Chapter 6
Role of Mycorrhizal Symbioses in Phosphorus Cycling

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6.1 Introduction

6.1.1 Mycorrhizal Symbiosis: Definition, Partners, Diversity

Mycorrhizal symbioses are associations of plant roots or rhizoids with fungi that, at least under some conditions, are beneficial to both partners. Arbuscular mycorrhizal (AM) symbiosis was established at the dawn of terrestrial plant evolution, some 400–500 million years ago, between ancestral vascular plants (*Cooksonia*, *Rhynia*, *Aglaophyton*) and fungi belonging to the phylum Glomeromycota (Pirozynski and Dalpé 1989; Redecker et al. 2000; Schüßler et al. 2001). AM symbiosis has been identified in thousands of plant species among all major plant lineages including bryophytes, ferns, gymno- and angiosperms (Brundrett 2009; Wang and Qiu 2006). It is the most widespread type of mycorrhizal symbiosis with respect to the number of plant species it involves (Trappe 1987; Wang and Qiu 2006) and can be found in virtually all ecosystems on Earth. Despite its broad host range, the fungal diversity is limited to a few hundred species (Redecker and Raab 2006), inferring that the

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association is particularly species-unspecific. Quantitative preferences for root colonization have, however, been repeatedly found between some plant and the fungal species (Jansa et al. 2002; Öpik et al. 2009; Sýkorová et al. 2007; Vandenkoornhuyse et al. 2003) and it is possible that a broader specificity between some fungal and plant genotypes does exist. This remains difficult to test experimentally, given the current limitations in the understanding of AM fungal genomic organization and molecular diversity (Croll and Sanders 2009; Martin et al. 2008).

Evolutionarily more recent types of mycorrhizal associations include ectomycorrhizas (ECM), ericoid mycorrhizas (ERM), and orchid mycorrhizas (Cairney 2000). These types are restricted to narrower groups of plant taxa, and involve fungi from the phyla Basidiomycota, Ascomycota, and Zygomycota. Some of these fungi form quite species-specific associations (e.g., *Cortinarius* and *Suillus* associate with rather a narrow range of plant species, such as *Pseudotsuga*, *Betula*, *Larix*, and *Pinus*), whereas others (e.g., *Cenococcum* spp.) may colonize roots of a broad range of plant species (Bruns et al. 2002; Smith and Read 2008; Tedersoo et al. 2008). A few plant species (such as eucalyptuses, willows, and alders) have the capacity to interact with both AM and ECM fungi. This can give rise to root systems simultaneously colonized by mycorrhizal fungi belonging to different types (Adams et al. 2006; van der Heijden and Vosátka 1999). The different types of mycorrhizal symbioses have also shown predominance for different plant biomes (Read and Perez-Moreno 2003; Smith and Read 2008 and references therein). Plants in polar regions and at high altitudes are usually not mycorrhizal, but often have roots extensively colonized by dark septate fungal endophytes with unclear function (Mandyam and Jumpponen 2005; Newsham et al. 2009). By definition, endophytes live solely within the plant tissues, and often fulfill their entire lifecycle including reproduction inside the plant body (Faeth and Fagan 2002). Mycorrhizal fungi, in contrast, inhabit and interconnect two kinds of environment, namely the inner volume of the plant roots and the surrounding soil (Jansa and Gryndler 2010). The status of many root-inhabiting fungi is unclear because it is inherently difficult to demonstrate absence of hyphal growth outside the roots. Heathlands (here we refer to heathlands at both high latitudes and altitudes as well as nutrient-limited and wildfire-prone ecosystems in Mediterranean climates, known as fynbos, chaparral, maquis or matorral in different parts of the world) are usually dominated by ERM, and Taiga (coniferous boreal forest) is dominated by the ECM (Read et al. 2004; Thormann et al. 1999). Most trees in deciduous forests establish ECM symbiosis, although the understorey plants are primarily colonized by AM fungi (Helgason et al. 2002). Most plants in grasslands and in tropical forests also establish AM symbiosis (Castillo et al. 2006; Treseder and Cross 2006). Plants inhabiting highly weathered and severely phosphorus (P)-impoverished soils (as in Western Australia) are often devoid of mycorrhizas; these plants have other adaptations, such as cluster roots, that fulfill their P requirements (Lambers et al. 2008). Under field conditions, the root system of a single plant is usually colonized by different mycorrhizal fungal species simultaneously (Burke et al. 2005; Jansa et al. 2003b; Merryweather and Fitter 1998; Miller et al. 1991). This diversity could have important consequences

for acquisition of nutrients as well as for maximizing symbiotic benefits for the plants (Baxter and Dighton 2001; Jansa et al. 2008; Koide 2000).

6.1.2 Mycorrhizal Functioning

The unequivocal importance of mycorrhizal symbioses to plants (and soils) is inherently difficult to demonstrate because the mycorrhizal condition is normal, and absence is rare under natural settings (Merryweather and Fitter 1995). Establishing non-mycorrhizal control treatments in pot experiments or in the field is a great challenge and may potentially introduce experimental artefacts (Jones and Smith 2004; Kahiluoto et al. 2000a). Soil sterilization by steaming or autoclaving, for example, changes chemical soil properties (Serrasolses et al. 2008). It also eliminates other soil organisms, introducing further confounding effects. While these artefacts should always be considered in the interpretation of experimental results, there have been numerous independent studies comparing the performance of mycorrhizal and non-mycorrhizal plants under a range of environmental conditions. These experiments have collectively demonstrated that plants benefit from their mycorrhizal associations through improved nutrient acquisition, mainly of elements with low mobility in the soil (e.g., P, zinc, and copper), and through greater resistance to drought and biotic stresses (Clark and Zeto 2000; Jansa et al. 2003a; Marschner 1995; Redon et al. 2009; Sikes et al. 2009).

The benefits of mycorrhizal colonization to the plants result from expansion and/or complementation of the root function. Mycorrhizal fungi colonize two environments: the inner root volume (sometimes extending to the hyphal sheath on the root surface) and the surrounding soil, thus directly connecting the root system with a greater soil volume. By increasing soil contact, the plants are able to acquire resources from zones lying far beyond the direct reach of the roots and the root hairs. This effect is not trivial because the hyphae of some AM fungi can extend many centimeters away from the root surface, unlike root hairs, which only extend a few millimeters (Jakobsen et al. 1992; Jansa et al. 2003a, 2005). ECM fungal mycelium can bridge even greater distances, particularly if the fungi form thick rhizomorphs (Allen et al. 2003). P transport through the ECM hyphae over distances up to 40 cm has been documented (Finlay and Read 1986; Timonen et al. 1996). In contrast, some mycorrhizal fungi establish very dense mycelial networks in the vicinity of the roots, growing only a few millimeters from their host (Smith et al. 2004). These mycelial networks significantly expand the capacity of the plant to acquire mineral nutrients from the soil. In addition, in the case of ECM fungi, these mycelial networks also play an important role in acquisition of water by the plants from the soil (Allen 2007; George and Marschner 1996). Root colonization by mycorrhizal fungi and their mycelial networks may also be important for interactions between plants and soil-borne pathogens. This is due to (1) changes in plant nutritional status upon mycorrhiza development, (2) direct competition for plant carbohydrates between the mycorrhizal fungi and the pathogens, and/or (3) changes

in the activity and composition of the microbial communities in the rhizosphere (Fitter 2005; Graham 2001; Newsham et al. 1995; Toljander et al. 2007).

Many ERM and ECM fungi are also thought to be involved in mineralization of organic nutrients (Bueé et al. 2007; Finlay 2008; Tibbett and Sanders 2002) and bioweathering of recalcitrant inorganic nutrients from carbonates, micas, and apatites (Blum et al. 2002; Wallander 2000). It appears, however, that even in some of the well-documented case studies, other soil microorganisms (particularly the prokaryotes) might have played important roles in the release of nutrients from minerals or organic compounds. Therefore, the contribution of mycorrhizal fungi to these processes remains, in most cases, poorly quantified (Finlay 2008; Koele et al. 2009). Evidence for direct involvement of AM fungi in mineralization of significant amounts of organic P is still inconsistent. In particular, the role of other soil microorganisms associated with the mycorrhizal mycelium, which might be very important under nonsterile soil conditions, is not properly understood (Finlay 2008; Joner and Jakobsen 1995; Joner and Johansen 2000; Koide and Kabir 2000; Tarafdar and Marschner 1994; Toljander et al. 2006). The presence of mycorrhizal fungi also significantly modifies soil conditions in the rooting zone (aggregation, wettability, biological activity), modulates intra- and interspecific competition within the plant community, and affects soil microbial communities (Barea 2000; Facelli et al. 1999; Johansson et al. 2004; Rillig and Mummey 2006).

Mycorrhizal fungi are invariably heterotrophic organisms, and they mostly derive the organic carbon needed for their growth, respiration, and biological maintenance directly from their host plants in the form of recently fixed photosynthates. Some of the fungi (especially those forming ECM and ERM associations) are currently considered capable of limited saprophytic growth (Azcón-Aguilar and Barea 1995; Gibson and Mitchell 2004; Koide et al. 2008; Zeller et al. 2008), though under natural conditions its widespread realization has recently been questioned (Baldrian 2009; Taylor and Alexander 2005). The dependence of the fungi on the host plant for organic carbon can, depending on environmental conditions (e.g., availability of soil P, availability of light and CO_2 to the plants, plant density, and possibly other factors), cause the association to vary from highly beneficial to apparently parasitic (Johnson et al. 1997; Schroeder and Janos 2004; Smith and Smith 1996; West et al. 1993; Whitbeck 2001). For example, under very low soil P availability (<0.2 mg P kg^{-1}, extractable with 0.5 M $NaHCO_3$) caused either by low total P levels or high P sorption in highly weathered soils, mycorrhizal symbiosis may be less beneficial in terms of net P acquisition than if small amounts of P were added to the soil (Bolan 1991; Bolan et al. 1983). Therefore, under very low soil P availability, plants specialized in modes of P mobilization and uptake other than mycorrhizal symbiosis (e.g., those forming cluster roots) can dominate the plant communities (Lambers et al. 2008). In contrast, under conditions of very high soil P availability (>50 mg kg^{-1}, extractable with 0.5 M $NaHCO_3$), such as following application of high rates of water-soluble P-fertilizers, the plant can gain access to enough P with its root system, resulting in little or no net demand for mycorrhizal P uptake (Kahiluoto et al. 2000b; Sorensen et al. 2003). In such situations, the extent of mycorrhizal development in roots is often reduced (Bolan

et al. 1984; Jansa et al. 2009; Youpensuk et al. 2008). In addition, depending on the plant species and soil and climatic conditions, the association with AM fungi could have negative effects on plant growth (Jifon et al. 2002; Morgan et al. 2005; Ryan and Graham 2002; Kahiluoto et al. 2000b). Under conditions where P availability limits plant growth ($NaHCO_3$-extractable P levels typically between 5 and 20 mg kg^{-1}), mineral nutrient acquisition benefits conferred to the plants by the AM fungi will usually far outweigh the costs of carbon supply to the fungus and will result in a net growth benefit to the plant (Jakobsen 1995; Li et al. 2005; Morgan et al. 2005; Ortas et al. 2002). These studies indicate that the benefits to the plants of association with AM fungi across a range of environmental conditions (Fig. 6.1) are best described by a bell-shaped (or unimodal) response curve (Bolan et al. 1984; Gange and Ayres 1999; Picone 2002). Even so, plants may benefit from mycorrhizal symbiosis even though the growth and/or nutritional benefits (such as net P uptake) may not be apparent, and special techniques such as isotopic labeling are necessary to demonstrate mycorrhizal function in these cases (Fitter 2005; Grace et al. 2009; Smith et al. 2004, 2009).

Although negative effects of some ECM fungi on host plant growth have been occasionally reported (Burgess et al. 1993; Corrêa et al. 2008), the great majority of

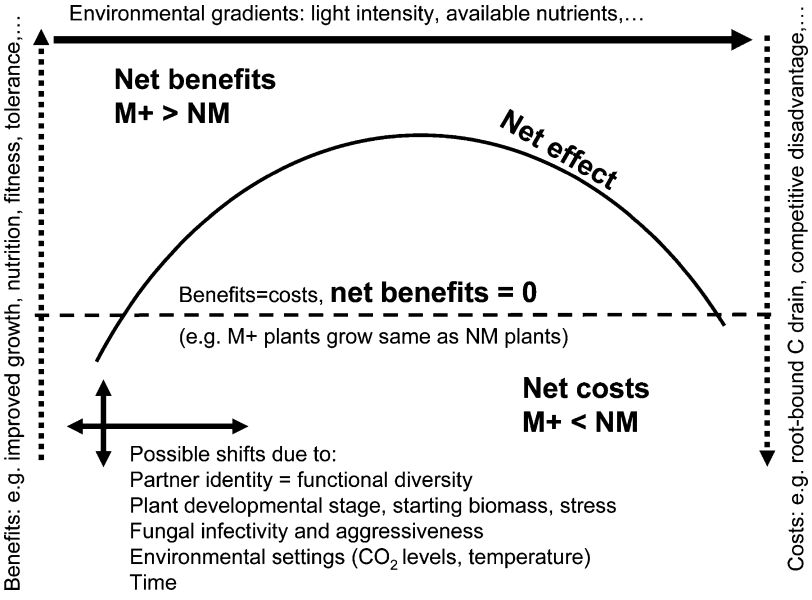

Fig. 6.1 Conceptual model of whole-plant effects of the interactions between a plant, mycorrhizal fungi, and the environment. This scheme delineates interdependencies between mycorrhizal costs and benefits, resulting in a continuum of outcomes, ranging from highly beneficial to potentially detrimental effects. This scheme is based mainly on the evidence gathered for arbuscular mycorrhizas, but also appears to be generally applicable to ectomycorrhizas. Processes in other mycorrhizal types (especially orchid mycorrhizas and mycorrhizas of achlorophylous plants) may follow different trajectories. *M+* mycorrhizal plant, *NM* non-mycorrhizal plant

studies on both ECM and ERM associations report growth benefits to the host plants upon colonization of the roots by the symbiotic fungi (Choi et al. 2005; Diedhiou et al. 2005; Finlay et al. 1992; Jansa and Vosátka 2000). The extent of root colonization by the different fungi and the magnitude of benefits, however, depend on a broader environmental context and not only on the P availability (Hoeksema et al. 2010). Additional factors that determine the extent of root colonization and mycorrhizal benefits are: soil nitrogen (N) levels, seed size and nutrient reserves contained in the seed, plant age and growth rate, and the identity of both plant and fungal species (Corrêa et al. 2006; Duponnois et al. 2008; Egerton-Warburton and Allen 2001).

