Azospirillum,* complementation of $AcdS^-$ strains with an *acdS* gene from *P. putida* enhanced the plant-beneficial effects of these PGPR on both tomato (*Lycopersicon esculentum* Mill.) and canola (Holguin and Glick 2001; Holguin and Glick 2003). Similar results were obtained following the introduction of the *Pseudomonas acdS* gene into $AcdS^-$ *Escherichia coli, Agrobacterium tumefaciens* and biocontrol strains of *Pseudomonas* spp., where expression of ACC deaminase promoted root elongation, inhibition of crown gall development and improved protection against phytopathogens, respectively (Hao et al. 2007; Shah et al. 1998; Wang et al. 2000). From a number of studies it appears that the growth promotion effect of ACC deaminase in rhizobacteria is most effective in stress environments such as in flooded, heavy-metal contaminated or saline soils (Cheng et al. 2007; Farwell et al. 2007) and in response to phytopathogens (Wang et al. 2000).

Cross-talk between plant-growth promoting pathways in plants

It is evident that plant regulatory molecules (e.g. auxin, ethylene, NO, gibberellin etc) do not act alone but interact with one another in a variety of complex ways (Fu and Harberd 2003; Glick et al. 2007a; Lamattina et al. 2003). Moreover, it is clear that the PGPR effect occurs as a result of a combination of different mechanisms (additive hypothesis). For example, a model has been proposed by Glick et al. 2007a to describe cross-talk between auxin and ethylene in both PGPR and plants. In response to root exudates containing tryptophan, PGPR produce IAA that can be taken up by plant cells. Besides the direct effect of IAA on plant cell proliferation and elongation, it also induces the synthesis of ACC synthase in plants (Abel et al. 1995) and thereby the production of ethylene. A negative feedback loop, involving inhibition by ethylene of the transcription of auxin response factors, would lead *in fine* to a slow down of ACC synthase activity and decrease of ACC and ethylene biosynthesis (Glick et al. 2007a). Other close interactions between IAA and ethylene pathways have been recently reported. It appears that ethylene triggers the accumulation of auxin in the root apex (Stepanova et al. 2005) and that the transport of auxin from the apex to the elongation zone of roots is required for ethylene to inhibit root growth (Swarup et al. 2007). Overall, the molecular mechanisms by which ethylene and auxin interact to competitively regulate root development remain largely unknown and future prospects will aim to clarify their respective contribution. AcdS- and IAA-producing PGPR might promote root growth by both a lowering of plant ethylene production and ethylene-dependent signalling pathways, and through an increase in an ethylene-independent manner, of the content of IAA in roots.

Facilitating plant iron and vitamins absorption

In addition to phytohormones, PGPR may influence the growth of plant roots through the production of siderophores and vitamins. Roots of strategy II type plants (e.g. the Graminaceae; Marschner 1995; Robin et al. 2008) secrete phytosiderophores (Fe-chelators) which bind Fe^{3+} and maintain its concentration in soil solution (see Lemanceau et al. 2009). At the root

surface chelated Fe^{3+} can then be directly taken up as a phytosiderophore-Fe complex (strategy II; see Lemanceau et al. 2009), whereas in non-graminaceous species (strategy I type plants; Marschner 1995; Robin et al. 2008) Fe^{3+} must first be reduced to Fe^{2+} prior to being absorbed by the plant (Lemanceau et al. 2009). Rhizobacteria (and fungi) also produce siderophores and it has been shown that plants can absorb bacterial-Fe^{3+} complexes, which includes strategy I species possibly by endocytosis (Bar-Ness et al. 1991; Vansuyt et al. 2007). The capture of these bacterial complexes by plants may play a significant role in nutrition and growth, especially in alkaline and calcareous soils where Fe availability is low (Bar-Ness et al. 1991; Masalha et al. 2000). Moreover, this mechanism is involved in biocontrol activities of PGPR and has been linked to competitive effects with phytopathogens and other detrimental rhizosphere microorganisms (Duijff et al. 1993; Longxian et al. 2005; Robin et al. 2008).

