

SPECIAL ISSUE REVIEW PAPER

Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical mycelium

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Abstract

Different symbiotic mycorrhizal associations between plants and fungi occur, almost ubiquitously, in a wide range of terrestrial ecosystems. Historically, these have mainly been considered within the rather narrow perspective of their effects on the uptake of dissolved mineral nutrients by individual plants. More recent research has placed emphasis on a wider, multifunctional perspective, including the effects of mycorrhizal symbiosis on plant and microbial communities, and on ecosystem processes. This includes mobilization of N and P from organic polymers, release of nutrients from mineral particles or rock surfaces via weathering, effects on carbon cycling, interactions with myco-heterotrophic plants, mediation of plant responses to stress factors such as drought, soil acidification, toxic metals, and plant pathogens, as well as a range of possible interactions with groups of other soil micro-organisms. Mycorrhizal fungi connect their plant hosts to the heterogeneously distributed nutrients required for their growth, enabling the flow of energy-rich compounds required for nutrient mobilization whilst simultaneously providing conduits for the translocation of mobilized products back to their hosts. In addition to increasing the nutrient absorptive surface area of their host plant root systems, the extraradical mycelium of mycorrhizal fungi provides a direct pathway for translocation of photosynthetically derived carbon to micro-sites in the soil and a large surface area for interaction with other micro-organisms. The detailed functioning and regulation of these mycorrhizosphere processes is still poorly understood but recent progress is reviewed and potential benefits of improved understanding of mycorrhizosphere interactions are discussed.

Key words: Arbuscular mycorrhiza, biotic interactions, carbon flow, ectomycorrhiza, ericoid mycorrhiza, mycelium, nutrient uptake, symbiosis, weathering.

Introduction

Fungi play a central role in many microbiological and ecological processes, influencing soil fertility, decomposition, cycling of minerals and organic matter, as well as plant health and nutrition. Fungi are heterotrophs, requiring external sources of carbon for energy and cellular synthesis and they have adopted three different trophic strategies to obtain this carbon, occurring as saprotrophs, necrotrophs, and biotrophs. Mycorrhizal symbiosis is the most ancient, widespread form of fungal symbiosis with plants. The term 'mycorrhiza' was first used in 1885 by Frank (see Frank, 2005, for a translation) to describe the modified root structures of forest trees, and has since been extended to cover a range of mutualistic, symbiotic associations between fungi and plant roots (Smith and Read, 2008). Seven different categories of mycorrhizal symbiosis have been distinguished on the basis of their morphological characteristics and the fungal and plant species involved.

Arbuscular mycorrhiza is the most ancient and widespread form. Paleobotanical and molecular sequence data suggest that the first land plants formed associations with Glomalean fungi from the Glomeromycota about 460 million years ago (Redecker *et al.*, 2000). This is estimated to be some 300–400 million years before the appearance of root nodule symbioses with nitrogen-fixing bacteria. Arbuscular mycorrhizal (AM) symbioses can be formed with a very wide range of plant species, as many as 250 000. Only 150–200 species of AM fungi have so

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far been distinguished on the basis of morphology, but DNA-based studies suggest the true diversity of these symbionts may be very much higher (Fitter, 2005; Santos-González *et al.*, 2006). The symbiosis is characterized by highly branched fungal structures, *arbuscules*, which grow intracellularly without penetrating the host plasmalemma.

Ericoid mycorrhiza are formed in three plant families, the Ericaceae, Empetraceae, and Epacridaceae, all belonging to the order Ericales. These plants grow principally as dwarf shrubs in upland and lowland heaths and other nutrient-impooverished areas, such as the understorey vegetation of boreal forests. Ericoid mycorrhizas also occur in warm Mediterranean climate zones in chaparral vegetation systems throughout the world, suggesting that nutritional, rather than climatic, factors determine their distribution. Around 3400 plant species form this type of mycorrhizal association with various fungi from the Ascomycota but only one species, *Rhizoscyphus ericae* (earlier known as *Hymenoscyphus ericae*) has been studied in detail. This fungus penetrates the cell walls of roots and forms coiled structures within each cell without penetrating the host plasmalemma. Recent evidence suggests that basidiomycetes belonging to clade B Sebaciales are also common ericoid mycorrhizal fungi (Selosse *et al.*, 2007).

Many long-lived perennial plants and trees form a third type of mycorrhiza, *ectomycorrhiza*. The fungi are predominantly from the Basidiomycota and Ascomycota and as many as 10 000 fungal species and 8000 plant species may be involved, globally (Taylor and Alexander, 2005). Although this represents only a small fraction of the total number of terrestrial plants, these species often form the dominant components of forest ecosystems occupying a disproportionately large area. The plant species involved are usually trees or shrubs from cool, temperate boreal or montane forests, but also include arctic-alpine dwarf shrub communities, Mediterranean/chaparral vegetation, and many species in the Dipterocarpaceae and leguminous Caesalpinoideae in tropical forests. The fungi do not penetrate the host cells, and the symbiosis is characterized by the presence of a fungal mantle or sheath around each of the short roots, as well as a network of intercellular hyphae penetrating between the epidermal and cortical cells, the so-called Hartig net. Like the arbuscules in arbuscular mycorrhiza, this interface is an effective way of increasing the surface area of contact between the fungus and its plant host. The mantle is usually connected to a more or less well-developed extraradical mycelium which may extend for many centimetres from the root into the soil. This extraradical mycelium may form a significant fraction of the total microbial biomass in forest soils and estimates of 700–900 kg ha⁻¹ have been published (Wallander *et al.*, 2001).

In most types of mycorrhizal symbiosis the fungal symbionts depend upon their autotrophic plant hosts to supply carbon, however in the *orchid mycorrhiza* formed

by orchids this dependency may be reversed. The family Orchidaceae is the largest in the plant kingdom and estimated to contain 30 000 species. Although most orchids have green leaves and are autotrophic when fully established, about 100 species are achlorophyllous as adults and all pass through a germination and early development phase when they are dependent on an external supply of nutrients and organic carbon. They have minute dust like seeds with no reserves, and are initially entirely dependent upon the supply of carbon and nitrogen from fungi. In total, more than 400 plant species are achlorophyllous and described as ‘*myco-heterotrophic*’, obtaining their carbon from fungi. The fungi colonizing these plants were originally thought to be effective saprotrophs or parasites, but DNA-based studies of the fungi have now shown that most of them are mycorrhizal fungi simultaneously colonizing other autotrophic plants (Leake, 2004). These plants are effectively ‘cheaters’ or epiparasites that in fact derive their carbon and nutrients via mycorrhizal connection with adjacent autotrophs (Bidartondo *et al.*, 2002; Leake, 2004), however, Bidartondo (2005) has also discussed the semantic problems of using such terms, which include the difficulty of making unequivocal statements about fitness costs of ‘cheaters’ and mycorrhizal fungi. The carbon supplies of green orchids are normally met by association with basidiomycetous *Rhizoctonia* species characterized as saprophytes or plant parasites, but in fully myco-heterotrophic orchids there is evidence that this ancestral trait has been abandoned in favour of association with other basidiomycete species that are obligate ectomycorrhizal symbionts of autotrophic trees and shrubs (Leake, 2005).