6.2 Different Forms of P in the Soil and Their Accessibility to Mycorrhizas

6.2.1 Forms of P

Phosphorus is present in different forms in the soil. Inorganic forms (crystalline apatites; amorphous phosphates of calcium, potassium, iron and aluminum, and other phosphates; inorganic polyphosphate; and orthophosphate) differ greatly in their solubility in water and in their chemical reactivity (Dou et al. 2009; Holford 1997). P is also a component of an array of organic compounds present in the soil, such as nucleic acids, phospholipids, inositol phosphates, and many metabolic intermediates (see also Doolette and Smernik 2011; Bünemann et al. 2011). In contrast to the diversity of P forms present in the soil, the only form taken up in significant amounts across the plasmalemma of both the plant and mycorrhizal fungal cells is orthophosphate (P_i), preferentially as $H_2PO_4^-$ ions (Rausch and Bucher 2002; Smith 2002). Although various organic P forms have been reported as potentially utilizable by some microorganisms, it appears that their enzymatic cleavage to P_i actually occurs before the cross-membrane uptake, in the close vicinity of the microbial cells (Heath 2005). Therefore, P_i in the soil solution close to the plant and/or fungal cells plays a pivotal role in the uptake of P by the plants, both via the direct and the mycorrhizal pathways (Smith 2002; Smith et al. 2004). Direct P uptake pathway refers to acquisition of P_i by the plants from the soil solution through rhizodermis cells or root hairs. Mycorrhizal P uptake pathway refers to acquisition of P from the soil solution by mycorrhizal hyphae, translocation of P throught the extraradical mycelium, release of P from the mycorrhizal hyphae within the roots, and uptake of this released P by the root cells (usually in the cortical layer).

6.2.2 Kinetics of P Acquisition by Hyphae

Uptake of P from the soil solution to the cells (either of plant roots or mycorrhizal fungal hyphae) is mediated by P_i transporters (Rausch and Bucher 2002; Smith 2002; Tatry et al. 2009). These transporters are large proteins with several

transmembrane domains and are responsible for the proton or sodium symport of phosphate molecules across the membrane and against a steep electrochemical gradient (Karandashov and Bucher 2005; Smith 2002). These proteins have been most studied in AM fungi, but recently, two P_i transporters from ECM fungus *Hebeloma cylindrosporum* have also been characterized (Tatry et al. 2009). The first mycorrhizal P_i transporter was identified from cDNA libraries of *Medicago truncatula* roots colonized by *Glomus versiforme*, using hybridization with a probe derived from a yeast P_i transporter (Harrison and van Buuren 1995). Further experiments, including expression of this P_i transporter in a yeast P_i transporter (*pho84*)-mutant, indicated Michaelis–Menten kinetics with an apparent K_m value of 18 μM. This value is one to two orders of magnitude higher than that predicted for high-affinity P transporter systems of AM fungi (Schweiger and Jakobsen 1999; Smith et al. 2001; Thomson et al. 1990). The discrepancy, however, could easily be due to problems with heterologous gene expression, as suggested earlier (Smith et al. 2001). Recently reported K_m values for the two P_i transporters of the ECM fungus *Hebeloma cylindrosporum* (4 and 55 μM) were closer to the values predicted from earlier hydroponic experiments (Tatry et al. 2009; van Tichelen and Colpaert 2000). All other reported details on P_i transporters from different AM fungi only refer to the so-called high-affinity transporter family, important for uptake of P_i from the soil solution, where the P_i concentration does normally not exceed 10 μM (Harrison 1999; Marschner 1995). The other (low-affinity) P_i transporter system, apparently operating in germ tubes of *Gigaspora margarita* (Thomson et al. 1990), has not yet been characterized at the gene level.

The described P_i transporters of both AM and ECM fungi show a high degree of structural conservation and other similarities to the P_i transporters of other organisms (Karandashov and Bucher 2005; Schachtman et al. 1998). The energetic expenditure of this high-affinity P_i acquisition is not fully resolved, but the estimates are between two and four protons per molecule of phosphate (Jennings 1996; Leggewie et al. 1997; Rausch and Bucher 2002 and references therein), with the proton gradient being generated by H^+-ATPases (Requena et al. 2003; Smith and Read 2008 and references therein). The other aspect of P_i uptake kinetics is the P_i inflow per unit of hyphal biomass or hyphal surface. Previous studies indicate some interspecies variation in both the AM and ECM fungal groups (Smith and Read 2008; van Tichelen and Colpaert 2000). This might relate to the kinetic parameters of the different P_i transporters and their expression patterns in the fungal mycelium in the soil. The uptake of P_i into the hyphae may further be modulated by possible differences between the different fungal species and genotypes in the intensity of hyphal proliferation and the dynamics of the hyphal networks.

Improved acquisition of P by mycorrhizal plants appears to be derived from several characteristics. The mycorrhizal hyphae are capable of penetrating smaller soil pores (5–30 μm) than the roots (>50–100 μm), thus expanding access to the soil. In addition, due to their size, the formation of a prominent P depletion zone around the individual hyphae is minimal. Mycorrhizal hyphae are also more efficient at spatial exploration of the soil volume (up to 50 m hyphae g^{-1}) as compared to roots (up to 0.1 m roots g^{-1}) and have a lower carbon cost per unit

of hyphal surface as compared to the root surface (Gregory 2006; Jansa et al. 2003a, 2005; Li et al. 1991; Schnepf et al. 2008; Tinker 1975). In contrast, a poorly studied aspect is the dynamics of the hyphal networks (de Vries et al. 2009; Fitter et al. 2004). It appears that short-lived hyphal structures, like the branched-absorbing structures described for AM fungi from the genus *Glomus*, can provide a highly flexible pathway for acquisition of P and other nutrients to the plants from the soil. These structures have rather high turnover rates (7–35 days from initiation to death under axenic conditions) as compared to backbone hyphal strands, which retain cytoplasm over 3 months under axenic culture conditions (Bago et al. 1998, 2004; de Vries et al. 2009). Hyphal turnover of AM fungi from genus *Glomus*, as estimated by isotopic signature of carbon supplied to the plants and recovered in the AM hyphae, was only about 5–6 days (Staddon et al. 2003). These results are congruent with the time-span of the fine and short-lived hyphal structures, as presented above, as well as with previous estimates (5–7 days) based on microscopy of soil hyphae (Friese and Allen 1991). The rates of hyphal turnover in ECM and ERM networks are not well known, but are probably lower than in the AM fungi. Estimates from a carbon-flux study comparable to the study of Staddon et al. (2003) indicated an average lifespan for ECM mycelium of about 9 days, whereas rhizomorphs of some ECM fungi were observed to live for a number of months (Godbold et al. 2006 and references therein). Great levels of variability with respect to the hyphal growth and/or turnover rates have been recognized within each mycorrhizal type and between different fungal taxa (Downes et al. 1992; Godbold et al. 2006; Wallander 2006). Possibly, part of this variability could be explained by the different P acquisition strategies of the different mycorrhizal fungi. For example, soil P mining (defined here as accessing recalcitrant P sources through solubilizing or hydrolyzing exudates according to Lambers et al. 2008) would assume longer-lived mycelium in the same soil patch, whereas P scavenging (defined here as collecting the easily available P beyond the reach of roots) could more efficiently be carried out by fungi with fast hyphal turnover, expanding rapidly into uncolonized soil patches. This hypothesis remains to be tested experimentally within each of the mycorrhizal types as well as between the different types.

6.2.3 Access to Recalcitrant P Forms, Weathering, and Mineralization

Varying amounts of information are known about different mycorrhizal types and their effects on release of P from recalcitrant forms present in soil. Many ECM fungi have been shown to be able to release P_i from poorly soluble P sources such as apatite. This function has been demonstrated in numerous pure culture, pot, and microcosm studies, and was recently reviewed by Rosling (2009). The relevance of pure culture studies has, however, been questioned because large amounts of added organic carbon can induce production of acids at higher rates than under natural conditions. Pot and microcosm studies are also difficult to interpret because other

microorganisms (some of them having the capacity to solubilize sorbed phosphate and/or the capacity to produce exocellular phosphatases) are usually present in the system (Jones and Smith 2004; Vessey 2003). These factors imply that the ECM could potentially take up P_i primarily released by the other microbes and transfer it to plants. In extreme cases, this could lead to measurable elevation of plant P uptake from recalcitrant sources, even when the involved mycorrhizal fungus was incapable of solubilization of the recalcitrant P on its own. However, Smits et al. (2008) recently demonstrated fungal-induced weathering of apatite in sterile microcosms with *Pinus sylvestris* seedlings colonized by the ECM fungus *Paxillus involutus*. Fungal colonization of apatite grains (Fig. 6.2) increased weathering rates threefold, and ^{14}C simultaneously supplied to the plant was preferentially allocated to apatite patches colonized by the fungus. The proposed mechanism for apatite dissolution is enhanced acidification and chelation of calcium cations from the apatite through fungal exudation of oxalic acid. Complexation of calcium with oxalic acid would then lead to formation of calcium oxalate crystals on the surface of the fungal hyphae in contact with the apatite. These crystals have previously been observed (Allen et al. 1996; Landeweert et al. 2001), as have the elevated levels of oxalic acid in the ectomycorrhizal mats of forest soils (Griffiths et al. 1994).

This relationship is supported by the observation that apatite grains introduced into forest soil usually become heavily colonized by ECM hyphae (Hagerberg et al. 2003; Turpault et al. 2009). Furthermore, Wallander and Thelin (2008) demonstrated that this fungal colonization became more intense when P levels of Norway spruce needles dropped below 1.5 mg P g^{-1} dry weight. This value is close to P-limiting conditions (1.3 mg P g^{-1} dry weight) according to Linder (1995), suggesting that carbon allocation to fungal-colonized nutrient patches is regulated by the nutrient status of the tree. In spite of these studies, direct evidence that ECM fungi enhance the rates of apatite weathering is still limited. For example, Turpault et al. (2009) incubated apatite grains in mesh bags for 4 years in a beech forest in

Fig. 6.2 Apatite grains (1 mm diameter) colonized by ectomycorrhizal fungus *Paxillus involutus* in sterile microcosms. Reproduced from Smits et al. (2008), with permission

western France. Half of the bags were placed in trenched plots to which roots and mycorrhizal hyphae had no access and the other half were placed at different depths in soil accessible to roots and mycorrhizal hyphae. Apatite grains in untrenched plots were heavily colonized by fungal hyphae (presumably ECM) and, in contrast to the grains without roots, showed many weathering marks (as assessed by electron microscopy). However, with exception of the treatment at a soil depth of 25 cm (0.2% apatite weight loss over 4 years without mycorrhizal roots versus 0.5% weight loss with the roots), the apatite dissolution measured as a loss of mass was seemingly unaffected by the presence of mycorrhizal roots when compared to the trenched plots established in the same soil. Similarly, in a study by Wallander and Thelin (2008), apatite grains from P-limited forests did not dissolve significantly faster than apatite grains from P-sufficient forests, based on the amount of rare earth elements (La, Nd, Sm, Eu, Tb and Yb) from the apatite that accumulated in mycorrhizal roots surrounding the mesh bags. Both the above studies, however, were carried out under acidic soil conditions (pH $\leq$4.3), which can preclude strong mycorrhizal effects on apatite solubilization through mycorrhizosphere acidification.

Although it seems indisputable that ECM fungi have the potential to release P from phosphorus-containing minerals under laboratory conditions, the extent to which this has an influence on field weathering rates of apatite is still the subject of much debate (Hutchens 2009; Rosling et al. 2009; Sverdrup et al. 2002; van Scholl et al. 2008). Uptake of elements from apatite by ECM fungi under field conditions has been previously demonstrated (Blum et al. 2002; Hagerberg et al. 2003), but the quantitative role of this process, operating on very long time scales (for contemporary science), is difficult to estimate.