Plants under optimal growing conditions synthesize vitamins but when grown in stressed environments, vitamin-producing rhizobacteria may stimulate plant growth and yield. In particular, production of vitamins of the B group (e.g. thiamine, biotin, riboflavine, niacin) has been documented in some *Azospirillum*, *Azotobacter*, *Pseudomonas fluorescens* and *Rhizobium* strains (Marek-Kozaczuk and Skorupska 2001; Revillas et al. 2000; Rodelas et al. 1993; Sierra et al. 1999). There is evidence that exogenous supply of B-group vitamins to plants favours root development (Mozafar and Oertli 1992), but there is presently no direct evidence (e.g. using mutants) that PGPR can stimulate plant growth through this mechanism (Marek-Kozaczuk and Skorupska 2001), although further work is warranted.

Interactions between plant growth promoting microorganisms

Mycorrhizal associations

Microbial populations in the rhizosphere, including known PGPR, can either interfere with or benefit the formation and function of mycorrhizal symbioses (Gryndler 2000). A typical beneficial effect is that exerted by 'mycorrhizal-helper-bacteria' (MHB) which stimulate mycelial growth and/or enhance mycorrhizal formation (Garbaye 1994). This applies both to ectomycorrhizal fungi (Frey-Klett et al. 2005) and to AM fungi (Barea et al. 2005b; Johansson et al. 2004) and involves a range of bacterial species, commonly including *Bacillus* and *Pseudomonas*. Responses to MHB are associated with both the production of compounds that increase root cell permeability and rates of root exudation, which either stimulate AM fungal mycelia in the rhizosphere or facilitate root penetration by the fungus, and the production of phytohormones that influence AM establishment (Barea et al. 2005b). Specific rhizobacteria are also known to affect the pre-symbiotic stages of AM development, such as spore germination and rate of mycelial growth (Barea et al. 2005b). Recently, Frey-Klett et al. (2007) revisited the significance of MHB and differentiated the effects based on either AM formation or AM function, including nutrient mobilization, N_2 fixation and protection of plants against root pathogens.

Given that the external mycelium of mycorrhizas act as a link between roots and the surrounding soil, the fungus can also synergistically interact with soil microorganisms that mobilize soil P, through either solubilization or mineralization (Azcon et al. 1976; Barea 1991; Barea et al. 2005a; Kucey 1987; Tarafdar and Marschner 1995). Such interactions have been investigated with ^{32}P-based methodologies using reactive rock phosphate in a non-acidic soil (Toro et al. 1997) and in an experiment conducted by Barea et al. (2002) using various treatments that included i) AM inoculation, ii) PSB inoculation, iii) AM plus PSB dual inoculation and iv) non-inoculated controls in a soil containing natural populations of both AM fungi and PSB (Fig. 5). Soils were either un-amended (without P application) or fertilized with rock phosphate. Both rock phosphate addition and microbial inoculation improved biomass production and P accumulation in plants, with dual inoculation being the most effective (Barea et al. 2002; Fig. 5). Independent of rock phosphate addition, AM-inoculated plants showed lower specific activity for ^{32}P than compared to non-AM inoculated controls, particularly when inoculated with PSB, suggesting that the PSB were effective in releasing P from sparingly soluble sources either directly from the soil or from added rock phosphate. Other studies have similarly showed a positive interaction between ectomycorrhizal fungi and the presence of bacterial isolates that show potential for the weathering of soil minerals and its associated release of nutrients for plant uptake (Uroz et al. 2007). On such evidence it suggested that mycor-