The Monotropaceae are mycoheterotrophic plants that form a fifth type of mycorrhizal association, *monotropoid mycorrhiza*. Structurally, these are like ectomycorrhizas, often with a well-developed mantle but with a more superficial Hartig net, with single hyphae growing into the epidermal cells, forming peg-like structures. The achlorophyllous monotropoid plants are wholly dependent on the fungi for reduced carbon and soil nutrients, and it appears that the carbon comes indirectly from autotrophic host plants which are also attached to the same ectomycorrhizal mycelium (Leake, 2004; Bidartondo, 2005). Two other types of mycorrhizal association have been distinguished, the *arbutoid mycorrhiza* and *ectendomycorrhiza*. The former associations are formed between fungi that are normally ectomycorrhizal and plants in the genera *Arbutus*, *Arctostaphylos*, and the family Pyrolaceae, where intracellular fungal penetration occurs. Ectendomycorrhizas have features of both ectomycorrhizas and endomycorrhizas, a sheath which may be reduced or absent, a Hartig net that is usually well developed, but also intracellular penetration. Some of the fungi that form ectendomycorrhizas with *Pinus* and *Larix* also form ectomycorrhizas with other tree species. Ectendo-, arbutoid

and monotropoid mycorrhizas can, to some extent, be seen as more specialized cases of the general mycorrhizal habit and the rest of this article will focus on AM, ericoid, and ectomycorrhizas, with some mention of orchid mycorrhizas in relation to carbon flow and effects on plant communities.

Historically, mycorrhizal research has mainly been focused within the rather narrow perspective of the effects of the symbiosis on individual plants, in particular, the improved acquisition of dissolved mineral nutrients such as P. It is fairly well accepted that arbuscular mycorrhizal and ectomycorrhizal mycelia improve the acquisition of mineral nutrients which are already in solution and that they do so by means of an extraradical mycelium which is a physical extension of the root system and increases the surface area across which nutrients can be taken up. This increase is achieved at a low synthetic cost to the host and by virtue of their small diameter the hyphae are also able to penetrate soil microsites which are inaccessible to plant roots. Ericoid associations appear to have a less well-developed extraradical mycelial phase but are able to mobilize organic nutrients which are not accessible to the host roots. Examples of improved vegetative growth and nutrient status of individual plants following mycorrhizal inoculation abound, especially in pot experiments, but the effects of mycorrhizal fungi on plant *fitness* are more difficult to demonstrate.

More recent research has widened the context in which mycorrhizal symbiosis is viewed and placed greater emphasis on the effects of mycorrhizal symbiosis on plant communities and ecosystems. Increasing attention has been paid to the role of the extraradical mycelial phase of the symbiosis (Finlay, 2005; Anderson and Cairney, 2007) and the importance of using realistic substrates to answer relevant, ecological questions (Read and Perez-Moreno, 2003). Many authors have highlighted the multifunctional nature of mycorrhizal effects (Newsham *et al.*, 1995; Finlay, 2004), including interactions with bacteria (Johansson *et al.*, 2004; Frey-Klett *et al.*, 2007), weathering of minerals (Landeweert *et al.*, 2001; Finlay and Rosling, 2006; Wallander, 2006), carbon cycling (Johnson *et al.*, 2002), effects on plant communities (van der Heijden *et al.*, 1998), tripartite syntheses with mycoheterotrophs (Leake, 2004; Bidartondo, 2005), and mediation of plant responses to stress (Finlay *et al.*, 2008) (Fig. 1). Effects of mycorrhizal symbiosis are more difficult to demonstrate in the field, but much progress has been made. In the following sections, the various types of multifunctionality associated with effects of extraradical mycelia of mycorrhizal fungi are reviewed and some of their ecological consequences are discussed.

Weathering and dissolution of minerals

Although it is well accepted that mycorrhiza assist in the acquisition of mineral nutrients already in the soil solution,

there has recently been increasing interest in the idea that mycorrhizal mycelia, either by themselves, or in association with bacteria or other fungi, may actively release nutrients from mineral particles and rock surfaces through weathering (Landeweert *et al.*, 2001; Finlay and Rosling, 2006; Wallander, 2006). Evidence for arbuscular mycorrhizal (AM) fungi is conflicting and although there is some evidence of increased use of relatively insoluble forms of inorganic P such as rock phosphate, these effects could depend upon synergistic interactions with other P-solubilizing micro-organisms (see section on Biotic interactions). Low molecular weight (LMW) organic acids have been proposed to play a role in weathering of minerals and there have been frequent reports of their production by ectomycorrhizal fungi (Ahonen-Jonnarh *et al.*, 2000).

Jongmans *et al.* (1997) published evidence suggesting that weatherable minerals in podzol surface soils and shallow granitic rock under European coniferous forests were commonly criss-crossed by networks of tubular pores 3–10 µm in diameter. The aetiology of these has still not been established but the authors speculated that they might be caused by hyphae of ectomycorrhizal fungi exuding organic acids at their tips. According to the theory, the host trees would provide important sinks for the nutrients released through dissolution in the pores and mycorrhizal hyphae would provide direct conduits for translocation of nutrients to plants from microsites isolated from the bulk soil solution. Van Breemen *et al.* (2000) pointed out that this would have implications for measurements based on bulk soil solution chemistry, making base cation/Al ratios, for example, less reliable indicators of critical loads of acidic deposition. Although it was initially postulated that mineral tunnelling by fungal hyphae might contribute substantially to weathering, measurements by Smits *et al.* (2005) have now shown that the contribution to total feldspar weathering is less than 1%, suggesting that the weathering of mineral surfaces is quantitatively more important. There is clearly a large potential for interaction between mycorrhizal hyphae and mineral surfaces and recent research by Rosling *et al.* (2003) revealed that at least 50% of the mycorrhizal fungal taxa found in a podzol soil in the north of Sweden were *exclusively* associated with the mineral soil horizons. Surprisingly, this was the first detailed study to consider ectomycorrhizal taxa *throughout* the soil profile since almost all studies are confined to the upper organic horizons. Further studies of different fungi and their responses to different mineral substrates (Mahmood *et al.*, 2001; Rosling *et al.*, 2004a, b) have revealed significant variation in the responses of different fungi. Studies by Wallander *et al.* (2002) using particle-induced X-ray emission (PIXE) analysis of element contents of fungal rhizomorphs also suggested that an ectomycorrhizal *Rhizopogon* species had the ability to mobilize