Different approaches have been used to examine the roles played by different mycorrhizal fungi in mobilizing P (and N) from organic substrates and these have been reviewed by Read and Perez-Moreno (2003), among others. These approaches range from axenic systems in which the fungal hyphae are exposed to identified model compounds, to microcosm and field studies using more natural biological substrates. ERM fungi produce a range of organic polymer-degrading enzymes that can attack molecules such as chitin, lignins, polyphenols, and tannins, which either contain N or protect access to organically bound or spatially inaccessible N and P sources (organic or inorganic). Detected enzymes include lignases, polyphenol oxidases, laccase, and catechol oxidase, and the ability to degrade hydrolyzable polyphenols appears to be more extensively developed in ERM than in ECM fungi (Bending and Read 1996a, b). In addition to degrading structural components of plant litter, the ERM fungi also produce enzymes that hydrolyze P-containing molecules. Experiments performed under axenic conditions using DNA as a sole P source (Leake and Miles 1996; Myers and Leake 1996) have shown that phosphodiesters can be used by the ERM fungi as sole P sources without the intervention of other saprotrophs. These findings were corroborated by studies of the ERM fungi isolated from *Woollsia pungens* roots (Chen et al. 1999). All four of the studied isolates were able to utilize various organic compounds as a sole carbon and N source, and two of the isolates were able to grow on DNA or inositol sodium hexaphosphate as sole sources of P, with higher biomass production than

Hymenoscyphus (now *Rhizoscyphus*) *ericae*. The relevance of the above results for the rates of acquisition of P by the ERM fungi and associated host plants from complex organic substrates under nonsterile soil conditions needs, in many cases, to be refined by coupling enzymatic assays and isotope labeling, as in the N studies of Wurzburger and Hendrick (2006, 2009).

Similar studies to those on ERM listed above have also been conducted on ECM fungi involving "natural" substrates. In these studies, pollen grains or dead nematodes were added to microcosms containing mycorrhizal (*Paxillus involutus*) or non-mycorrhizal *Betula pendula* seedlings (Perez-Moreno and Read 2001a, b). More than 96% of the P in pollen (measured as P concentration in the pollen-enriched soil patches) added to mycorrhizal microcosms was removed and, on average, 25% of this was transferred to the mycorrhizal seedlings (calculated from the system P budget, comparing mycorrhizal and non-mycorrhizal plants and assuming no significant contribution of seed P to the plant P content). In contrast, only 25% of the P in pollen added to non-mycorrhizal microcosms was removed and only 7% of this ended up in the non-mycorrhizal plants, suggesting that ECM fungal hyphae play an important role in resource capture from organic substrates. In the study with nematodes, 65% of the P originally present in the nematodes was removed from the site of addition and 73% of this was transferred to the mycorrhizal *B. pendula* plants. In non-mycorrhizal systems, the plants gained half as much P as the mycorrhizal systems, representing only 22% of the total originally present in the nematodes. In earlier studies, Bending and Read (1995a, b) examined the structure and function of the ECM fungal mycelium in relation to nutrient mobilization from forest litter. In microcosms containing *Pinus sylvestris* seedlings, colonization of organic material from the fermentation horizon by *Suillus bovinus* reduced concentrations of P by 22%, but colonization by *Thelephora terrestris* had no effect. Activities of nutrient-mobilizing enzymes in birch litter colonized by *Paxillus involutus* were studied and phosphomonoesterase activity increased 28–50 days but decreased again between 50 and 98 days after the initial colonization of the organic patches by the fungal mycelia. The final levels of activity were below those of uncolonized litter, but in these unsterile substrates it was not possible to distinguish between the activities of mycorrhizal fungi and those of saprotrophs. Another study addressing the utilization of inositol hexaphosphate by ECM fungi (Colpaert et al. 1997) demonstrated substantial extracellular acid phosphatase activity associated with mycelia of *Thelephora terrestris* and *Suillus luteus* that was correlated with mycelial biomass and increasing P nutrition of the mycorrhizal plants. Phytase activity of the mycelium could not be detected, but activity at the surface of mycorrhizal roots was higher than that at the surface of non-mycorrhizal roots, though the relative contributions of plant roots and fungi to hydrolysis of soluble inositol hexaphosphate were unclear. Tibbett and Sanders (2002) have shown that colonization of willow roots by *Hebeloma syrjense* resulted in substantial improvement of P capture by the plants from plant litter (8% of the added P transferred to the shoots within 35 days in mycorrhizal plants as compared with only 1% in the non-mycorrhizal plants). This may be due to either the short-circuiting of the organic P re-cycling between soil and plants via mycorrhizal

hyphae, or secondarily through the effects of the ECM on other components of the system involved in P cycling (such as bacteria, saprophytic fungi, mites, collembolans etc.). In this context, it is interesting to mention an earlier study that documented efficient transfer of P from the mycelium of the saprophytic fungus *Hypholoma fasciculare* to the ECM fungi *Suillus variegatus* or *Paxillus involutus* (Lindahl et al. 1999). In this study, up to 25% of the ^{32}P contained in the hyphae of *Hypholoma* appeared in the mycorrhizal plants, whereas transfer from the mycorrhizal fungi to the saprophyte was at least one order of magnitude lower.

Studies of the extraradical hyphae of *Glomus intraradices* (Koide and Kabir 2000) have demonstrated that this AM fungus can hydrolyze organic P and transfer it through the mycelium. The magnitude of these processes under unsterile soil conditions, however, remains poorly quantified, and the importance of organic P mineralization by the AM fungi themselves has been called into question by other experiments (Joner and Jakobsen 1995; Joner and Johansen 2000). In another study, wheat was grown in chambers composed of several compartments. These compartments permitted both root and mycorrhizal hyphae growth, or, blocked root access and allowed for only hyphal growth. The soils in different compartments were then supplemented with large amounts of P (200 mg kg^{-1} soil) in inorganic or organic forms. Control chambers without mycorrhizal fungi were also established. Elevated phosphatase activity was observed in the root-free soil colonized by *Glomus mosseae* when compared to AM-free soil, particularly upon organic P addition (Tarafdar and Marschner 1994). Similarly designed experiments using red clover and *Glomus versiforme* suggest that AM fungal colonization of a root-free soil amended with organic P makes a significant contribution to plant uptake of P from sources such as lecithin, RNA, and sodium phytate (Feng et al. 2003). On the other hand, the study by Antibus et al. (1997) demonstrated that field-collected AM roots of red maple had consistently lower levels of phosphatase activity than ECM roots of the same plant species.

Tarafdar et al. (2001) showed that fungal (*Aspergillus* spp.) acid phosphatases were more efficient than plant enzymes at mobilizing P from lecithin and phytate. This could be interpreted, on one hand, as proof of the capacity of fungi in general to efficiently hydrolyze organic P in the soil or, on the other hand, as a demonstration of the capacity of certain specific fungal groups (particularly the soil saprophytes) to hydrolyze such substrates. It is now clear from a range of studies that ERM and ECM fungi have the saprotrophic capacity to intervene in microbial mobilization–immobilization cycles and to sequester both N and P from the organic complexes formed during the decomposition of microbial, faunal, and plant remains. In heathland and forest ecosystems, these are the dominant sources of both N and P, and the enzymatic capacity to sequester these nutrients from complex organic substrates is probably most highly developed in the ERM fungi (Smith and Read 2008). The evidence for AM fungi is less clear and is complicated by the need to distinguish between the physiological activity of the AM hyphae and that of other fungi or bacteria that might be associated with them. Experiments by Hodge et al. (2001) demonstrated accelerated decomposition and N uptake from organic material associated with AM hyphae, but the potential contribution of other

soil saprotrophs was unclear. Further experiments by Leigh et al. (2009) have shown uptake of P and N associated with patches of organic material, but again, additional uptake of P from bone-meal and Terragreen substrate present within the microcosms cannot be ruled out. The ambiguity here indicates the need for further experiments investigating the potential role of mycorrhiza-associated bacteria. The role of mycorrhizal fungal hyphae as primers of soil microbial activity has been discussed by a number of authors (e.g., Jones et al. 2004; Talbot et al. 2008; Toljander et al. 2007), but so far our understanding of how this regulates nutrient acquisition and transfer within the mycorrhizosphere is limited.

6.2.4 Mycorrhizas as Compound-Specific Filters

In an overwhelming number of studies, the role of mycorrhizal symbiosis in plant acquisition of P has been documented under a wide range of environmental conditions, in different ecosystems and for different host plants (Arihara and Karasawa 1998; Cardoso and Kuyper 2006; Jansa et al. 2009 and references therein; Smith and Read 2008 and references therein). Nevertheless, to regard mycorrhizas only as P pumps would be utterly incorrect, particularly if considering ECM and ERM fungi in comparison to the most abundant form of mycorrhizal symbiosis formed by the AM fungi. In addition to their role in P nutrition, ECM, ERM and, to a lesser extent, AM fungi are involved in acquisition of N by plants, both from inorganic and organic sources (Finlay et al. 1992; Johansen et al. 1992; Mäder et al. 2000; Read et al. 2004). Involvement of ECM in plant water uptake has been shown (Allen 2007; Plamboeck et al. 2007) and the mycorrhizas are also known to alleviate deficiencies in micronutrients such as zinc and copper. In addition, at least some genotypes of mycorrhizal fungi have the capacity to protect their host plants from acquisition of soil pollutants such as radiocaesium (de Boulois et al. 2008; Joner et al. 2004; Ladeyn et al. 2008) and heavy metals (Joner et al. 2000; Martino et al. 2000; Sharples et al. 1999; Sudová et al. 2008), while maintaining the P and/or zinc supply to the plants (Joner et al. 2004; Soares and Siqueira 2008).

6.3 Translocation of P Within the Hyphae and Its Release to the Plants

6.3.1 Transport Within the Hyphae

The P taken up by mycorrhizal fungi from the soil solution is used to meet the physiological demand of the fungus, with the remainder transported to the plants or stored in the hyphae. Transport of P to the plant implies a long-distance transfer through the hyphal network, which, in both ECM and AM fungi, is assumed to involve polyphosphates (Bucking and Heyser 2003; Ezawa et al. 2002). The short-chain polyphosphates, resulting from depolymerization of longer polyphosphate

chains transferred over long distances, appear to be the immediate source of P for the plants (Ohtomo and Saito 2005; Solaiman et al. 1999; Takanishi et al. 2009). Rapid transfer rates of P via mycorrhizal fungal hyphae have been measured either using radioisotope labeling or microscopy (Bago et al. 2002; Cooper and Tinker 1978; Cox et al. 1980; Nielsen et al. 2002; Rhodes and Gerdemann 1978; Timonen et al. 1996). Together with the capacity of some ECM and ERM fungi to release P from recalcitrant sources, this rapid transfer represents what has been referred to as a mycorrhizal short-circuit in soil–plant P cycling, bypassing release from minerals or organic sources by free-living soil microorganisms (Johnson et al. 2005; Pankow et al. 1991).

6.3.2 Release of P to the Plant

The mechanics of how the P is released from the fungi to the plants has not yet been described for any mycorrhizal type. It is also not yet known whether this process is through passive leakage or an active transport system. It is likely that some fungi can, to different extents, retain P in their mycelium during translocation, resulting in partial immobilization and perhaps storage of P on the way from the soil to the plants (Boddington and Dodd 1999; Chilvers and Harley 1980; Harley and McCready 1981; Solaiman et al. 1999) – either as a result of slow transfer within the hyphae or due to limited release to the plant. In either case, P cycling between soil and plant is slowed down and the P could potentially also be released back to soil from the fungal hyphae or transferred to other soil organisms upon hyphal death due to soil disturbance, parasitism, or grazing. On the other hand, transitional storage of P in the fungal mycelium may function as a buffer ensuring continuous supply of P into long-lived plants such as trees or perennial herbs in a changing environment (Genet et al. 2000; Lussenhop and Fogel 1999; Read 1984). Thus, in the long run, the rapid provision of P to the host plants by fungi may not necessarily be the most beneficial system.

The plant side of the transfer, namely the mycorrhiza-inducible P_i transporters expressed in the close vicinity of fungal structures such as hyphal coils or arbuscules, has already been characterized for several plant species establishing AM symbiosis (e.g., Glassop et al. 2005; Javot et al. 2007; Nagy et al. 2005; Paszkowski et al. 2002; Rausch et al. 2001). Similar transporters are also likely to exist in ECM and ERM plants, but have not yet been characterized at the molecular level.

6.3.3 Consequences of Mycorrhizal P Acquisition for the Plants and for Maintenance of Mutualism

The efficiency of P acquisition by the mycorrhizal fungi, the temporary P immobilization in the fungal biomass, and the controlled P release to the plants all have

important consequences for plant P nutritional status and growth. Although large improvements of plant P uptake have been reported upon mycorrhizal colonization of the roots by certain AM fungal species, association with other fungi may yield negative growth responses, and thus qualify the relationship as parasitic (Johnson et al. 1997; Smith et al. 2004). The potential for fungal control of P release to the plants points to one possible mechanism for maintaining the mycobiont diversity and mutualistic nature of the symbiosis through diversification of the benefits of carbon trading between the plant and the mycorrhizal fungi (Cowden and Peterson 2009; Helgason and Fitter 2009; Kiers and van der Heijden 2006).