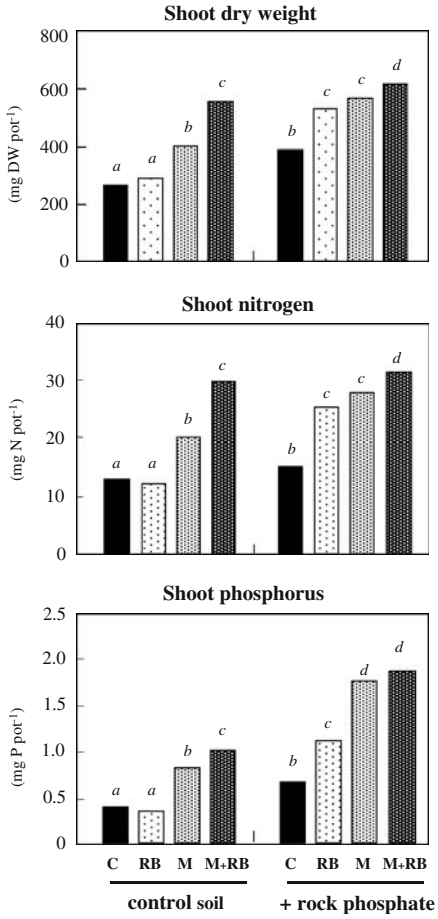

Fig. 5 Growth, N and P content of shoots of lucerne (alfalfa; *Medicago sativa* L.) inoculated with plant growth promoting rhizobacteria (PGPR). The plants were inoculated with *Rhizobium meliloti* and grown in a Cambisol soil (Granada; Spain) with either no added P (control) or supplied with rock phosphate (Riecito Venezuela; 11.4% P provided at 100 mg P kg^{-1} soil). Additionally, plants were grown as either control (C) or were further inoculated with a phosphate-solubilizing bacteria (RB; *Enterobacter* sp.), an arbuscular mycorrhizal fungi (M; *Glomus mosseae*) or with a comibantion of both microorganisms (M+RB). For each panel, columns not designated with the same letter are significantly ($P<0.05$) different (data taken from Barea et al. 2002)

rhizas are highly effective for improving the capture of mobilized nutrients in soil, especially in relation to the mobilization and capture of soil P.

Microbial interactions and enhanced nitrogen fixation

Interaction between mycorrhizal fungi, PGPR and diazotrophs, including both rhizobia and associative N-fixers, has also received considerable attention. In legumes it is evident that AM can improve both nodulation and N_2 fixation within nodules (Barea et al. 2005a; Barea et al. 2005b). Co-inoculation of *Rhizobium* sp. with AM fungi gave greater growth promotion in lucerne (alfalfa) and pea than inoculation of either symbiont alone (Höflich et al. 1994). The physiological and biochemical basis of AM fungal x *Rhizobium* interactions in improving legume productivity suggests that the main effect of AM in enhancing nodule activity is through a generalized stimulation of host nutrition, but specific hormonal effects on root and nodule development may also occur (Barea et al. 2005a).

Several reports have demonstrated a direct PGPR effect on legume nodulation. Various PGPR including *Azotobacter vinelandii, A. brasilense, Bacillus* sp., *Pseudomonas* sp., and *Serratia* spp. increased root and shoot growth, the number and mass of nodules, N_2 fixation and plant N content, and grain yield in various legumes when co-inoculated with *Rhizobium* sp. (Burdman et al. 1996; Parmar and Dadarwal 1999; Sivaramaiah et al. 2007). The most commonly implicated mechanism involved the production of IAA (Molla et al. 2001). PGPR stimulation of root growth potentially provides more infection sites for nodule initiation and, through their ability to induce flavonoid production in the plant (Burdman et al. 1996), an induction in the expression of rhizobial *nod* genes. Co-inoculation of *Rhizobium* sp. with *Pseudomonas fluorescens* (strain PsIA12), which is able to promote the development of roots and protect against root pests, also has been shown to improve the benefit of rhizobia on various legumes including, lucerne, pea and broad bean (*Vicia faba* var *major* Harz.) (Höflich et al. 1994).