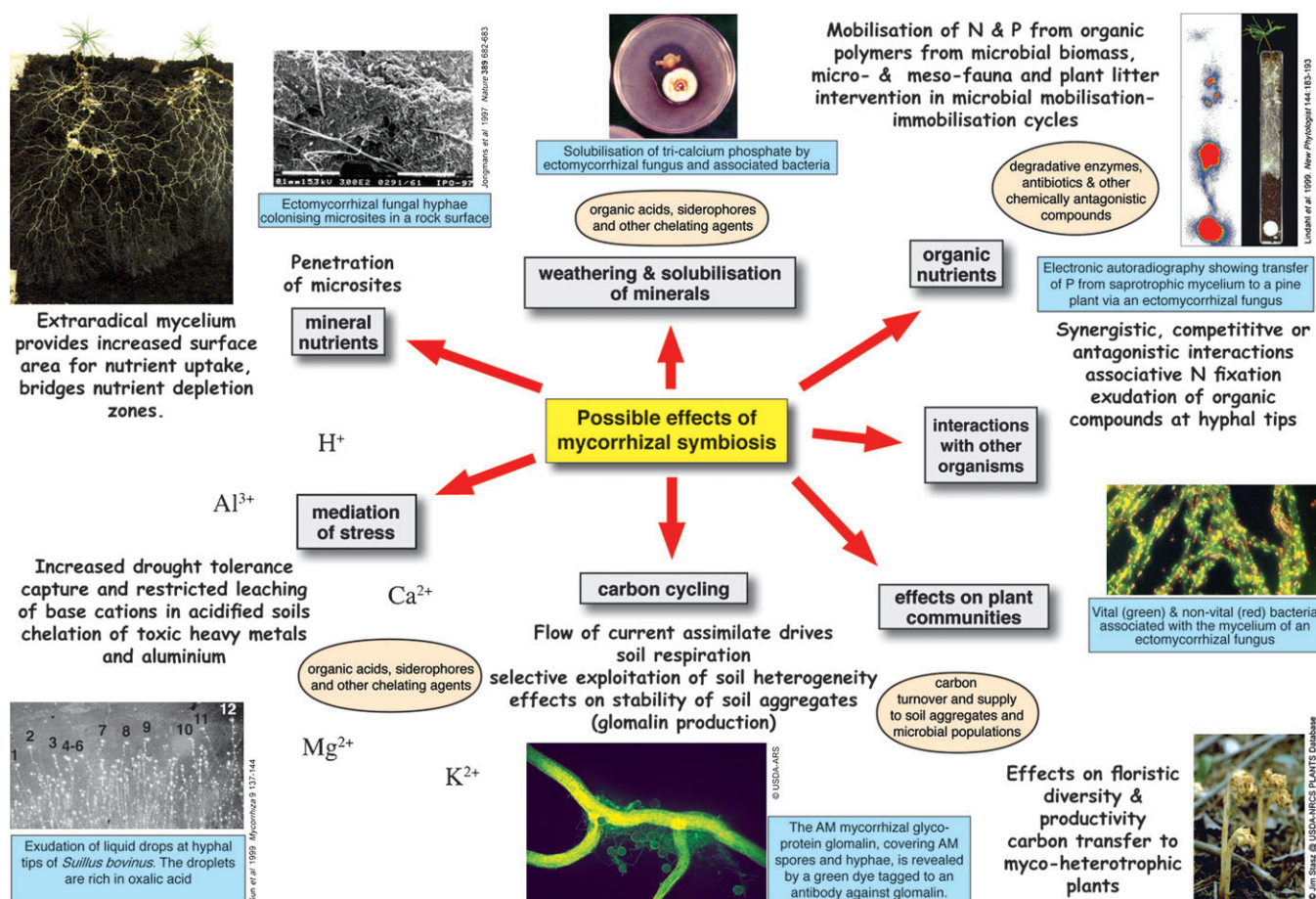


Fig. 1. Schematic representation indicating the diversity of possible interactions involving the extraradical mycelia of mycorrhizal associations. Adapted with permission from Macmillan Publishers Ltd: *Nature* **389**, 682–683, copyright 1999. *Mycorrhiza* **9**, 137–144 Sun *et al.* with kind permission from Springer Science and Business Media. From Lindahl *et al.*, 1999, *New Phytologist* **144**, 183–193, with permission.

significant amounts of P and K from the minerals apatite and biotite and probably plays a significant role in transporting these to trees.

The roles of fungi in general (Gadd, 2006), and mycorrhizal fungi in particular, in geochemical processes have often been neglected, and their potential role in weathering interactions is still the subject of some debate. However, it is fairly well accepted that lichens participate in weathering interactions by producing organic acids that are manufactured with carbon derived from the photobiont but delivered to mineral surfaces by the mycobiont (the fungal symbiotic partner) (Banfield *et al.*, 1999). It is not unlikely that parallel processes occur in ectomycorrhizal symbioses, the only differences being that the size of the photosynthetic apparatus to provide the energy for nutrient mobilization, as well as the size of the plant sink for mobilized nutrients, are both much bigger. However, only a fraction of the total number of mycorrhizal species has been investigated and further studies are still required to determine the extent of mycorrhizal weathering and the range of species involved.

Nutrient mobilization from organic substrates

In addition to improving plant uptake of mineral nutrients, many mycorrhizal fungi may play a significant role in mobilizing nutrients from organic substrates. The main effect of significance to host plants is the mobilization of nutrients such as N and P from structural and other polymers which are otherwise unavailable to plant roots. Sequestration of N and P by mycorrhizal fungi from a range of biologically relevant substrates such as pollen (Perez-Moreno and Read, 2001a), dead nematodes (Perez-Moreno and Read, 2001b), collembola (Klironomos and Hart, 2001), and saprotrophic mycelia (Lindahl *et al.*, 1999) has been demonstrated and the subject has been elegantly reviewed by Read and Perez-Moreno (2003). Intervention by different groups of mycorrhizal fungi in microbial mobilization–immobilization cycles results in mobilization of N and P from microbial, micro-faunal, meso-faunal, and plant litter, enabling the development of distinctive plant communities along altitudinal or latitudinal gradients. This is particularly evident in the ericoid

mycorrhizal fungi colonizing heathland ecosystems and in ectomycorrhizal fungi colonizing boreal forest ecosystems. In these ecosystems, where N and P are sequestered in organic forms that are not readily available to autotrophs, the dominant plant species are highly dependent on mycorrhizal symbionts for their nutrient supply. Lindahl *et al.* (2005) reviewed enzymatic activities of mycorrhizal mycelia and concluded that wider recognition of the ability of many mycorrhizal fungi to mobilize nutrients from complex organic sources is a necessary step in the further development of nutrient cycling models, particularly in ecosystems with low nutrient availability. Abuzinadah *et al.* (1986) suggested that the ability of ectomycorrhizal fungi to utilize organic forms of N would restrict losses to decomposer populations and lead to tighter nutrient cycling. Bending and Read (1995) were able to show mobilization of N from patches of organic material from the fermentation horizon of a pine forest soil by mycelia of the ectomycorrhizal fungus *Suillus bovinus*. Further experiments by Read (1991) demonstrated that mobilization of N from such patches by the ectomycorrhizal fungi *Boletinus cavipes* and *S. bovinus* was associated with increases in the N concentration of leaves of larch and pine seedlings, respectively. The negative effects of ectomycorrhizal fungi on decomposers, postulated to explain increases in decomposition following removal of mycorrhizal fungi by trenching (Gadgil and Gadgil, 1971) have been suggested to depend upon competition for nitrogen or water (Koide and Wu, 2003), but very little is known about the detailed interactions of ectomycorrhizal and saprotrophic fungi in forest ecosystems. Lindahl *et al.* (1999) were able to demonstrate uptake by ectomycorrhizal mycelia of ^{32}P -labelled phosphate sequestered from the mycelium of the wood decomposing fungus *Hypholoma fasciculare* in laboratory microcosms containing interacting mycelia. In other experiments, Lindahl *et al.* (2001) demonstrated that the direction and amount of transfer of ^{32}P -labelled P between interacting saprotrophic and ectomycorrhizal fungal mycelia was influenced by the size of the resources available to them. The intervention of ectomycorrhizal fungi in decomposition cycles presumably involves competitive interactions with saprotrophs and it has been assumed that they occur in close proximity to each other, but little is known about the spatial or temporal dynamics of interaction between these two groups of fungi in natural ecosystems. Recent experiments by Lindahl *et al.* (2007) suggest that the degrading and nutrient-mobilizing components of the fungal community in boreal forests may be temporally and spatially separated. These authors studied changes in fungal community composition along vertical profiles through a *Pinus sylvestris* forest soil. In the study, PCR, cloning, T-RFLP, and sequence analysis were combined with ^{14}C dating of the organic matter, analyses of carbon:nitrogen (C:N) ratios, and ^{15}N natural abun-

dance measurements. Saprotrophic fungi were primarily confined to relatively recently (<4 year) shed litter components on the surface of the forest floor, where organic carbon was mineralized while nitrogen was retained. Mycorrhizal fungi dominated in the underlying, more decomposed litter and humus, where they apparently mobilized N and made it available to their host plants. These observations thus suggest that saprotrophs with a full complement of litter-degrading enzymes are needed during the initial stages of decomposition and that N mobilized by these fungi is retained within their mycelia. As the C:N ratio of the litter decreases, the saprotrophs presumably become less competitive in relation to mycorrhizal species which are directly supplied with host assimilates. The dominance of ectomycorrhizal fungi in the lower, well degraded litter and humus, suggests that mycorrhizal hyphae play a significant role in mobilizing N from well-decomposed organic matter in boreal forest soils and that labile C entering the soil via roots and associated mycorrhizal fungi may play an important role in driving mobilization of this N.