In cases where the roots are colonized simultaneously by several species and/or genotypes of the mycorrhizal fungi, there is some evidence for preferential carbon distribution to more beneficial mycorrhizal symbionts (Bever et al. 2009; Fitter 2006). This preference is probably dependent upon the rates of P transfer within the specific root cells or fragments colonized by the different fungi. This is corroborated by physiological studies that showed that the release of P from intraradical hyphae of *Gigaspora* increased upon glucose addition (Solaiman and Saito 2001). However, there is also experimental evidence that some AM fungi can gain carbon from plants in spite of the net P gain of the host plant being very limited, such as under P- and N-sufficient conditions (Hoeksema et al. 2010; Pearson and Jakobsen 1993; Smith et al. 2003, 2004, 2009). Additionally, the existence of mycoheterotrophic plants, where the plants apparently receive both mineral nutrients and carbon from the fungus (Bidartondo et al. 2002; Imhof 2009; Taylor et al. 2004), is difficult to reconcile with the hypothesis of preferential carbon allocation to the most beneficial fungal symbiont. Possibly, some of the processes are regulated at the ecosystem level and not at a single plant level. This may mean that the answers are hidden in plant community ecology, source–sink relationships and so called "common mycorrhizal networks" interconnecting different plants (Bever 1999; Bever et al. 2009), although little evidence is so far available about mycorrhiza-mediated transfer of P and carbon between plants (Newman and Ritz 1986; Philip and Simard 2008; Robinson and Fitter 1999; Selosse et al. 2006; Yao et al. 2003). Furthermore, experimental data have recently been gathered showing a more inconspicuous contribution of mycorrhizas to the P acquisition by the plants without detectable plant growth or net P uptake improvements (Smith et al. 2003, 2004). These effects are, however, only seen in carefully designed radioisotope experiments, using non-mycorrhizal mutant genotypes, or expression analyses of fungal and plant P transporters (Burleigh and Bechmann 2002; Grace et al. 2009; Li et al. 2008; Poulsen et al. 2005; Smith et al. 2009). Results of the above studies showed that the symbiosis may be fully functional, even if traditional measurements of mycorrhizal "benefits" such as growth or net P uptake improvements were not able to detect its contribution (Facelli et al. 2009). They also indicate that the definition of the symbiosis, currently often implicating measurable benefits to both partners, may need to be broadened to cover these cases of association with no obvious "benefits" (Cavagnaro et al. 2004; Jones and Smith 2004).

6.4 Functional Diversity of Mycorrhizas with Respect to P Uptake

In addition to major functional differences between the different mycorrhizal types, variation in P uptake patterns and efficiency have been recognized between species and genotypes of both AM and the ECM fungi (Boddington and Dodd 1999; Cairney 1999; Cavagnaro et al. 2005; Jansa et al. 2005; Munkvold et al. 2004; Smith et al. 2003). In these studies, radioisotope labeling has proven to be a particularly important approach (see also Frossard et al. 2011). The recorded functional diversity among the different mycorrhizal fungi appears to be important for understanding mycorrhizal functioning in the field. This is because roots of most plants are colonized by a mixture of mycorrhizal fungal species, usually, but not always, belonging to the same type (van der Heijden and Vosátka 1999; van der Heijden et al. 1998).

It has been postulated that fungi differing in P acquisition strategies could complement each other when sharing the same root system, resulting in greater symbiotic benefits than those conferred by each of the fungi in isolation (Koide 2000). Although this may well be the case, direct experimental evidence for functional complementarity in P acquisition within mycorrhizal communities is still limited (Jansa et al. 2008; Maherali and Klironomos 2007). Better understanding of the components of the mycorrhizal uptake pathway in different mycorrhizal fungi (e.g., numbers of alternative P transporters, their regulation and expressional dynamics, dynamics of the polyphosphate pool in the fungal hyphae) and how the functional diversity is structured within fungal communities, will be necessary before more general conclusions can be drawn. A combination of approaches spanning molecular biology (Burleigh et al. 2002; Grace et al. 2009; Jansa et al. 2008; Tatry et al. 2009), isotopic labeling (Jakobsen et al. 1992; Jansa et al. 2005), carefully designed pot experiments (Maherali and Klironomos 2007; Smith et al. 2004), and modeling (Antoninka et al. 2009; Deressa and Schenk 2008; Schnepf et al. 2008, 2011) is essential for further progress in this area. Likewise, interactions between mycorrhizal P uptake, carbon costs, and cycling of other nutrients such as N at the whole plant or plant community levels must be considered for an ecologically relevant picture (Grelet et al. 2009; Johnson et al. 2010; Smith et al. 2009).

6.5 Human Impact on the Mycorrhizal Pathway of P Acquisition by Plants

Agricultural activities, pollution, climate change, and other anthropogenic environmental influences affect mycorrhizal symbioses and their role in P acquisition by plants. Substantial information has been accumulated on these influences over the years; however, only a fraction is discussed here. For a more detailed overview, the

reader is referred to other sources (Allen et al. 2003; Allison and Treseder 2008; Drigo et al. 2008; Jansa et al. 2006).

In agricultural systems, the application of water-soluble mineral P and N fertilizers usually reduces the dependency of plants on nutrient uptake via the mycorrhizal pathway. This forced selection may eventually promote fungi that are less beneficial to plants or promote an abundance of plants that are less mycorrhiza-dependent (Covacevich et al. 2007; Jansa et al. 2006; Johnson 1993). Crop breeding efforts for high yields have been shown to inadvertently select for lower mycorrhizal dependencies, probably through selection for greater dependency on mineral fertilizer inputs (Hetrick et al. 1993; Tawaraya 2003; Zhu et al. 2001). These effects are not limited to agricultural plants and soils as nutrients, and pollutants often leach into natural ecosystems from agricultural fields, inappropriate waste management, and/or industrial activities. These effects are especially pronounced in forests and heathlands. The activity of fungi sensitive to elevated nutrient availability and pollutants decreases, and plant species or genotypes are favored that can better tolerate the pollution and/or depend less on nutrient acquisition via mycorrhizal fungi (Dighton 1995; Egerton-Warburton and Allen 2000; Kieliszewska-Rokicka 1999; Rejšek 1991; Robertson et al. 2007).

Elevation of CO_2 levels in the atmosphere may transiently increase the biomass and metabolic activities of mycorrhizal fungi, such as P transfer from soil to plants, due to a reduction of carbon limitation and through creating a greater requirement for P and other nutrients by the plants (Alberton and Kuyper 2009; Millard et al. 2007). In a longer perspective, however, this may result in a more rapid exploitation of soil nutrient reserves and an increased sensitivity of ecosystems to disturbance events (Pritchard et al. 2008). Global warming and redistribution of precipitation patterns may also change the activity of soil microorganisms in general and mycorrhizal fungi in particular (Fitter et al. 2004), but the future prospects remain rather blurred – usually the availability of water and not soil nutrients appears to be the primary driver of the expected ecosystem changes (Aerts et al. 2009; Allison and Treseder 2008; Heinemeyer et al. 2007). If water availability is not limiting the microbial activity, decay of roots and plant debris may be accelerated by global warming, which could in turn speed up mycorrhizal P capture from these sources (e.g., Carleton and Read 1991) thus speeding up the P cycling. Nevertheless, genotypic differences in temperature tolerance and acclimation between different mycorrhizal fungi might also contribute to the variability in the observed responses in mycorrhizal community composition and functioning to climatic changes (Malcolm et al. 2008).

A final aspect of human activity worth mentioning here is the phenomenon of plant invasion. It has been proposed that non-mycorrhizal alien plants, such as *Hakea* spp. that form cluster roots, could gain a P-acquisition advantage in ecosystems normally dominated by mycorrhizal plants (Allsopp and Holmes 2001; Sousa et al. 2007). For alien plants like *Centaurea maculosa* in Northern American grasslands, a different mode of action has been proposed: invasive plants could tap into the existing mycorrhizal networks and divert the flux of resources, such as P, to individuals with this ability (Batten et al. 2008; Callaway et al. 2004; Zabinski

et al. 2002). Another scenario is that the native mycorrhizal fungi could be suppressed by (non-mycorrhizal) alien plants (e.g., *Alliaria petiolata* in North America), which would in turn result in suppression of the native plants that rely on their (native) mycorrhizal symbionts (Callaway et al. 2008; Mitchell et al. 2006). Although experimental evidence for these processes and their importance in the phenomenon of ecological invasions is still equivocal, it is becoming more and more apparent that underground processes, nutrient balances, and associated microflora including mycorrhizal fungi might all be important players in plant invasions, and thus relevant topics for further study.

6.6 Conclusions

Mycorrhizal symbioses are highly diverse in their relationships with plants and ecosystems and are involved in different P cycling processes. Although evidence is accumulating to suggest that some ECM fungi have the capacity to induce or accelerate weathering of P-bearing minerals, thus affecting P inputs into the biological P cycling within the ecosystems, these processes are still largely unquantified. It is therefore unclear how important these processes are compared to the other input pathways such as aerial deposition, sedimentation, abiotic weathering, and anthropogenic inputs via fertilization and pollution, and how they vary amongst different ecosystems and on different geographic and time scales (Johnson et al. 2010; Newman 1995; Smits et al. 2008). To solve these issues, precise measurement of P fluxes should be continued, using radio- and stable isotope methods (Frossard et al. 2011), as well as complementary modeling efforts and long-term observations (Rosling 2009; Rosling et al. 2009; Schnepf et al. 2011). Soil and environmental conditions must always be taken into account when interpreting experimental results (e.g., little biotic effect on solubilization of apatite through acidification should be expected for strongly acidic soil conditions). Additionally, chemical reactivity and other relevant information (chemical composition, crystallinity, grain size, provenance) of compounds such as apatite used for experimental studies should always be assessed and reported to allow strict reproducibility of results.

The importance of mycorrhizal symbiosis in plant P uptake has been established in hundreds of studies published over many decades (Smith and Read 2008). This extends from traditional comparisons of small (non-mycorrhizal) and big (mycorrhizal) plants, where the differences in net P uptake are easily demonstrable; through more inconspicuous cases, where improvements of net P uptake are not always translated into improved plant growth (Jansa et al. 2005); to the extreme cases, where net P uptake of the plant is not different between mycorrhizal and non-mycorrhizal plants, although the mycorrhizal P uptake pathway is fully operational (Grace et al. 2009; Smith et al. 2004, 2009).

In spite of some well-documented model cases, the mechanisms governing the transfer of P within the common mycorrhizal networks interconnecting different

plants, as well as the involvement of other soil microorganisms in soil–mycorrhiza-plant P transfer are still only fragmentarily understood (Finlay 2008; Lindahl et al. 1999; Toljander et al. 2006). Extensive use of mineral P fertilizers and breeding for high-yielding crop varieties under fertilized soil conditions has seemingly led to selection of genotypes that are less responsive to mycorrhizal symbiosis than some of the older cultivars (Hetrick et al. 1993). This might be of concern regarding efficient use of natural resources in the future (Sawers et al. 2008).

Major differences in the accessibility of different soil P pools to different mycorrhizal types explain the distribution of the different mycorrhizal types in ecosystems: AM fungi appear to access mainly orthophosphate in the soil solution, ECM can access both inorganic and organic P in soil, and ERM appear to be able to access mainly the P contained in organic substrates (Read and Perez-Moreno 2003). Direct acquisition of P from decaying plant biomass or other organic substrates via mycorrhizal pathway effectively short-circuits the soil–plant P cycling, in which the largest portion of P mineralization would otherwise have to be accomplished by free-living soil decomposers before being accessed by roots or the mycorrhizal hyphae (Carleton and Read 1991). Through efficient P recycling from organic forms, capture of P_i from soil solution, and by improving soil mechanical stability, mycorrhizal symbiosis has the potential to contribute substantially to reduction of P loss through leaching and erosion (Asghari et al. 2005; Cardoso and Kuyper 2006). On the other hand, in agricultural and other ecosystems where management includes intentional removal of some plant products (green biomass, grains, fibers, wood), mycorrhizal symbiosis alone cannot guarantee long-term sustainability of production without adequate P inputs in the form of mineral or organic fertilizers, plant residues, or products resulting from wastewater treatment or municipal waste processing (Jansa et al. 2006; Oberson et al. 2011).