Interaction between AM fungi and various PGPR has also been reported and in many cases shown to be beneficial for plant growth (see review by Barea et al. 2005a). For example, increased root colonization by AM fungi was observed when coinoculated with a range of PGPR including *Azospirillum*, *Azotobacter croococcum*, *Bacillus polymyxa* and *Pseudomonas stricta* (Artursson et al. 2006; Gamalero et al. 2004; Toro et al. 1997). Barea et al. (1983) similarly showed that maize and ryegrass inoculated with *A. brasilense* and mycorrhizal fungi had comparable N and P contents as to plants grown with fertilizer. Inoculation of plants with *Azospirillum* enhanced mycorrhizal formation and conversely, *Azospirillum* establishment

in the rhizosphere was also shown to be improved (Barea et al. 2005a). However, increased N acquisition by dual-inoculated plants was attributed to greater N uptake capacity by mycorrhizal infected roots, rather than a direct effect through N_2 fixation. Multi-level interactions between AM fungi, *Azospirillum* and PSB have also been reported with indication of synergistic effects when inoculated simultaneously (Muthukumar et al. 2001). However, it is important to also consider that relationships between PGPR and mycorrhizas may not always be positive (Walley and Germida 1997).

Conclusions and future directions

The acquisition of nutrients from soils is governed by root growth and its interaction with the abiotic and biotic components of soil. This interaction is manifest largely by the physical, chemical and biological properties of the rhizosphere (Hinsinger et al. 2009). Through better understanding of rhizosphere interactions and how roots associate with soil microorganisms there is opportunity for enhancing the efficiency of nutrient uptake by plants (Rengel and Marschner, 2005). This may occur through either direct plant selection, manipulation of root growth or by management of indigenous microbial communities and/or specific symbiotic and associative interactions through inoculation.

Manipulation of roots

Growth and development of roots and formation of the rhizosphere through root hairs or via the capacity to associate with mycorrhizas is of critical importance for effective soil exploration and access to nutrients. Indeed identification of germplasm and its use in breeding programs that are directed at modifications to root architecture have been successful in improving nutrient efficiency under field conditions through either direct plant selection (Gahoonia et al. 1999; Liao et al. 2006; Lynch and Brown 2001) or by intercropping of different plant species for enhanced N and P nutrition (e.g. Li et al. 2007; Knudsen et al. 2004). Further success can be expected as molecular tools become available that allow root traits to be more readily identified and manipulated, such as genome-wide analyses and the development of molecular markers for specific root traits and/or the identification of key regulatory genes including transcription factors that are involved in root development (Wissuwa et al. 2009). For example, genes associated with branching and lateral root growth, proliferation in N-rich regions and root hair development in response to nutrient deficiency have been identified, some of which are associated with hormonal responses in plants (Grierson et al. 2001; Yi et al. 2005; Zhang and Forde 2000). Ultimately such genes may be used to manipulate root growth for greater nutrient acquisition. Alternatively, it is possible that biochemical traits of roots may also be manipulated to influence the availability of nutrients in soil. For example, microbial phytase genes have been expressed in plant roots and when grown in controlled environments these plants have increased ability to access organic forms of P when supplied as inositol phosphates (George et al. 2005a; Richardson et al. 2001b). Genes that encode for the synthesis and transport of organic anions in plants have similarly been identified and, in some cases, used to enhance the release of organic anions from roots with benefits reported in terms of tolerance to Al (de la Fuente-Martínez et al. 1997; Delhaize et al. 2004) and improved access to soil P (Lopez-Bucio et al. 2000). However, the reliability of over-expressing genes for organic anion biosynthesis as a general means to improve organic anion release from roots has been questioned (Delhaize et al. 2001). In addition there is a need to demonstrate widespread applicability of such approaches for plants when grown in different soil environments where restricted performance has either been observed or where growth may be impeded by other limitations (George et al. 2005b). There is also a need to better understand the importance of spatial and temporal variations in root growth and rhizosphere function in different soil environments in relation to the uptake of specific nutrients (primarily N and P, but also for micronutrients), so that plant manipulations and breeding objectives are directed at appropriate traits for maximum benefit. Indeed the use of appropriate models have shown that small changes to root growth or rhizosphere processes can have significant effect on the acquisition of N and P by different plant species (Wissuwa 2003; Dunbabin et al. 2006). Likewise, the importance of microbial-mediated processes for nutrient mobilization in the rhizosphere and

their interaction with plant mechanisms needs to be considered along with the significance of rhizosphere interactions under field conditions (Watt et al., 2006).