More research is needed on arbuscular mycorrhizal fungi and it is possible that relevant species have not yet been investigated since there has been a general concentration on agricultural systems in which additions of inorganic fertilizers, pesticides, and plant breeding may have selected against arbuscular mycorrhizal fungi with the capacity to mobilize organic substrates. Hodge (2006) pointed out that AM fungi should theoretically be better able to compete for nutrients in patchy soils than the rest of the microbes. Reynolds *et al.* (2005) found no evidence that AM fungi promote plant N acquisition and growth of old-field perennials under conditions of low N supply, but AM fungi may be associated with decaying organic matter in some ecosystems, and Hodge *et al.* (2001) demonstrated enhanced decomposition and N capture from decaying grass leaves in the presence of AM fungi. However, further research is still needed to distinguish between the direct capacity of AM fungi to mobilize organic substrates and their possible, indirect effects on decomposition and plant nutrient uptake, caused by stimulation of decomposers and subsequent uptake of their decomposition products by mycorrhizal hyphae. This problem is further discussed below in relation to interactions with other micro-organisms.

Carbon flow

Loss of energy-rich carbon compounds from plant roots to soil microbial populations constitutes a fundamental supply process to the soil ecosystem and the effects of mycorrhizal fungi on carbon flow to the soil have been reviewed by Finlay and Söderström (1992). Significant amounts of carbon flow through mycorrhizal mycelia to

different components of the soil ecosystem and the cost of maintaining ectomycorrhizal associations has been estimated by different authors to be between 15% and 28% of net carbon fixation. Recent experiments by Högborg *et al.* (2001) used girdling of forest trees to distinguish the relative contributions of roots and ectomycorrhizal fungi and free-living microbial heterotrophs (decomposers) to soil respiration. Decreases of over 50% in soil respiration were found following girdling, suggesting that the flow of current assimilates is a major driver of soil respiration. Apart from direct respiratory loss, energy rich carbon compounds are required for most biological processes and further information is needed about the amounts and types of different compounds and the mechanisms regulating their translocation and ultimate partitioning. Potential effects include production of enzymes, organic acids, and other compounds influencing the degradation of organic substrates or solubilization of mineral substrates (Rosling *et al.*, 2004a, b) and production of antibiotic substances involved in chemical defence or antagonism. Production of glycoproteins such as glomalin that are involved in the formation and stability of soil aggregates may also have an important influence on other micro-organisms associated with the arbuscular mycorrhizal mycelium (Johansson *et al.*, 2004) (see the section on Biotic interactions). Although allocation of carbon may be increased in ectomycorrhizal mycelia colonizing patches of decomposing plant litter, Leake *et al.* (2001) showed that the allocation of carbon to the mycorrhizal mycelia interacting with the mycelium of the wood decomposer *Phanerochaete velutina* was reduced. There has been intensive discussion and controversy about the ultimate fate of carbon reaching the mycorrhizal mycelium and the possible significance of any transfer between plants connected by shared hyphal networks. Some authors (Simard *et al.*, 1997) contend that the amounts of C transferred can be ecologically significant, while other authors (Robinson and Fitter, 1999) question the significance of the process, or advocate a more mycogenic viewpoint (Fitter *et al.*, 2000). Finlay and Söderström (1992) pointed out that connection of plants to a common mycelial network could be of significance without needing to invoke any arguments concerning net interplant transfer of carbon, since seedlings could gain access to a large absorptive network of hyphae with minimal investment of carbon. The results of Högborg *et al.* (1999) are consistent with the above argument since the authors found that promiscuous ectomycorrhizal fungi forming associations with several tree species had natural signatures of ^{13}C closer to those of overstorey trees, suggesting that the overstorey trees partly or wholly support the carbon demands of the nutrient-absorbing mycelia of their alleged competitors, the understorey trees. Transfer of carbon may also occur between green plants and non-photosynthetic, myco-heterotrophic plants sharing the mycelium (see the

section on Effects on plant communities and ecosystems). Flow of carbon through mycelia of AM fungi in grassland ecosystems has been demonstrated by Johnson *et al.*, (2002) to be more rapid and quantitatively important than previously appreciated, although it has also been shown to be disrupted by soil invertebrate grazing (Johnson *et al.* 2005). Low molecular weight compounds produced by mycorrhizal hyphae may contribute significantly to the total CO_2 efflux from forest soils (van Hees *et al.*, 2005). Allocation of recent photoassimilates through mycorrhizal mycelia influences nutrient dynamics and microbial populations in the mycorrhizosphere (Jones *et al.*, 2004; Finlay and Rosling, 2006) and Högborg and Read (2006) have pointed out that this physiological continuity and dynamic interdependence of the plant–microbe–soil system challenge the widespread view that soil activity is dominated by decomposer organisms using older detrital material and that root litter inputs equal those of above-ground litter.

Bioremediation

Evidence on the roles mycorrhizal mycelia might play in bioremediation of soil pollutants is still conflicting. Meharg and Cairney (2000) reviewed possible ways in which ectomycorrhizal fungi might influence rhizosphere remediation of persistent organic pollutants (POPs). Many of the fungi screened for degradation of POPs such as polyhalogenated biphenyls, polyaromatic hydrocarbons, chlorinated phenols, and pesticides, are able to transform these compounds, but relatively few mycorrhizal taxa have been tested. Donnelly *et al.* (1993) demonstrated degradation of two chlorinated aromatic herbicides (2,4-dichlorophenoxyacetic acid and atrazine) by ericoid and ectomycorrhizal fungi. Meharg *et al.* (1997a) showed that degradation of 2,4-dichlorophenol by the two ectomycorrhizal fungi *Paxillus involutus* and *Suillus variegatus* was higher when the fungi were growing in symbiosis with *Pinus sylvestris* than when they were grown in pure culture. In other experiments (Meharg *et al.*, 1997b), *S. variegatus* has been shown to be effective in degrading 2,4,6-trinitrotoluene. A potential advantage of using mycorrhizal fungi in bioremediation is that they receive a direct supply of carbon from their plant hosts to support growth into contaminated substrates. Some of this carbon may subsequently be available to bacteria associated with the mycorrhizal mycelium (Sun *et al.*, 1999) and this may have consequences for bioremediation in the mycorrhizosphere. Attempts to introduce micro-organisms with biocontrol or bioremediation properties often fail because the inoculants fail to establish themselves. Mycorrhizal hyphae may facilitate the establishment of some bacteria and Sarand *et al.* (1998) suggested that mycorrhizal hyphae were able to support microbial biofilms of catabolic