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References

Adams F, Reddell P, Webb MJ, Shipton WA (2006) Arbuscular mycorrhizas and ectomycorrhizas on *Eucalyptus grandis* (Myrtaceae) trees and seedlings in native forests of tropical north-eastern Australia. Aust J Bot 54:271–281

Aerts R, Callaghan TV, Dorrepaal E, van Logtestijn RSP, Cornelissen JHC (2009) Seasonal climate manipulations result in species-specific changes in leaf nutrient levels and isotopic composition in a sub-arctic bog. Funct Ecol 23:680–688

Alberton O, Kuyper TW (2009) Ectomycorrhizal fungi associated with *Pinus sylvestris* seedlings respond differently to increased carbon and nitrogen availability: implications for ecosystem responses to global change. Glob Change Biol 15:166–175

Allen MF (2007) Mycorrhizal fungi: highways for water and nutrients in arid soils. Vadose Zone J 6:291–297

Allen MF, Figueroa C, Weinbaum BS, Barlow SB, Allen EB (1996) Differential production of oxalate by mycorrhizal fungi in arid ecosystems. Biol Fertil Soils 22:287–292

Allen MF, Swenson W, Querejeta JI, Egerton-Warburton LM, Treseder KK (2003) Ecology of mycorrhizae: a conceptual framework for complex interactions among plants and fungi. Annu Rev Phytopathol 41:271–303

Allison SD, Treseder KK (2008) Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. Glob Change Biol 14:2898–2909

Allsopp N, Holmes PM (2001) The impact of alien plant invasion on mycorrhizas in mountain fynbos vegetation. S Afr J Bot 67:150–156

Antibus RK, Bower D, Dighton J (1997) Root surface phosphatase activities and uptake of ^{32}P-labelled inositol phosphate in field-collected gray birch and red maple roots. Mycorrhiza 7:39–46

Antoninka A, Wolf JE, Bowker M, Classen AT, Johnson NC (2009) Linking above- and below-ground responses to global change at community and ecosystem scales. Glob Change Biol 15:914–929

Arihara J, Karasawa T (1998) Phosphorus nutrition in cropping systems through arbuscular mycorrhizal management. In: Ae N, Arihara J, Okada K, Srinivasan A (eds) International workshop on plant nutrient acquisition. Tsukuba, Japan. Conference proceedings. Springer, Berlin, pp 319–337

Asghari HR, Chittleborough DJ, Smith FA, Smith SE (2005) Influence of arbuscular mycorrhizal (AM) symbiosis on phosphorus leaching through soil cores. Plant Soil 275:181–193

Azcón-Aguilar C, Barea JM (1995) Saprophytic growth of arbuscular mycorrhizal fungi. In: Varma A, Hock B (eds) Mycorrhiza: structure, function, molecular biology and biotechnology. Springer, Berlin, pp 391–407

Bago B, Azcón-Aguilar C, Goulet A, Piché Y (1998) Branched adsorbing structures (BAS): a feature of the extraradical mycelium of symbiotic arbuscular mycorrhizal fungi. New Phytol 139:375–388

Bago B, Pfeffer PE, Zipfel W, Lammers P, Shachar-Hill Y (2002) Tracking metabolism and imaging transport in arbuscular mycorrhizal fungi. Metabolism and transport in AM fungi. Plant Soil 244:189–197

Bago B, Cano C, Azcón-Aguilar C, Samson J, Coughlan AP, Piché Y (2004) Differential morphogenesis of the extraradical mycelium of an arbuscular mycorrhizal fungus grown monoxenically on spatially heterogeneous culture media. Mycologia 96:452–462

Baldrian P (2009) Ectomycorrhizal fungi and their enzymes in soils: is there enough evidence for their role as facultative soil saprotrophs? Oecologia 161:657–660

Barea JM (2000) Rhizosphere and mycorrhiza of field crops. In: Balazs E, Galante E, Lynch JM, Schepers JS, Toutant JP, Werner D, Werry PAT (eds) Conference on biological resource management – connecting science and policy, Paris. France. Conference proceedings. Springer, Berlin, pp 81–92

Batten KM, Scow KM, Espeland EK (2008) Soil microbial community associated with an invasive grass differentially impacts native plant performance. Microb Ecol 55:220–228

Baxter JW, Dighton J (2001) Ectomycorrhizal diversity alters growth and nutrient acquisition of grey birch (*Betula populifolia*) seedlings in host-symbiont culture conditions. New Phytol 152:139–149

Bending GD, Read DJ (1995a) The structure and function of the vegetative mycelium of ectomycorrhizal plants. V. Foraging behaviour and translocation of nutrients from exploited litter. New Phytol 130:401–409

Bending GD, Read DJ (1995b) The structure and function of the vegetative mycelium of ectomycorrhizal plants. VI. Activities of nutrient mobilizing enzymes in birch litter colonized by *Paxillus involutus* (Fr.) Fr. New Phytol 130:411–417

Bending GD, Read DJ (1996a) Effects of the soluble polyphenol tannic acid on the activities of ericoid and ectomycorrhizal fungi. Soil Biol Biochem 28:1595–1602
Bending GD, Read DJ (1996b) Nitrogen mobilization from protein-polyphenol complex by ericoid and ectomycorrhizal fungi. Soil Biol Biochem 28:1603–1612
Bever JD (1999) Dynamics within mutualism and the maintenance of diversity: inference from a model of interguild frequency dependence. Ecol Lett 2:52–62
Bever JD, Richardson SC, Lawrence BM, Holmes J, Watson M (2009) Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. Ecol Lett 12:13–21
Bidartondo MI, Redecker D, Hijri I, Wiemken A, Bruns TD, Dominguez L, Sersic A, Leake JR, Read DJ (2002) Epiparasitic plants specialized on arbuscular mycorrhizal fungi. Nature 419:389–392
Blum JD, Klaue A, Nezat CA, Driscoll CT, Johnson CE, Siccama TG, Eagar C, Fahey TJ, Likens GE (2002) Mycorrhizal weathering of apatite as an important calcium source in base-poor forest ecosystems. Nature 417:729–731
Boddington CL, Dodd JC (1999) Evidence that differences in phosphate metabolism in mycorrhizas formed by species of *Glomus* and *Gigaspora* might be related to their life-cycle strategies. New Phytol 142:531–538
Bolan NS (1991) A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. Plant Soil 134:189–207
Bolan NS, Robson AD, Barrow NJ (1983) Plant and soil factors including mycorrhizal infection causing sigmoidal response of plants to applied phosphorus. Plant Soil 73:187–201
Bolan NS, Robson AD, Barrow NJ (1984) Increasing phosphorus supply can increase the infection of plant roots by vesicular arbuscular mycorrhizal fungi. Soil Biol Biochem 16:419–420
Brundrett MC (2009) Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320:37–77
Bruns TD, Bidartondo MI, Taylor DL (2002) Host specificity in ectomycorrhizal communities: what do the exceptions tell us? Integr Comp Biol 42:352–359
Bucking H, Heyser W (2003) Uptake and transfer of nutrients in ectomycorrhizal associations: interactions between photosynthesis and phosphate nutrition. Mycorrhiza 13:59–68
Bueé M, Courty PE, Mignot D, Garbaye J (2007) Soil niche effect on species diversity and catabolic activities in an ectomycorrhizal fungal community. Soil Biol Biochem 39:1947–1955
Bünemann EK, Prusisz B, Ehlers K (2011) Characterization of phosphorus forms in soil microorganisms. In: Bünemann EK, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_2
Burgess TI, Malajczuk N, Grove TS (1993) The ability of 16 ectomycorrhizal fungi to increase growth and phosphorus uptake of *Eucalyptus globulus* Labill and *E. diversicolor* F. Muell. Plant Soil 153:155–164
Burke DJ, Martin KJ, Rygiewicz PT, Topa MA (2005) Ectomycorrhizal fungi identification in single and pooled root samples: terminal restriction fragment length polymorphism (T-RFLP) and morphotyping compared. Soil Biol Biochem 37:1683–1694
Burleigh SH, Bechmann IE (2002) Plant nutrient transporter regulation in arbuscular mycorrhizas. Plant Soil 244:247–251
Burleigh SH, Cavagnaro T, Jakobsen I (2002) Functional diversity of arbuscular mycorrhizas extends to the expression of plant genes involved in P nutrition. J Exp Bot 53:1593–1601
Cairney JWG (1999) Intraspecific physiological variation: implications for understanding functional diversity in ectomycorrhizal fungi. Mycorrhiza 9:125–135
Cairney JWG (2000) Evolution of mycorrhiza systems. Naturwissenschaften 87:467–475
Callaway RM, Thelen GC, Barth S, Ramsey PW, Gannon JE (2004) Soil fungi alter interactions between the invader *Centaurea maculosa* and North American natives. Ecology 85:1062–1071

Callaway RM, Cipollini D, Barto K, Thelen GC, Hallett SG, Prati D, Stinson K, Klironomos J (2008) Novel weapons: invasive plant suppresses fungal mutualists in America but not in its native Europe. Ecology 89:1043–1055

Cardoso IM, Kuyper TW (2006) Mycorrhizas and tropical soil fertility. Agric Ecosyst Environ 116:72–84

Carleton TJ, Read DJ (1991) Ectomycorrhizas and nutrient transfer in conifer-feather moss ecosystems. Can J Bot 69:778–785

Castillo CG, Borie F, Godoy R, Rubio R, Sieverding E (2006) Diversity of mycorrhizal plant species and arbuscular mycorrhizal fungi in evergreen forest, deciduous forest and grassland ecosystems of Southern Chile. J Appl Bot Food Qual 80:40–47

Cavagnaro TR, Smith FA, Hay G, Carne-Cavagnaro VL, Smith SE (2004) Inoculum type does not affect overall resistance of an arbuscular mycorrhiza-defective tomato mutant to colonisation but inoculation does change competitive interactions with wild-type tomato. New Phytol 161:485–494

Cavagnaro TR, Smith FA, Smith SE, Jakobsen I (2005) Functional diversity in arbuscular mycorrhizas: exploitation of soil patches with different phosphate enrichment differs among fungal species. Plant Cell Environ 28:642–650

Chen A, Chambers SM, Cairney JWG (1999) Utilisation of organic nitrogen and phosphorus sources by mycorrhizal endophytes of *Woollsia pungens* (Cav.) F. Muell. (Epacridaceae). Mycorrhiza 8:181–187

Chilvers GA, Harley JL (1980) Visualization of phosphate accumulation in beech mycorrhizas. New Phytol 84:319–326

Choi DS, Quoreshi AM, Maruyama Y, Jin HO, Koike T (2005) Effect of ectomycorrhizal infection on growth and photosynthetic characteristics of *Pinus densiflora* seedlings grown under elevated CO_2 concentrations. Photosynthetica 43:223–229

Clark RB, Zeto SK (2000) Mineral acquisition by arbuscular mycorrhizal plants. J Plant Nutr 23:867–902

Colpaert JV, van Laere A, van Tichelen KK, van Assche JA (1997) The use of inositol hexaphosphate as a phosphorus source by mycorrhizal and non-mycorrhizal Scots pine (*Pinus sylvestris*). Funct Ecol 11:407–415

Cooper KM, Tinker PB (1978) Translocation and transfer of nutrients in vesicular-arbuscular mycorrhizas. II. Uptake and translocation of phosphorus, zinc and sulphur. New Phytol 81:43–52

Corrêa A, Strasser RJ, Martins-Loução MA (2006) Are mycorrhiza always beneficial? Plant Soil 279:65–73

Corrêa A, Strasser RJ, Martins-Loução MA (2008) Response of plants to ectomycorrhizae in N-limited conditions: which factors determine its variation? Mycorrhiza 18:413–427

Covacevich F, Echeverria HE, Aguirrezabal LAN (2007) Soil available phosphorus status determines indigenous mycorrhizal colonization of field and glasshouse-grown spring wheat from Argentina. Appl Soil Ecol 35:1–9

Cowden CC, Peterson CJ (2009) A multi-mutualist simulation: applying biological market models to diverse mycorrhizal communities. Ecol Modell 220:1522–1533

Cox G, Moran KJ, Sanders F, Nockolds C, Tinker PB (1980) Translocation and transfer of nutrients in vesicular-arbuscular mycorrhizas. 3. Polyphosphate granules and phosphorus translocation. New Phytol 84:649–659

Croll D, Sanders IR (2009) Recombination in *Glomus intraradices*, a supposed ancient asexual arbuscular mycorrhizal fungus. BMC Evol Biol 9:13

de Boulois HD, Joner EJ, Leyval C, Jakobsen I, Chen BD, Roos R, Thiry Y, Rufyikiri G, Delvaux B, Declerck S (2008) Role and influence of mycorrhizal fungi on radiocesium accumulation by plants. J Environ Radioactiv 99:785–800

de Vries FT, Bååth E, Kuyper TW, Bloem J (2009) High turnover of fungal hyphae in incubation experiments. FEMS Microbiol Ecol 67:389–396

Deressa TG, Schenk MK (2008) Contribution of roots and hyphae to phosphorus uptake of mycorrhizal onion (*Allium cepa* L.) – a mechanistic modeling approach. J Plant Nutr Soil Sci 171:810–820

Diedhiou AG, Gueye O, Diabate M, Prin Y, Duponnois R, Dreyfus B, Ba AM (2005) Contrasting responses to ectomycorrhizal inoculation in seedlings of six tropical African tree species. Mycorrhiza 16:11–17

Dighton J (1995) Nutrient cycling in different terrestrial ecosystems in relation to fungi. Can J Bot 73:S1349–S1360

Doolette AL, Smernik RJ (2011) Soil organic phosphorus speciation using spectroscopic techniques. In: Bünemann EK, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_1

Dou ZX, Ramberg CF, Toth JD, Wang Y, Sharpley AN, Boyd SE, Chen CR, Williams D, Xu ZH (2009) Phosphorus speciation and sorption-desorption characteristics in heavily manured soils. Soil Sci Soc Am J 73:93–101

Downes GM, Alexander IJ, Cairney JWG (1992) A study of aging of spruce [*Picea sitchensis* (Bong) Carr] ectomycorrhizas. 1. Morphological and cellular changes in mycorrhizas formed by *Tylospora fibrillosa* (Burt) Donk and *Paxillus involutus* (Batsch ex Fr) Fr. New Phytol 122:141–152