Interaction with microorganisms, management and development of inocula

Understanding of the interaction of roots with soil microorganisms that are associated with enhanced nutrient acquisition has also advanced in recent years. For instance, significant progress in knowledge of mycorrhizal symbioses and their role in agro-ecosystem function have been made, but further research, particularly in relation to the potential contribution of AM fungi to agricultural systems, is required. This includes better understanding of; (i) population biology and diversity of mycorrhizal fungi in soils, (ii) identifying genetic determinants involved in the compatibility and synergism between plant and fungal partners, (iii) examining ecological traits that control the beneficial effects of the fungus on plant growth and soil quality, (iv) increased knowledge of interactions within the mycorrhizosphere, particularly those involving other PGPR, including phosphate-mobilizing microorganisms, and (v) improved management systems for realizing mycorrhizal benefits for both sustainable agricultural production systems and in natural and restoration ecosystems. For AM fungi in particular, this includes improved methods for production of inocula and development of appropriate management practices (e.g. either by crop rotation, intercropping or with inclusion of various PGPR, including mycorrhiza helper bacteria) to promote the presence and function of various AM in different environments.

Effort has also been directed at understanding of the ecology and management of PGPR in soil, yet their development as inoculants (with the exception of rhizobia which have been successful over many decades) remains a considerable challenge. Whilst biocontrol products based on specific strains of *Pseudomonas* or *Bacillus* have been developed successfully, exploitation of phytostimulatory (or biofertilizer) PGPR-based inoculants remains less advanced. One exception is *Azospirillum*, which has now been commercialized widely as an inoculant and shown considerable promise in different agriculture environments. In this case it is evident that growth promotion occurs primarily through phytostimulation and enhanced root growth, rather than direct effects on N_2 fixation. A number of soil fungi, originally isolated and characterized on the basis of their capacity to solubilize inorganic soil P under laboratory conditions, have similarly been developed as commercial biofertilizer inoculants. However, again it is evident that these inoculants appear to promote plant growth through stimulation of root growth rather than directly through P-mobilization (Wakelin et al. 2006). Increased root growth subsequently allows greater soil exploration and thus increased P uptake which results in an apparent increase in P efficiency. In contrast, Wakelin et al. (2007) have recently reported the isolation of a wider range of soil fungi (predominantly *Penicillium* sp.) that show greater potential for direct P mobilization. With these few examples it is evident that growth promotion and microbial interaction with roots is a complex phenomenon and that better understanding of the various mechanisms involved and how they interact with roots is required. Indeed it is generally accepted that greater nutrient uptake by plants in response to PGPR appears to occur generally as a result of stimulated root growth as compared to direct effects on increased plant uptake of nutrients.

Paramount to further success of PGPR is a need to better understanding the ecology of microorganisms, either indigenous or introduced, within the rhizosphere both as individual organisms and through their interaction with other microorganisms (e.g. N_2-fixing rhizobacteria or endophytic diazotrophs with P-mobilizing AM fungi) and directly with host plants. Inconsistent response of PGPR in different environments and on various hosts remains as a significant impediment to their widespread development and application (Richardson 2001). Identification of traits involved in the ability of specific organisms to establish themselves in the rhizosphere (rhizosphere competence) at levels sufficient to exert effects on plant growth, to effectively compete with indigenous microorganisms or to cooperative with other beneficial organisms, and understanding of the signalling processes that occur between plants and microorganisms is required. Moreover, methods of inoculation (e.g. use of carriers, rates, and product longevity etc) and opportunity for developing microbial consortia as inocula needs to be considered. Opportunities for this will be advanced by development and application of molecular techniques and biotechnological approaches to microbial ecology. This includes non-disruptive *in situ* visualization techniques

(e.g. confocal laser scanning microscopy and fluorescent tagged DNA probes, proteins, or microorganisms), functional genomics and analysis of the molecular basis of root colonization and signaling in the rhizosphere. In addition there is need for better understanding of the actual mechanisms that contribute to growth promotion and interaction with plants roots, including the possibility for genetic modification of specific microorganisms or plants.

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