plasmid (Tol⁺) harbouring bacteria which could be active in bioremediation of petroleum-contaminated soil. In further experiments, these authors (Sarand *et al.*, 2000) demonstrated that the number of Tol⁺ bacteria was higher in mycorrhizospheric soil compared with bulk soil, and inoculation with bacteria had a positive effect on plant and fungal development. The presence of easily available plant-derived carbon sources did not impede the degradation of the *m*-toluate by the bacteria (Sarand *et al.*, 1999). However, in other experiments Genney *et al.* (2004) found that degradation of the polycyclic aromatic hydrocarbon fluorene was retarded in a Scots pine ectomycorrhizosphere. Joner *et al.* (2006) also demonstrated impeded phytoremediation of polycyclic aromatic hydrocarbons (PAHs) by the ectomycorrhizal mycelium of *S. bovinus* that was attributed to nutrient depletion by the scavenging fungus. In general, the role of arbuscular mycorrhizal fungi is less well investigated with respect to bioremediation, but experiments by Joner *et al.* (2001) suggest that dissipation of polycyclic aromatic hydrocarbons (PAHs) may be enhanced in the presence of arbuscular mycorrhizas, and that changes in the composition of the mycorrhiza-associated microflora may be responsible for the observed decreases in PAH concentrations.

Mediation of plant stress

Mycorrhizal fungi have a range of effects which contribute to the amelioration of different types of stress experienced by their plant hosts, including metal toxicity, oxidative stress, water stress, and effects of soil acidification. These have recently been reviewed by Colpaert (2008) and Finlay *et al.* (2008).

The ability of ectomycorrhizal fungi to capture base cations and restrict their loss through leaching, and to release nutrients through weathering of mineral surfaces, may be important in environments influenced by soil acidification (Ahonen-Jonnarth *et al.*, 2003). In such soils the toxicity of the resulting elevated concentrations of Al and other toxic metals may be reduced by increased production of chelating agents such as oxalic acid (Ahonen-Jonnarth *et al.*, 2000). Fomina *et al.* (2005) investigated solubilization of toxic metal minerals and metal tolerance by ericoid and ectomycorrhizal fungi. In general, metal-tolerant fungi grew and solubilized toxic metal minerals better than non-tolerant isolates. Metal dissolution by fungi may take place through proton-promoted or ligand-promoted mechanisms and organic acids provide both a source of protons for solubilization and metal-chelating anions to complex the metal cations. Toxic metals may also cause oxidative stress and several studies of mycorrhizal fungal responses suggested that the fungi may be able to regulate genes providing protection against reactive oxygen species (ROS). Lanfranco *et al.* (2005) present evidence of a functional arbuscular

mycorrhizal CuZn superoxide dismutase which may provide protection against localized host defence responses involving ROS. Other studies (Ott *et al.*, 2002; Schützendübel and Polle, 2002) suggest that ectomycorrhizal fungi improve protection against toxic metal-induced oxidative stress through strongly induced glutathione synthesis.

Extracellular and cellular mechanisms promoting metal tolerance in ectomycorrhizal fungi have been reviewed by Bellion *et al.* (2006) and there is no doubt that metal tolerance does exist in ectomycorrhizal fungi. However, Colpaert (2008) points out that very little is still known about how fungal metal tolerance affects metal transfer to the host plant and that scientists are 'still at the dawn of the elucidation of the molecular mechanisms involved in metal homeostasis, detoxification and tolerance in filamentous fungi'. Metal tolerant AM fungi have also been reported (Leyval *et al.*, 2002) and assumed to have potential in phytoremediation of metal-contaminated soils, but there are still gaps in our knowledge of the mechanisms involved.

The effects of mycorrhizal fungi on plant responses to drought stress have been discussed by a number of authors (Smith and Read, 2008), but it is difficult to separate nutritional effects from direct effects on water transport since the hyphal contribution to nutrient uptake becomes more important as soil dries. Experiments by Querejeta *et al.* (2003), however, have shown nocturnal water translocation from plant roots to mycorrhizal fungi in association with hydraulic lift. Supply of water in this way would be an important way of maintaining mycorrhizal activity and improving nutrient uptake by deep-rooted plants, even when the fertile upper soil horizons are dry. The exudation of liquid droplets at ectomycorrhizal hyphal tips has also been discussed by Sun *et al.* (1999) who suggested that this would help to maintain better continuity between hyphal tips and the adjacent substrate, as well as more stable conditions for microbial interactions at this interface. Effects of mycorrhizal fungi on tolerance of water stress are difficult to study since the supply of poorly diffusible nutrients such as P in dry soil will become limited by the increasing tortuosity of the diffusion path and mycorrhizal hyphae will make an increasingly important contribution to P uptake as the soil dries, confounding the effects of water and nutrients. However, several studies suggest that enhanced tolerance of AM plants to water deficit may involve modulation of drought-induced plant genes (Ruis-Lozano *et al.*, 2006). Down-regulation of genes encoding plasma membrane aquaporins has been shown by Porcel *et al.* (2006) and this may play a role in the increased tolerance of AM plants to both water and salt stress.

Effects on plant communities and ecosystems

The floristic diversity and productivity of reconstructed grassland communities have been shown to depend upon

the presence of a species-rich assemblage of arbuscular mycorrhizal species (van der Heijden *et al.*, 1998). In these experiments increasing fungal diversity resulted in greater species diversity and higher productivity, suggesting that changes in below-ground diversity of mycorrhizal symbionts can drive changes in above-ground diversity and productivity. The mechanism behind these effects is likely to be differential effects of specific plant–fungus combinations on the growth of different plant species. This is consistent with the idea emerging from many molecular studies, that the degree of mycorrhizal specificity may be higher than hitherto supposed. If the addition of new fungal species leads to increases in the survival and vigour of more plant species that are responsive to mycorrhizal colonization then there may be a positive feedback on the mycorrhizal fungi, leading to more efficient resource utilization and increases in overall productivity. These effects are context dependent and Vogelsang *et al.* (2006) suggest that plant diversity and productivity are more responsive to AMF identity than to AMF diversity *per se*, and that AMF identity and P environment can interact in complex ways to alter community-level properties. Although Vogelsang *et al.* (2006) found little support for AMF-facilitated complementarity in P use, recent experiments by Jansa *et al.* (2008) provide direct evidence of functional complementarity among species within the AMF community colonizing a single root system. Leek plants colonized by a mixture of *Glomus claroideum* and *Glomus intraradices* acquired more P than with either of the two AMF separately. Competition among the species is a major challenge in interpreting experiments with mixed inoculations, but the relative colonization of the two species was determined by the use of real-time PCR. Ultimately, as van der Heijden and Scheublin (2007) argue, defining functionally distinct AMF groups is essential if we want to understand fully the interactions between plant and AMF communities in agricultural and natural ecosystems.

The ecological significance of the possible transfer of photosynthetically derived carbon between different plant species is still questioned by some scientists (Robinson and Fitter, 1999). Pfeffer *et al.* (2004) found no evidence to support the movement of carbon between interconnected roots of AM plants but there is substantial evidence to suggest that it may be of great significance to myco-heterotrophic plant species. Although the fungal associates and carbon sources of most myco-heterotrophic plants have so far not been identified, several more closely examined non-photosynthetic plant species have been revealed to be effectively epiparasitic on green plants, obtaining their carbon via hyphal connections with shared arbuscular (Bidartondo *et al.*, 2002) or ectomycorrhizal fungal associates (Taylor and Bruns, 1997; McKendrick *et al.*, 2000). Epiparasitic plants have consistently been revealed to have extremely high levels of fungal specific-

ity, irrespective of the major groups of mycorrhizal fungi with which they associate. In each case, only a very narrow range of fungi is involved and the fungal distribution appears to control the plant distribution, providing a clear example of the way in which mycorrhizal community structure may control the success of plant species.