Drigo B, Kowalchuk GA, van Veen JA (2008) Climate change goes underground: effects of elevated atmospheric CO_2 on microbial community structure and activities in the rhizosphere. Biol Fertil Soils 44:667–679

Duponnois R, Kisa M, Prin Y, Ducousso M, Plenchette C, Lepage M, Galiana A (2008) Soil factors influencing the growth response of *Acacia holosericea* A. Cunn. ex G. Don to ectomycorrhizal inoculation. New Forest 35:105–117

Egerton-Warburton LM, Allen EB (2000) Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. Ecol Appl 10:484–496

Egerton-Warburton L, Allen MF (2001) Endo- and ectomycorrhizas in *Quercus agrifolia* Nee. (Fagaceae): patterns of root colonization and effects on seedling growth. Mycorrhiza 11:283–290

Ezawa T, Smith SE, Smith FA (2002) P metabolism and transport in AM fungi. Plant Soil 244:221–230

Facelli E, Facelli J, McLaughlin MJ, Smith SE (1999) An experimental study of the interactive effects of mycorrhizal symbiosis, intraspecific competition and resource availability using *Trifolium subterraneum* L. cv Mt Barker. New Phytol 141:535–547

Facelli E, Smith SE, Smith FA (2009) Mycorrhizal symbiosis – overview and new insights into roles of arbuscular mycorrhizas in agro- and natural ecosystems. Australas Plant Pathol 38:338–344

Faeth SH, Fagan WF (2002) Fungal endophytes: common host plant symbionts but uncommon mutualists. Integr Comp Biol 42:360–368

Feng G, Song YC, Li XL, Christie P (2003) Contribution of arbuscular mycorrhizal fungi to utilization of organic sources of phosphorus by red clover in a calcareous soil. Appl Soil Ecol 22:139–148

Finlay RD (2008) Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical mycelium. J Exp Bot 59:1115–1126

Finlay RD, Read DJ (1986) The structure and function of the vegetative mycelium of ectomycorrhizal plants. II. The uptake and distribution of phosphorus by mycelial strands interconnecting host plants. New Phytol 103:157–165

Finlay RD, Frostegård Å, Sonnerfeldt AM (1992) Utilization of organic and inorganic nitrogen sources by ectomycorrhizal fungi in pure culture and in symbiosis with *Pinus contorta* Dougl. Ex Louds. New Phytol 120:105–115

Fitter AH (2005) Darkness visible: reflections on underground ecology. J Ecol 93:231–243

Fitter AH (2006) What is the link between carbon and phosphorus fluxes in arbuscular mycorrhizas? A null hypothesis for symbiotic function. New Phytol 172:3–6

Fitter AH, Heinemeyer A, Husband R, Olsen E, Ridgway KP, Staddon PL (2004) Global environmental change and the biology of arbuscular mycorrhizas: gaps and challenges. Can J Bot 82:1133–1139

Friese CF, Allen MF (1991) The spread of VA mycorrhizal fungal hyphae in the soil: inoculum types and external hyphal architecture. Mycologia 83:409–418

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

Gange AC, Ayres RL (1999) On the relation between arbuscular mycorrhizal colonization and plant 'benefit'. Oikos 87:615–621

Genet P, Prevost A, Pargney JC (2000) Seasonal variations of symbiotic ultrastructure and relationships of two natural ectomycorrhizae of beech (*Fagus sylvatica*/*Lactarius blennius* var. *viridis* and *Fagus sylvatica*/*Lactarius subdulcis*). Trees Struct Funct 14:465–474

George E, Marschner H (1996) Nutrient and water uptake by roots of forest trees. J Plant Nutr Soil Sci 159:11–21

Gibson BR, Mitchell DT (2004) Nutritional influences on the solubilization of metal phosphate by ericoid mycorrhizal fungi. Mycol Res 108:947–954

Glassop D, Smith SE, Smith FW (2005) Cereal phosphate transporters associated with the mycorrhizal pathway of phosphate uptake into roots. Planta 222:688–698

Godbold DL, Hoosbeek MR, Lukac M, Cotrufo MF, Janssens IA, Ceulemans R, Polle A, Velthorst EJ, Scarascia-Mugnozza G, De Angelis P, Miglietta F, Peressotti A (2006) Mycorrhizal hyphal turnover as a dominant process for carbon input into soil organic matter. Plant Soil 281:15–24

Grace EJ, Cotsaftis O, Tester M, Smith FA, Smith SE (2009) Arbuscular mycorrhizal inhibition of growth in barley cannot be attributed to extent of colonization, fungal phosphorus uptake or effects on expression of plant phosphate transporter genes. New Phytol 181:938–949

Graham JH (2001) What do root pathogens see in mycorrhizas? New Phytol 149:357–359

Gregory PJ (2006) Plant roots: growth, activity and interaction with soils. Blackwell, Oxford

Grelet GA, Johnson D, Paterson E, Anderson IC, Alexander IJ (2009) Reciprocal carbon and nitrogen transfer between an ericaceous dwarf shrub and fungi isolated from *Piceirhiza bicolorata* ectomycorrhizas. New Phytol 182:359–366

Griffiths RP, Baham JE, Caldwell BA (1994) Soil solution chemistry of ectomycorrhizal mats in forest soil. Soil Biol Biochem 26:331–337

Hagerberg D, Thelin G, Wallander H (2003) The production of ectomycorrhizal mycelium in forests: relation between forest nutrient status and local mineral sources. Plant Soil 252:279–290

Harley JL, McCready CC (1981) Phosphate accumulation in *Fagus* mycorrhizas. New Phytol 89:75–80

Harrison MJ (1999) Biotrophic interfaces and nutrient transport in plant fungal symbioses. J Exp Bot 50:1013–1022

Harrison MJ, van Buuren ML (1995) A phosphate transporter from the mycorrhizal fungus *Glomus versiforme*. Nature 378:626–629

Heath RT (2005) Microbial turnover of organic phosphorus in aquatic systems. In: Turner BL, Frossard E, Baldwin DS (eds) Organic phosphorus in the environment. CABI, Wallingford, pp 185–204

Heinemeyer A, Hartley IP, Evans SP, de la Fuente JAC, Ineson P (2007) Forest soil CO_2 flux: uncovering the contribution and environmental responses of ectomycorrhizas. Glob Change Biol 13:1786–1797

Helgason T, Fitter AH (2009) Natural selection and the evolutionary ecology of the arbuscular mycorrhizal fungi (Phylum Glomeromycota). J Exp Bot 60:2465–2480

Helgason T, Merryweather JW, Denison J, Wilson P, Young JPW, Fitter AH (2002) Selectivity and functional diversity in arbuscular mycorrhizas of co-occurring fungi and plants from a temperate deciduous woodland. J Ecol 90:371–384

Hetrick BAD, Wilson GWT, Cox TS (1993) Mycorrhizal dependence of modern wheat cultivars and ancestors – a synthesis. Can J Bot 71:512–518

Hodge A, Campbell CD, Fitter AH (2001) An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. Nature 413:297–299

Hoeksema JD, Chaudhary VB, Gehring CA, Johnson NC, Karst J, Koide RT, Pringle A, Zabinski C, Bever JD, Moore JC, Wilson GWT, Klironomos JN, Umbanhowar J (2010) A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecol Lett 13:394–407

Holford ICR (1997) Soil phosphorus: its measurement, and its uptake by plants. Aust J Soil Res 35:227–239

Hutchens E (2009) Microbial selectivity on mineral surfaces: possible implications for weathering processes. Fungal Biol Rev 23:115–121. doi:10.1016/j.fbr.2009.10.002

Imhof S (2009) Arbuscular, ecto-related, orchid mycorrhizas-three independent structural lineages towards mycoheterotrophy: implications for classification? Mycorrhiza 19:357–363

Jakobsen I (1995) Transport of phosphorus and carbon in VA mycorrhizas. In: Varma A, Hock B (eds) Mycorrhiza: structure, function, molecular biology and biotechnology. Springer, Berlin, pp 297–324

Jakobsen I, Abbott LK, Robson AD (1992) External hyphae of vesicular-arbuscular mycorrhizal fungi associated with *Trifolium subterraneum* L. 1. Spread of hyphae and phosphorus inflow into roots. New Phytol 120:371–380

Jansa J, Gryndler M (2010) Biotic environment of the arbuscular mycorrhizal fungi in soil. In: Koltai H, Kapulnik Y (eds) Arbuscular Mycorrhizas: Physiology and Function, 2nd edn. Springer, Heidelberg, 209–236. doi: 10.1007/978-90-481-9489-6_10

Jansa J, Vosátka M (2000) *In vitro* and *post vitro* inoculation of micropropagated Rhododendrons with ericoid mycorrhizal fungi. Appl Soil Ecol 15:125–136

Jansa J, Mozafar A, Anken T, Ruh R, Sanders IR, Frossard E (2002) Diversity and structure of AMF communities as affected by tillage in a temperate soil. Mycorrhiza 12:225–234

Jansa J, Mozafar A, Frossard E (2003a) Long-distance transport of P and Zn through the hyphae of an arbuscular mycorrhizal fungus in symbiosis with maize. Agronomie 23:481–488

Jansa J, Mozafar A, Kuhn G, Anken T, Ruh R, Sanders IR, Frossard E (2003b) Soil tillage affects the community structure of mycorrhizal fungi in maize roots. Ecol Appl 13:1164–1176

Jansa J, Mozafar A, Frossard E (2005) Phosphorus acquisition strategies within arbuscular mycorrhizal fungal community of a single field site. Plant Soil 276:163–176

Jansa J, Wiemken A, Frossard E (2006) The effects of agricultural practices on arbuscular mycorrhizal fungi. In: Frossard E, Blum WEH, Warkentin BP (eds) Function of soils for human societies and the environment. Geological Society, London, pp 89–115

Jansa J, Smith FA, Smith SE (2008) Are there benefits of simultaneous root colonization by different arbuscular mycorrhizal fungi? New Phytol 177:779–789

Jansa J, Oberholzer H-R, Egli S (2009) Environmental determinants of the arbuscular mycorrhizal fungal infectivity of Swiss agricultural soils. Eur J Soil Biol 45:400–408

Javot H, Penmetsa RV, Terzaghi N, Cook DR, Harrison MJ (2007) A *Medicago truncatula* phosphate transporter indispensable for the arbuscular mycorrhizal symbiosis. Proc Natl Acad Sci U S A 104:1720–1725

Jennings DH (1996) The physiology of fungal nutrition. Cambridge University Press, Cambridge

Jifon JL, Graham JH, Drouillard DL, Syvertsen JP (2002) Growth depression of mycorrhizal *Citrus* seedlings grown at high phosphorus supply is mitigated by elevated CO_2. New Phytol 153:133–142

Johansen A, Jakobsen I, Jensen ES (1992) Hyphal transport of ^{15}N-labelled nitrogen by a vesicular-arbuscular mycorrhizal fungus and its effect on depletion of inorganic soil N. New Phytol 122:281–288

Johansson JF, Paul LR, Finlay RD (2004) Microbial interactions in the mycorrhizosphere and their significance for sustainable agriculture. FEMS Microbiol Ecol 48:1–13

Johnson NC (1993) Can fertilization of soil select less mutualistic mycorrhizae? Ecol Appl 3:749–757

Johnson NC, Graham JH, Smith FA (1997) Functioning of mycorrhizal associations along the mutualism-parasitism continuum. New Phytol 135:575–585

Johnson D, Ijdo M, Genney DR, Anderson IC, Alexander IJ (2005) How do plants regulate the function, community structure, and diversity of mycorrhizal fungi? J Exp Bot 56:1751–1760

Johnson NC, Wilson GWT, Bowker MA, Wilson JA, Miller RM (2010) Resource limitation is a driver of local adaptation in mycorrhizal symbioses. Proc Natl Acad Sci U S A 107:2093–2098

Joner EJ, Jakobsen I (1995) Uptake of ^{32}P from labelled organic matter by mycorrhizal and non-mycorrhizal subterranean clover (*Trifolium subterraneum* L). Plant Soil 172:221–227

Joner E, Johansen A (2000) Phosphatase activity of external hyphae of two arbuscular mycorrhizal fungi. Mycol Res 104:81–86

Joner EJ, Briones R, Leyval C (2000) Metal-binding capacity of arbuscular mycorrhizal mycelium. Plant Soil 226:227–234

Joner EJ, Roos P, Jansa J, Frossard E, Leyval C, Jakobsen I (2004) No significant contribution of arbuscular mycorrhizal fungi to transfer of radiocesium from soil to plants. Appl Environ Microbiol 70:6512–6517

Jones MD, Smith SE (2004) Exploring functional definitions of mycorrhizas: are mycorrhizas always mutualisms? Can J Bot 82:1089–1109

Jones DL, Hodge A, Kuzyakov Y (2004) Plant and mycorrhizal regulation of rhizodeposition. New Phytol 163:459–480

Kahiluoto H, Ketoja E, Vestberg M (2000a) Creation of a non-mycorrhizal control for a bioassay of AM effectiveness 1. Comparison of methods. Mycorrhiza 9:241–258

Kahiluoto H, Ketoja E, Vestberg M (2000b) Promotion of utilization of arbuscular mycorrhiza through reduced P fertilization 1. Bioassays in a growth chamber. Plant Soil 227:191–206

Karandashov V, Bucher M (2005) Symbiotic phosphate transport in arbuscular mycorrhizas. Trends Plant Sci 10:22–29

Kieliszewska-Rokicka B (1999) Phosphate status and acid phosphatase activity in soil and ectomycorrhizas in two mature stands of Scots pine (*Pinus sylvestris* L.) exposed to different levels of anthropogenic pollution. Acta Soc Bot Pol 68:311–317

Kiers ET, van der Heijden MGA (2006) Mutualistic stability in the arbuscular mycorrhizal symbiosis: exploring hypotheses of evolutionary cooperation. Ecology 87:1627–1636

Koele N, Turpault MP, Hildebrand EE, Uroz S, Frey-Klett P (2009) Interactions between mycorrhizal fungi and mycorrhizosphere bacteria during mineral weathering: budget analysis and bacterial quantification. Soil Biol Biochem 41:1935–1942

Koide RT (2000) Functional complementarity in the arbuscular mycorrhizal symbiosis. New Phytol 147:233–235

Koide RT, Kabir Z (2000) Extraradical hyphae of the mycorrhizal fungus *Glomus intraradices* can hydrolyse organic phosphate. New Phytol 148:511–517

Koide RT, Sharda JN, Herr JR, Malcolm GM (2008) Ectomycorrhizal fungi and the biotrophy–saprotrophy continuum. New Phytol 178:230–233

Ladeyn I, Plassard C, Staunton S (2008) Mycorrhizal association of maritime pine, *Pinus pinaster*, with *Rhizopogon roseolus* has contrasting effects on the uptake from soil and root-to-shoot transfer of ^{137}Cs, ^{85}Sr and ^{95m}Tc. J Environ Radioactiv 99:853–863

Lambers H, Raven JA, Shaver GR, Smith SE (2008) Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol 23:95–103

Landeweert R, Hoffland E, Finlay RD, Kuyper TW, van Breemen N (2001) Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. Trends Ecol Evol 16:248–254

Leake JR, Miles W (1996) Phosphodiesters as mycorrhizal P sources. 1. Phosphodiesterase production and the utilization of DNA as a phosphorus source by the ericoid mycorrhizal fungus *Hymenoscyphus ericae*. New Phytol 132:435–443

Leggewie G, Willmitzer L, Riesmeier J (1997) Two cDNA from potato are able to complement a phosphate uptake-deficient yeast mutant: identification of phosphate transporters from higher plants. Plant Cell 9:381–392

Leigh J, Hodge A, Fitter AH (2009) Arbuscular mycorrhizal fungi can transfer substantial amounts of nitrogen to their host plant from organic material. New Phytol 181:199–207

Li XL, George E, Marschner H (1991) Extension of the phosphorus depletion zone in VA-mycorrhizal white clover in a calcareous soil. Plant Soil 136:41–48

Li HY, Zhu YG, Marschner P, Smith FA, Smith SE (2005) Wheat responses to arbuscular mycorrhizal fungi in a highly calcareous soil differ from those of clover, and change with plant development and P supply. Plant Soil 277:221–232

Li HY, Smith SE, Ophel-Keller K, Holloway RE, Smith FA (2008) Naturally occurring arbuscular mycorrhizal fungi can replace direct P uptake by wheat when roots cannot access added P fertiliser. Funct Plant Biol 35:124–130

Lindahl B, Stenlid J, Olsson S, Finlay R (1999) Translocation of ^{32}P between interacting mycelia of a wood-decomposing fungus and ectomycorrhizal fungi in microcosm systems. New Phytol 144:183–193

Linder S (1995) Foliar analysis for detecting and correcting nutrient imbalance in Norway spruce. Ecol Bull 44:178–196

Lussenhop J, Fogel R (1999) Seasonal change in phosphorus content of *Pinus strobus–Cenococcum geophilum* ectomycorrhizae. Mycologia 91:742–746

Mäder P, Vierheilig H, Streitwolf-Engel R, Boller T, Frey B, Christie P, Wiemken A (2000) Transport of ^{15}N from a soil compartment separated by a polytetrafluoroethylene membrane to plant roots via the hyphae of arbuscular mycorrhizal fungi. New Phytol 146:155–161

Maherali H, Klironomos JN (2007) Influence of phylogeny on fungal community assembly and ecosystem functioning. Science 316:1746–1748

Malcolm GM, Lopez-Gutierrez JC, Koide RT, Eissenstat DM (2008) Acclimation to temperature and temperature sensitivity of metabolism by ectomycorrhizal fungi. Glob Change Biol 14:1169–1180

Mandyam K, Jumpponen A (2005) Seeking the elusive function of the root-colonising dark septate endophytic fungi. Stud Mycol 53:173–189

Marschner H (1995) Mineral nutrition of higher plants. Academic, London

Martin F, Gianinazzi-Pearson V, Hijri M, Lammers P, Requena N, Sanders IR, Shachar-Hill Y, Shapiro H, Tuskan GA, Young JPW (2008) The long hard road to a completed *Glomus intraradices* genome. New Phytol 180:747–750

Martino E, Turnau K, Girlanda M, Bonfante P, Perotto S (2000) Ericoid mycorrhizal fungi from heavy metal polluted soils: their identification and growth in the presence of zinc ions. Mycol Res 104:338–344

Merryweather J, Fitter A (1995) Phosphorus and carbon budgets – mycorrhizal contribution in *Hyacinthoides non-scripta* (L) Chouard Ex Rothm under natural conditions. New Phytol 129:619–627

Merryweather J, Fitter A (1998) The arbuscular mycorrhizal fungi of *Hyacinthoides non-scripta* – II. Seasonal and spatial patterns of fungal populations. New Phytol 138:131–142

Millard P, Sommerkorn M, Grelet GA (2007) Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. New Phytol 175:11–28

Miller SL, Koo CD, Molina R (1991) Characterization of red alder ectomycorrhizae – a preface to monitoring belowground ecological responses. Can J Bot 69:516–531

Mitchell CE, Agrawal AA, Bever JD, Gilbert GS, Hufbauer RA, Klironomos JN, Maron JL, Morris WF, Parker IM, Power AG, Seabloom EW, Torchin ME, Vazquez DP (2006) Biotic interactions and plant invasions. Ecol Lett 9:726–740

Morgan JAW, Bending GD, White PJ (2005) Biological costs and benefits to plant–microbe interactions in the rhizosphere. J Exp Bot 56:1729–1739

Munkvold L, Kjøller R, Vestberg M, Rosendahl S, Jakobsen I (2004) High functional diversity within species of arbuscular mycorrhizal fungi. New Phytol 164:357–364

Myers MD, Leake JR (1996) Phosphodiesters as mycorrhizal P sources. II. Ericoid mycorrhiza and the utilization of nuclei as a phosphorus and nitrogen source by Vaccinium macrocarpon. New Phytol 132:445–451

Nagy R, Karandashov V, Chague W, Kalinkevich K, Tamasloukht M, Xu GH, Jakobsen I, Levy AA, Amrhein N, Bucher M (2005) The characterization of novel mycorrhiza-specific phosphate transporters from *Lycopersicon esculentum* and *Solanum tuberosum* uncovers functional redundancy in symbiotic phosphate transport in solanaceous species. Plant J 42:236–250

Newman EI (1995) Phosphorus inputs to terrestrial ecosystems. J Ecol 83:713–726

Newman EI, Ritz K (1986) Evidence on the pathways of phosphorus transfer between vesicular-arbuscular mycorrhizal plants. New Phytol 104:77–87

Newsham KK, Fitter AH, Watkinson AR (1995) Multi-functionality and biodiversity in arbuscular mycorrhizas. Trends Ecol Evol 10:407–411

Newsham KK, Upson R, Read DJ (2009) Mycorrhizas and dark septate root endophytes in polar regions. Fungal Ecol 2:10–20

Nielsen JS, Joner EJ, Declerck S, Olsson S, Jakobsen I (2002) Phospho-imaging as a tool for visualization and noninvasive measurement of P transport dynamics in arbuscular mycorrhizas. New Phytol 154:809–819

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

Ohtomo R, Saito M (2005) Polyphosphate dynamics in mycorrhizal roots during colonization of an arbuscular mycorrhizal fungus. New Phytol 167:571–578

Öpik M, Metsis M, Daniell TJ, Zobel M, Moora M (2009) Large-scale parallel 454 sequencing reveals host ecological group specificity of arbuscular mycorrhizal fungi in a boreonemoral forest. New Phytol 184:424–437

Ortas I, Ortakçi D, Kaya Z, Çinar A, Önelge N (2002) Mycorrhizal dependency of sour orange in relation to phosphorus and zinc nutrition. J Plant Nutr 25:1263–1279

Pankow W, Boller T, Wiemken A (1991) The significance of mycorrhizas for protective ecosystems. Experientia 47:391–394

Paszkowski U, Kroken S, Roux C, Briggs SP (2002) Rice phosphate transporters include an evolutionarily divergent gene specifically activated in arbuscular mycorrhizal symbiosis. Proc Natl Acad Sci U S A 99:13324–13329

Pearson JN, Jakobsen I (1993) Symbiotic exchange of carbon and phosphorus between cucumber and three arbuscular mycorrhizal fungi. New Phytol 124:481–488

Perez-Moreno J, Read DJ (2001a) Nutrient transfer from soil nematodes to plants: a direct pathway provided by the mycorrhizal mycelial network. Plant Cell Environ 24:1219–1226

Perez-Moreno J, Read DJ (2001b) Exploitation of pollen by mycorrhizal mycelial systems with special reference to nutrient recycling in boreal forests. Proc Biol Sci 268:1329–1335

Philip LJ, Simard SW (2008) Minimum pulses of stable and radioactive carbon isotopes to detect belowground carbon transfer between plants. Plant Soil 308:23–35

Picone C (2002) Managing mycorrhizae for sustainable agriculture in the tropics. In: Vandermeer JH (ed) Tropical agroecosystems. CRC, Boca Raton, pp 95–132

Pirozynski KA, Dalpé Y (1989) Geological history of the Glomaceae with particular reference to mycorrhizal symbiosis. Symbiosis 7:1–35

Plamboeck AH, Dawson TE, Egerton-Warburton LM, North M, Bruns TD, Querejeta JI (2007) Water transfer via ectomycorrhizal fungal hyphae to conifer seedlings. Mycorrhiza 17:439–447

Poulsen KH, Nagy R, Gao LL, Smith SE, Bucher M, Smith FA, Jakobsen I (2005) Physiological and molecular evidence for Pi uptake via the symbiotic pathway in a reduced mycorrhizal colonization mutant in tomato associated with a compatible fungus. New Phytol 168:445–453

Pritchard SG, Strand AE, McCormack ML, Davis MA, Oren R (2008) Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO_2-enrichment. Glob Change Biol 14:1252–1264

Rausch C, Bucher M (2002) Molecular mechanisms of phosphate transport in plants. Planta 216:23–37

Rausch C, Daram P, Brunner S, Jansa J, Laloi M, Leggewie G, Amrhein N, Bucher M (2001) A phosphate transporter expressed in arbuscule-containing cells in potato. Nature 414:462–466

Read DJ (1984) The structure and function of the vegetative mycelium of mycorrhizal roots. In: Jennings DH, Rayner ADM (eds) The ecology and physiology of the fungal mycelium. Cambridge University Press, Cambridge, pp 215–240

Read DJ, Perez-Moreno J (2003) Mycorrhizas and nutrient cycling in ecosystems – a journey towards relevance? New Phytol 157:475–492

Read DJ, Leake JR, Perez-Moreno J (2004) Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. Can J Bot 82:1243–1263

Redecker D, Raab P (2006) Phylogeny of the Glomeromycota (arbuscular mycorrhizal fungi): recent developments and new gene markers. Mycologia 98:885–895

Redecker D, Kodner R, Graham LE (2000) Glomalean fungi from the Ordovician. Science 289:1920–1921

Redon PO, Beguiristain T, Leyval C (2009) Differential effects of AM fungal isolates on *Medicago truncatula* growth and metal uptake in a multimetallic (Cd, Zn, Pb) contaminated agricultural soil. Mycorrhiza 19:187–195

Rejšek K (1991) Acid phosphomonoesterase activity of ectomycorrhizal roots in Norway spruce pure stands exposed to pollution. Soil Biol Biochem 23:667–671

Requena N, Breuninger M, Franken P, Ocon A (2003) Symbiotic status, phosphate, and sucrose regulate the expression of two plasma membrane H+-ATPase genes from the mycorrhizal fungus *Glomus mosseae*. Plant Physiol 132:1540–1549

Rhodes LH, Gerdemann JW (1978) Translocation of calcium and phosphate by external hyphae of vesicular-arbuscular mycorrhizae. Soil Sci 126:125–126

Rillig MC, Mummey DL (2006) Mycorrhizas and soil structure. New Phytol 171:41–53

Robertson SJ, McGill WB, Massicotte HB, Rutherford PM (2007) Petroleum hydrocarbon contamination in boreal forest soils: a mycorrhizal ecosystems perspective. Biol Rev 82:213–240

Robinson D, Fitter A (1999) The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. J Exp Bot 50:9–13

Rosling A (2009) Trees, mycorrhiza and minerals – field relevance of *in vitro* experiments. Geomicrobiol J 26:389–401

Rosling A, Roose T, Hermann AM, Davidson FA, Finlay RD, Gadd GM (2009) Approaches to modelling mineral weathering by fungi. Fungal Biol Rev 23:138–144. doi:10.1016/j.fbr.2009.09.003