Biotic interactions

In addition to increasing the absorptive surface area of their host plant root systems, the hyphae of symbiotic fungi provide an increased surface area for interactions with other micro-organisms, and provide an important pathway for the translocation of energy-rich plant assimilates (products of photosynthesis) to the soil. The interactions may be synergistic, competitive or antagonistic and may have applied significance in areas such as sustainable agriculture (Johansson *et al.*, 2004), biological control or bioremediation. The potential of such interactions for stimulating plant growth has been reviewed by Artursson *et al.* (2006). Bacteria with the potential to fix nitrogen have been discovered growing endosymbiotically within tuberculate roots of ectomycorrhizal plants (Izumi *et al.*, 2006). Obviously such tripartite symbioses would be of significance in nitrogen-limited environments. Endosymbiotic bacteria have been reported in both AM fungi (Jargeat *et al.*, 2004) and the ectomycorrhizal fungus *Laccaria bicolor* (Bertaux *et al.*, 2003). These may be more common than is currently supposed and there is still only limited knowledge about their functional role in the symbiosis. Exudation and reabsorption of fluid droplets at ectomycorrhizal hyphal tips was demonstrated by Sun *et al.* (1999) who concluded that it might represent an important mechanism for conditioning the hyphal environment in the vicinity of tips, creating an interface for the exchange of nutrients and carbon compounds with the adjacent soil environment and its other micro-organisms. The extent to which interactions between mycorrhizal mycelia and other micro-organisms influence different organic or mineral substrates is still unclear and further experiments are needed to distinguish between the activity of mycorrhizal hyphae themselves and facilitated mycorrhizal uptake of compounds mobilized by the activities of other organisms. Experiments by Artursson *et al.* (2005) using T-RFLP and the nucleotide analogue bromodeoxyuridine demonstrate that inoculation with an AM fungus modified the active bacterial communities associated with mycorrhizal clover and wheat roots, suggesting that mycorrhizal fungi can influence bacterial community structure. It is also well known that bacteria may have an active influence on ectomycorrhizal root colonization (Frey-Klett *et al.*, 2007). Differential attachment of different bacterial taxa to vital and non-vital fungal hyphae (Toljander *et al.*, 2006) suggests that some

bacteria may function primarily as saprotrophs, consuming dead hyphae, whilst others depend more upon interactions with living hyphae. Detailed studies using *in vitro* systems show that AM fungal exudates have the potential to influence the vitality and community structure of mycorrhizosphere bacteria (Toljander *et al.*, 2007) and these types of effect may be of significance in relation to microbial priming or biological control of plant pathogens. New approaches based on stable isotope probing, RNA analysis, and metagenomics (Vandenkoornhuyzen *et al.*, 2007) indicate that there are many hitherto unidentified root symbionts and that bacteria and AM fungi occupying roots show differential activity in C consumption with much higher carbon flow to some fungi than others. Other recent experiments by Singh *et al.* (2008) suggest that AM fungi may influence bacterial assemblages in roots but that the effect is not reciprocal. AM fungal mycelia clearly play an important role in the microbial processes influencing ecosystem functioning but we still have much to learn about the detailed interactions of root-inhabiting microbes and how these are regulated.

Concluding remarks

It should be apparent from the preceding discussion that different types of mycorrhizal symbioses play fundamental roles in shaping terrestrial ecosystems and that the characteristic plant communities that dominate the major terrestrial biomes of the world today do so because selection has favoured different types of symbiotic association that are functionally adapted to the prevailing suites of edaphic and climatic conditions characterizing different environments. The real significance of mycorrhizal fungi is that they connect the primary producers of ecosystems, plants, to the heterogeneously distributed nutrients required for their growth, enabling the flow of energy-rich compounds required for nutrient mobilization whilst simultaneously providing conduits for the translocation of mobilized products back to their hosts. Elucidating the diversity of mechanisms involved, the range of interactions with other organisms, and the ways in which these are regulated remains the ultimate challenge in understanding the role of these fungi in biogeochemical cycles. New molecular tools have enabled identification of mycorrhizal fungal symbionts with a higher degree of resolution and have contributed to the realization that the degree of functional specificity in mycorrhizal associations may be higher than hitherto appreciated. Old views of mycorrhizal symbiosis, based solely on the mineral nutrition of individual plants, are giving way to new theories with a broader functional basis, using more ecologically relevant species and substrates. Comparative analysis of different systems will improve our understanding of responses to environmental

and climatic perturbations. This new knowledge is an important prerequisite for future, sustainable management of terrestrial ecosystems.

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References

- Abuzinadah RA, Finlay RD, Read DJ. 1986. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants. II. Utilization of protein by mycorrhizal plants of *Pinus contorta*. *New Phytologist* **103**, 495–506.
- Ahonen-Jonnarh U, Göransson A, Finlay RD. 2003. Growth and nutrient uptake of ectomycorrhizal *Pinus sylvestris* seedlings treated with elevated Al concentrations. *Tree Physiology* **23**, 157–167.
- Ahonen-Jonnarh U, Van Hees PAW, Lundström US, Finlay RD. 2000. Production of organic acids by mycorrhizal and non-mycorrhizal *Pinus sylvestris* L. seedlings exposed to elevated concentrations of aluminium and heavy metals. *New Phytologist* **146**, 557–567.
- Anderson IC, Cairney JWG. 2007. Ectomycorrhizal fungi: exploring the mycelial frontier. *FEMS Microbiology Reviews* **31**, 388–406.
- Artursson V, Finlay RD, Jansson J. 2006. Interactions between arbuscular mycorrhizal fungi and bacteria and their potential for stimulating plant growth. *Environmental Microbiology* **8**, 1–10.
- Artursson V, Finlay RD, Jansson J. 2005. Combined bromodeoxyuridine immunocapture and terminal-restriction fragment length polymorphism analysis highlights differences in the active soil bacterial metagenome due to *Glomus mosseae* inoculation or plant species. *Environmental Microbiology* **7**, 1952–1966.
- Banfield JF, Barker WW, Welch SA, Taunton A. 1999. Biological impact on mineral dissolution: application of the lichen model to understanding mineral weathering in the rhizosphere. *Proceedings of the National Academy of Sciences, USA* **96**, 3404–3411.
- Bellion M, Courbot M, Jacob C, Blaudez D, Chalot M. 2006. Extracellular and cellular mechanisms sustaining metal tolerance in ectomycorrhizal fungi. *FEMS Microbiology Letters* **254**, 173–181.
- Bidartondo MI. 2005. The evolutionary ecology of myco-heterotrophy. *New Phytologist* **167**, 335–352.
- Bidartondo MI, Redecker D, Hijri I, Wiemken A, Bruns TD, Domínguez L, Sérsic A, Leake JR, Read DJ. 2002. Epiparasitic plants specialized on arbuscular mycorrhizal fungi. *Nature* **419**, 389–392.
- Bending GD, Read DJ. 1995. The structure and function of the vegetative mycelium of ectomycorrhizal plants. V. Foraging behaviour and translocation of nutrients from exploited litter. *New Phytologist* **130**, 401–409.
- Bertaux J, Schmid M, Hutzler P, Hartmann A, Garbaye J, Frey-Klett P. 2005. Occurrence and distribution of endobacteria in the plant-associated mycelium of the ectomycorrhizal fungus *Laccaria bicolor* S238N. *Environmental Microbiology* **7**, 1786–1795.