Ryan MH, Graham JH (2002) Is there a role for arbuscular mycorrhizal fungi in production agriculture? Plant Soil 244:263–271

Sawers RJH, Gutjahr C, Paszkowski U (2008) Cereal mycorrhiza: an ancient symbiosis in modern agriculture. Trends Plant Sci 13:93–97

Schachtman DP, Reid RJ, Ayling SM (1998) Phosphorus uptake by plants: from soil to cell. Plant Physiol 116:447–453

Schnepf A, Roose T, Schweiger P (2008) Impact of growth and uptake patterns of arbuscular mycorrhizal fungi on plant phosphorus uptake – a modelling study. Plant Soil 312:85–99

Schnepf A, Leitner D, Klepsch S, Pellerin S, Mollier A (2011) Modelling phosphorus dynamics in the soil–plant system. In: Bünemann EK, Oberson A, Frossard E (eds) Phosphorus in action: biological processes in soil phosphorus cycling. Soil biology, vol 26. Springer, Heidelberg. doi:10.1007/978-3-642-15271-9_5

Schroeder MS, Janos DP (2004) Phosphorus and intraspecific density alter plant responses to arbuscular mycorrhizas. Plant Soil 264:335–348

Schüßler A, Schwarzott D, Walker C (2001) A new fungal phylum, the Glomeromycota: phylogeny and evolution. Mycol Res 105:1413–1421

Schweiger P, Jakobsen I (1999) The role of mycorrhizas in plant P nutrition: fungal uptake kinetics and genotype variation. In: Gissel-Nielsen G, Jensen A (eds) Plant nutrition – molecular biology and genetics. Kluwer, Dordrecht, pp 277–289

Selosse MA, Richard F, He XH, Simard SW (2006) Mycorrhizal networks: des liaisons dangereuses? Trends Ecol Evol 21:621–628

Serrasolses I, Romanya J, Khanna PK (2008) Effects of heating and autoclaving on sorption and desorption of phosphorus in some forest soils. Biol Fertil Soils 44:1063–1072

Sharples JM, Meharg AA, Chambers SM, Cairney JWG (1999) Arsenate sensitivity in ericoid and ectomycorrhizal fungi. Environ Toxicol Chem 18:1848–1855

Sikes BA, Cottenie K, Klironomos JN (2009) Plant and fungal identity determines pathogen protection of plant roots by arbuscular mycorrhizas. J Ecol 97:1274–1280

Smith FW (2002) The phosphate uptake mechanism. Plant Soil 245:105–114

Smith SE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic, New York

Smith FA, Smith SE (1996) Mutualism and parasitism: diversity in function and structure in the "arbuscular" (VA) mycorrhizal symbiosis. Adv Bot Res 22:1–43

Smith SE, Dickson S, Smith FA (2001) Nutrient transfer in arbuscular mycorrhizas: how are fungal and plant processes integrated? Aust J Plant Physiol 28:683–694

Smith SE, Smith FA, Jakobsen I (2003) Mycorrhizal fungi can dominate phosphate supply to plants irrespective of growth responses. Plant Physiol 133:16–20

Smith SE, Smith FA, Jakobsen I (2004) Functional diversity in arbuscular mycorrhizal (AM) symbioses: the contribution of the mycorrhizal P uptake pathway is not correlated with mycorrhizal responses in growth or total P uptake. New Phytol 162:511–524

Smith FA, Grace EJ, Smith SE (2009) More than a carbon economy: nutrient trade and ecological sustainability in facultative arbuscular mycorrhizal symbioses. New Phytol 182:347–358

Smits MM, Bonneville S, Haward S, Leake JR (2008) Ectomycorrhizal weathering, a matter of scale. Mineral Mag 72:135–138

Soares CRFS, Siqueira JO (2008) Mycorrhiza and phosphate protection of tropical grass species against heavy metal toxicity in multi-contaminated soil. Biol Fertil Soils 44:833–841

Solaiman MZ, Saito A (2001) Phosphate efflux from intraradical hyphae of *Gigaspora margarita in vitro* and its implication for phosphorus translocation. New Phytol 151:525–533

Solaiman MZ, Ezawa T, Kojima T, Saito M (1999) Polyphosphates in intraradical and extraradical hyphae of an arbuscular mycorrhizal fungus, *Gigaspora margarita*. Appl Environ Microbiol 65:5604–5606

Sorensen JN, Larsen J, Jakobsen I (2003) Management strategies for capturing the benefits of mycorrhizas in the production of field-grown vegetables. Acta Hortic 627:65–71

Sousa MF, Facanha AR, Tavares RM, Lino-Neto T, Geros H (2007) Phosphate transport by proteoid roots of *Hakea sericea*. Plant Sci 173:550–558

Staddon PL, Ramsey CB, Ostle N, Ineson P, Fitter AH (2003) Rapid turnover of hyphae of mycorrhizal fungi determined by AMS microanalysis of ^{14}C. Science 300:1138–1140

Sudová R, Doubková P, Vosátka M (2008) Mycorrhizal association of *Agrostis capillaris* and *Glomus intraradices* under heavy metal stress: combination of plant clones and fungal isolates from contaminated and uncontaminated substrates. Appl Soil Ecol 40:19–29

Sverdrup H, Hagen-Thorn A, Holmqvist J, Walman P, Warfinge P, Walse C, Alveteg M (2002) Biochemical processes and mechanisms. In: Sverdrup H, Stjernquist I (eds) Developing principles and models for sustainable forestry in Sweden. Managing forest ecosystems, vol 5. Kluwer, Dordrecht, pp 91–196

Sýkorová Z, Wiemken A, Redecker D (2007) Co-occurring *Gentiana verna* and *Gentiana acaulis* and their neighboring plants in two Swiss upper montane meadows harbor distinct arbuscular mycorrhizal fungal communities. Appl Environ Microbiol 73:5426–5434

Takanishi I, Ohtomo R, Hayatsu M, Saito M (2009) Short-chain polyphosphate in arbuscular mycorrhizal roots colonized by *Glomus* spp.: a possible phosphate pool for host plants. Soil Biol Biochem 41:1571–1573

Talbot JM, Allison SD, Treseder KK (2008) Decomposers in disguise: mycorrhizal fungi as regulators of soil C dynamics in ecosystems under global change. Funct Ecol 22:955–963

Tarafdar JC, Marschner H (1994) Phosphatase activity in the rhizosphere and hyphosphere of VA mycorrhizal wheat supplied with inorganic and organic phosphorus. Soil Biol Biochem 26:387–395

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

Tatry MV, Kassis EE, Lambilliotte R, Corratge C, van Aarle I, Amenc LK, Alary R, Zimmermann S, Sentenac H, Plassard C (2009) Two differentially regulated phosphate transporters from the symbiotic fungus *Hebeloma cylindrosporum* and phosphorus acquisition by ectomycorrhizal *Pinus pinaster*. Plant J 57:1092–1102

Tawaraya K (2003) Arbuscular mycorrhizal dependency of different plant species and cultivars. Soil Sci Plant Nutr 49:655–668

Taylor AFS, Alexander I (2005) The ectomycorrhizal symbiosis: life in the real world. Mycologist 19:102–112

Taylor DL, Bruns TD, Hodges SA (2004) Evidence for mycorrhizal races in a cheating orchid. Proc Biol Sci 271:35–43

Tedersoo L, Jairus T, Horton BM, Abarenkov K, Suvi T, Saar I, Koljalg U (2008) Strong host preference of ectomycorrhizal fungi in a Tasmanian wet sclerophyll forest as revealed by DNA barcoding and taxon-specific primers. New Phytol 180:479–490

Thomson BD, Clarkson DT, Brain P (1990) Kinetics of phosphorus uptake by the germ tubes of the vesicular arbuscular mycorrhizal fungus, *Gigaspora margarita*. New Phytol 116:647–653

Thormann MN, Currah RS, Bayley SE (1999) The mycorrhizal status of the dominant vegetation along a peatland gradient in southern boreal Alberta, Canada. Wetlands 19:438–450

Tibbett M, Sanders FE (2002) Ectomycorrhizal symbiosis can enhance plant nutrition through improved access to discrete organic nutrient patches of high resource quality. Ann Bot 89:783–789

Timonen S, Finlay RD, Olsson S, Söderström B (1996) Dynamics of phosphorus translocation in intact ectomycorrhizal systems: non-destructive monitoring using a beta-scanner. FEMS Microbiol Ecol 19:171–180

Tinker PB (1975) Soil chemistry of phosphorus and mycorrhizal effects on plant growth. In: Sanders FE, Mosse B, Tinker PB (eds) Endomycorrhizas. Academic, London, pp 353–371

Toljander JF, Artursson V, Paul LR, Jansson JK, Finlay RD (2006) Attachment of different soil bacteria to arbuscular mycorrhizal fungal extraradical hyphae is determined by hyphal vitality and fungal species. FEMS Microbiol Lett 254:34–40

Toljander JF, Lindahl BD, Paul LR, Elfstrand M, Finlay RD (2007) Influence of arbuscular mycorrhizal mycelial exudates on soil bacterial growth and community structure. FEMS Microbiol Ecol 61:295–304

Trappe JM (1987) Phylogenetic and ecologic aspects of mycotrophy in the angiosperms from an evolutionary standpoint. In: Safir GR (ed) Ecophysiology of VA mycorrhizal plants. CRC, Boca Raton, pp 5–25

Treseder KK, Cross A (2006) Global distributions of arbuscular mycorrhizal fungi. Ecosystems 9:305–316

Turpault M-P, Nys C, Calvaruso C (2009) Rhizosphere impact on the dissolution of test minerals in a forest ecosystem. Geoderma 153:147–154

van der Heijden EW, Vosátka M (1999) Mycorrhizal associations of *Salix repens* L. communities in succession of dune ecosystems. II. Mycorrhizal dynamics and interactions of ectomycorrhizal and arbuscular mycorrhizal fungi. Can J Bot 77:1833–1841

van der Heijden MGA, Klironomos JN, Ursic M, Moutoglis P, Streitwolf-Engel R, Boller T, Wiemken A, Sanders IR (1998) Mycorrhizal fungal diversity determines plant biodiversity, ecosystem variability and productivity. Nature 396:69–72

van Scholl L, Kuyper TW, Smits MM, Landeweert R, Hoffland E, van Breemen N (2008) Rock-eating mycorrhizas: their role in plant nutrition and biogeochemical cycles. Plant Soil 303:35–47

van Tichelen KK, Colpaert JV (2000) Kinetics of phosphate absorption by mycorrhizal and non-mycorrhizal Scots pine seedlings. Physiol Plant 110:96–103

Vandenkoornhuyse P, Ridgway KP, Watson IJ, Fitter AH, Young JPW (2003) Co-existing grass species have distinctive arbuscular mycorrhizal communities. Mol Ecol 12:3085–3095

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

Wallander H (2000) Uptake of P from apatite by *Pinus sylvestris* seedlings colonised by different ectomycorrhizal fungi. Plant Soil 218:249–256

Wallander H (2006) External mycorrhizal mycelia – the importance of quantification in natural ecosystems. New Phytol 171:240–242

Wallander H, Thelin G (2008) The stimulating effect of apatite on ectomycorrhizal growth diminishes after PK fertilization. Soil Biol Biochem 40:2517–2522

Wang B, Qiu YL (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16:299–363

West HM, Fitter AH, Watkinson AR (1993) Response of *Vulpia ciliata* ssp. *ambigua* to removal of mycorrhizal infection and to phosphate application under natural conditions. J Ecol 81:351–358

Whitbeck JL (2001) Effects of light environment on vesicular-arbuscular mycorrhiza development in *Inga leiocalycina*, a tropical wet forest tree. Biotropica 33:303–311

Wurzburger N, Hendrick RL (2006) Rhododendron thickets alter N cycling and soil extracellular enzyme activities in southern Appalachian hardwood forests. Pedobiologia 50:563–576

Wurzburger N, Hendrick RL (2009) Plant litter chemistry and mycorrhizal roots promote a nitrogen feedback in a temperate forest. J Ecol 97:528–536

Yao Q, Li XL, Ai WD, Christie P (2003) Bi-directional transfer of phosphorus between red clover and perennial ryegrass via arbuscular mycorrhizal hyphal links. Eur J Soil Biol 39:47–54

Youpensuk S, Lordkaew S, Rerkasem B (2008) Arbuscular mycorrhizal fungi associated with tangerine (*Citrus reticulata*) in Chiang Mai province, northern Thailand, and their effects on the host plant. Sci Asia 34:259–264

Zabinski CA, Quinn L, Callaway RM (2002) Phosphorus uptake, not carbon transfer, explains arbuscular mycorrhizal enhancement of *Centaurea maculosa* in the presence of native grassland species. Funct Ecol 16:758–765

Zeller B, Brechet C, Maurice JP, Le Tacon F (2008) Saprotrophic versus symbiotic strategy during truffle ascocarp development under holm oak. A response based on ^{13}C and ^{15}N natural abundance. Ann Forest Sci 65:607

Zhu YG, Smith SE, Barritt AR, Smith FA (2001) Phosphorus (P) efficiencies and mycorrhizal responsiveness of old and modern wheat cultivars. Plant Soil 237:249–255