- Colpaert JV.** 2008. Heavy metal pollution and genetic adaptations in ectomycorrhizal fungi. In: Avery S, Stratford M, van West P, eds. *Stress in yeasts and filamentous fungi*. Amsterdam: Elsevier, 157–173.
- Donnelly PK, Entry JA, Crawford DL.** 1993. Degradation of atrazine and 2,4-dichlorophenoxyacetic acid by mycorrhizal fungi at 3 nitrogen concentrations *in vitro*. *Applied and Environmental Microbiology* **59**, 2642–2647.
- Finlay RD.** 2004. Mycorrhizal fungi and their multifunctional roles. *Mycologist* **18**, 91–96.
- Finlay RD.** 2005. Action and interaction in the mycorrhizal hyphosphere: a re-evaluation of the role of mycorrhizal symbiosis in nutrient acquisition and plant ecology. In: BassiriRad H, ed. *Nutrient acquisition by plants: an ecological perspective*. Heidelberg: Springer-Verlag, 221–276.
- Finlay RD, Lindahl BD, Taylor AFS.** 2008. Responses of mycorrhizal fungi to stress. In: Avery S, Stratford M, van West P, eds. *Stress in yeasts and filamentous fungi*. Amsterdam: Elsevier, 201–220.
- Finlay RD, Rosling A.** 2006. Integrated nutrient cycles in forest ecosystems, the role of ectomycorrhizal fungi. In: Gadd GM, ed. *Fungi in biogeochemical cycles*. Cambridge, UK: Cambridge University Press, 28–50.
- Finlay RD, Söderström B.** 1992. Mycorrhiza and carbon flow to soil. In: Allen MF, ed. *Mycorrhizal functioning*. London: Chapman and Hall, 134–160.
- Fitter AH.** 2005. Darkness visible, reflections on underground ecology. *Journal of Ecology* **93**, 231–243.
- Fitter AH, Heinemeyer A, Staddon PL.** 2000. The impact of elevated CO₂ and global climate change on arbuscular mycorrhizas: a mycocentric approach. *New Phytologist* **147**, 179–187.
- Fomina MA, Alexander IJ, Colpaert JV, Gadd GM.** 2005. Solubilization of toxic metal minerals and metal tolerance of mycorrhizal fungi. *Soil Biology and Biochemistry* **37**, 851–866.
- Frank B.** 2005. On the nutritional dependence of certain trees on root symbiosis with belowground fungi. *Mycorrhiza* **15**, 267–275. (Translation of Frank's original 1885 paper.)
- Frey-Klett J, Garbaye J, Tarkka M.** 2007. The mycorrhiza helper bacteria revisited. *New Phytologist* **176**, 22–36.
- Gadd GM (ed.).** 2006. *Fungi in biogeochemical cycles*. Cambridge: Cambridge University Press.
- Gadgil RL, Gadgil PD.** 1971. Mycorrhiza and litter decomposition. *Nature* **233**, 133.
- Genney DR, Alexander IJ, Killham K, Meharg AA.** 2004. Degradation of the polycyclic aromatic hydrocarbon (PAH) fluorene is retarded in a Scots pine ectomycorrhizosphere. *New Phytologist* **163**, 641–649.
- Hodge A.** 2006. Plastic plants and patchy soils. *Journal of Experimental Botany* **57**, 401–411.
- Hodge A, Campbell CD, Fitter AH.** 2001. An arbuscular mycorrhizal fungus accelerates decomposition and acquires nitrogen directly from organic material. *Nature* **413**, 297–299.
- Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Löfvenius M, Read DJ.** 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* **411**, 789–792.
- Högberg P, Read DJ.** 2006. Towards a more plant physiological perspective on soil ecology. *Trends in Ecology and Evolution* **21**, 548–554.
- Izumi H, Anderson IC, Alexander IJ, Killam K, Moore ERB.** 2006. Diversity and expression of nitrogenase genes (*nifH*) from ectomycorrhizas of Corsican pine (*Pinus nigra*). *Environmental Microbiology* **8**, 2224–2230.
- Jansa J, Smith FA, Smith SE.** 2008. Are there benefits of simultaneous root colonization by different arbuscular mycorrhizal fungi? *New Phytologist* doi: 10.1111/j.1469–8137.2007.02294.x.
- Jargeat P, Cosseau C, Ola'h B, Jauneau A, Bonfante P, Batut J, Bécard G.** 2004. Isolation, free-living capacities, and genome structure of *Candidatus Glomeribacter gigasporarum*, the endocellular bacterium of the mycorrhizal fungus *Gigaspora margarita*. *Journal of Bacteriology* **186**, 6876–6884.
- Johansson J, Paul L, Finlay RD.** 2004. Microbial interactions in the mycorrhizosphere and their significance for sustainable agriculture. *FEMS Microbiology Ecology* **48**, 1–12.
- Johnson D, Krsek M, Wellington EMH, Stott AW, Cole L, Bardgett RD, Read DJ, Leake JR.** 2005. Soil invertebrates disrupt carbon flow through fungal networks. *Science* **309**, 1047.
- Johnson D, Leake JR, Ostle N, Ineson P, Read DJ.** 2002. *In situ* ¹³C pulse-labelling of upland grassland demonstrates that a rapid pathway of carbon flux from arbuscular mycorrhizal mycelia to the soil. *New Phytologist* **153**, 327–334.
- Joner EJ, Johansen A, Loibner AP, Cruz MAD, Szolar OHJ, Portal J-M, Leyval C.** 2001. Rhizosphere effects on microbial community structure and dissipation and toxicity of polycyclic aromatic hydrocarbons (PAHs) in spiked soil. *Environmental Science and Technology* **35**, 2773–2777.
- Joner EJ, Leyval C, Colpaert JV.** 2006. Ectomycorrhizas impede phytoremediation of polycyclic aromatic hydrocarbons (PAHs) both within and beyond the rhizosphere. *Environmental Pollution* **142**, 34–38.
- Jones DL, Hodge A, Kuzyakov Y.** 2004. Plant and mycorrhizal regulation of rhizodeposition. *New Phytologist* **163**, 459–480.
- Jongmans AG, van Breemen N, Lundström U, Finlay RD, van Hees PAW, Giesler R, Melkerud P-A, Olsson M, Srinivasan M, Unestam T.** 1997. Rock-eating fungi: a true case of mineral plant nutrition? *Nature* **389**, 682–683.
- Klironomos JN, Hart MM.** 2001. Animal nitrogen swap for plant carbon. *Nature* **41**, 651–652.
- Koide R, Wu T.** 2003. Ectomycorrhizas and retarded decomposition in a *Pinus resinosa* plantation. *New Phytologist* **158**, 401–407.
- Landeweert R, Hofflund E, Finlay RD, van Breemen N.** 2001. Linking plants to rocks: Ectomycorrhizal fungi mobilize nutrients from minerals. *Trends in Ecology and Evolution* **16**, 248–254.
- Lanfranco L, Novero M, Bonfante P.** 2005. The mycorrhizal fungus *Gigaspora margarita* possesses a CuZn superoxide dismutase that is up-regulated during symbiosis with legume hosts. *Plant Physiology* **137**, 1319–1330.
- Leake JR.** 2004. Myco-heterotroph/epiparasitic plant interactions with ectomycorrhizal and arbuscular mycorrhizal fungi. *Current Opinion in Plant Biology* **7**, 422–428.
- Leake JR.** 2005. Plants parasitic on fungi, unearthing the fungi in myco-heterotrophs and debunking the 'saprophytic' plant myth. *Mycologist* **19**, 113–122.
- Leake JR, Donnelly DP, Saunders EM, Boddy L, Read DJ.** 2001. Rates and quantities of carbon flux to ectomycorrhizal mycelium following ¹⁴C pulse labeling of *Pinus sylvestris* seedlings: effects of litter patches and interaction with a wood-decomposer fungus. *Tree Physiology* **21**, 71–82.
- Leyval C, Joner EJ, del Val C, Haselwandter K.** 2002. Potential of arbuscular mycorrhizal fungi for bioremediation. In: Gianinazzi S, Schüepp H, Barea JM, Haselwandter K, eds. *Mycorrhizal technology in agriculture. From genes to bioproducts*. Basel: Birkhäuser Verlag, 175–186.
- Lindahl BD, Finlay RD, Cairney JWG.** 2005. Enzymatic activities of mycelia in mycorrhizal fungal communities. In: Dighton J, Oudemans P, White J, eds. *The fungal community, its organization and role in the ecosystem*. New York: Marcel Dekker, 331–348.

- Lindahl BD, Ihrmark K, Boberg J, Trumbore S, Högberg P, Stenlid J, Finlay RD. 2007. Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in boreal forests. *New Phytologist* **173**, 611–620.
- Lindahl B, Olsson S, Stenlid J, Finlay RD. 2001. Effects of resource availability on mycelial interactions and ^{32}P -transfer between a saprotrophic and an ectomycorrhizal fungus in soil microcosms. *FEMS Microbiology Ecology* **38**, 43–52.
- Lindahl B, Stenlid J, Olsson S, Finlay RD. 1999. Translocation of ^{32}P between interacting mycelia of a wood decomposing fungus and ectomycorrhizal fungi in microcosm systems. *New Phytologist* **144**, 183–193.
- Mahmood S, Finlay RD, Erland S, Wallander H. 2001. Solubilization and colonization of wood ash by ecto-mycorrhizal fungi isolated from a wood ash fertilised spruce forest. *FEMS Microbiology Ecology* **35**, 151–161.
- McKendrick SL, Leake JR, Read DJ. 2000. Symbiotic germination and development of mycoheterotrophic plants in nature: transfer of carbon from ectomycorrhizal *Salix repens* and *Betula pendula* to the orchid *Corallorhiza trifida* through shared hyphal connections. *New Phytologist* **145**, 539–548.
- Meharg AA, Cairney JWG. 2000. Ectomycorrhizas: extending the capacities of rhizosphere remediation? *Soil Biology and Biochemistry* **32**, 1475–1484.
- Meharg AA, Cairney JWG, Maguire N. 1997a. Mineralization of 2,4-dichlorophenol by ectomycorrhizal fungi in axenic culture and in symbiosis with pine. *Chemosphere* **34**, 2495–2504.
- Meharg AA, Dennis GR, Cairney JWG. 1997b. Biotransformation of 2,4,6-trinitrotoluene (TNT) by ectomycorrhizal basidiomycetes. *Chemosphere* **35**, 513–521.
- Newsham KK, Fitter AH, Watkinson AR. 1995. Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends in Ecology and Evolution* **10**, 407–411.
- Ott T, Fritz E, Polle A, Schützendübel A. 2002. Characterization of antioxidative systems in the ectomycorrhiza-building basidiomycete *Paxillus involutus* (Bartsch) Fr. and its reaction to cadmium. *FEMS Microbiology Ecology* **42**, 359–366.
- Perez-Moreno J, Read DJ. 2001a. Exploitation of pollen by mycorrhizal mycelial systems with special reference to nutrient cycling in boreal forests. *Proceedings of the Royal Society B* **268**, 1329–1335.
- Perez-Moreno J, Read DJ. 2001b. Nutrient transfer from soil nematodes to plants: a direct pathway provided by the mycorrhizal mycelial network. *Plant, Cell and Environment* **24**, 1219–1226.
- Pfeffer PE, Douds DD, Bücking H, Schwartz DP, Shachar-Hill Y. 2004. The fungus does not transfer carbon to or between roots in an arbuscular mycorrhizal symbiosis. *New Phytologist* **163**, 617–627.
- Porcel R, Aroca R, Azcón R, Ruiz-Lozano JM. 2006. PIP aquaporin gene expression in arbuscular mycorrhizal *Glycine max* and *Lactuca sativa* plants in relation to drought stress tolerance. *Plant Molecular Biology* **60**, 389–404.
- Querejeta JJ, Egerton-Warburton LM, Allen MF. 2003. Direct nocturnal water transfer from oaks to their mycorrhizal symbionts during severe soil drying. *Oecologia* **134**, 55–64.
- Read DJ. 1991. Mycorrhizas in ecosystems. *Experientia* **47**, 376–390.
- Read DJ, Perez-Moreno J. 2003. Mycorrhizas and nutrient cycling in ecosystems: a journey towards relevance? *New Phytologist* **157**, 475–492.
- Redecker D, Kodner R, Graham LE. 2000. Glomalean fungi from the Ordovician. *Science* **289**, 1920–1921.
- Reynolds HL, Hartley AE, Vogelsang KM, Bever JD, Schultz PA. 2005. Arbuscular mycorrhizal fungi do not enhance nitrogen acquisition and growth of old-field perennials under low nitrogen supply in glasshouse culture. *New Phytologist* **167**, 869–880.
- Robinson D, Fitter AH. 1999. The magnitude and control of carbon transfer between plants linked by a common mycorrhizal network. *Journal of Experimental Botany* **50**, 9–13.
- Rosling A, Landeweert R, Lindahl BD, Larsson K-H, Kuypers TW, Taylor AFS, Finlay RD. 2003. Vertical distribution of ectomycorrhizal fungal taxa in a podzol profile determined by morphotyping and genetic verification. *New Phytologist* **159**, 775–783.
- Rosling A, Lindahl BD, Finlay RD. 2004a. Carbon allocation in intact mycorrhizal systems of *Pinus sylvestris* L. seedlings colonizing different mineral substrates. *New Phytologist* **162**, 795–802.
- Rosling A, Lindahl BD, Taylor AFS, Finlay RD. 2004b. Mycelial growth and substrate acidification of ectomycorrhizal fungi in response to different minerals. *FEMS Microbiology Ecology* **47**, 31–37.
- Ruiz-Lozano JM, Porcel R, Aroca R. 2006. Does the enhanced tolerance of arbuscular mycorrhizal plants to water deficit involve modulation of drought-induced plant genes? *New Phytologist* **171**, 693–698.
- Santos-González JC, Finlay RD, Tehler A. 2007. Seasonal dynamics of arbuscular mycorrhizal root colonization in a semi-natural grassland. *Applied and Environmental Microbiology* **73**, 5613–5623.
- Sarand I, Haario H, Jørgensen KS, Romantschuk M. 2000. Effect of inoculation of a TOL plasmid containing mycorrhizosphere bacterium on development of Scots pine seedlings, their mycorrhizosphere and the microbial flora in m-toluene-amended soil. *FEMS Microbiology Ecology* **31**, 127–141.
- Sarand I, Timonen S, Koivula T, Peltola R, Haahtela K, Sen R, Romantschuk M. 1999. Tolerance and biodegradation of m-toluene by Scots pine, a mycorrhizal fungus and fluorescent pseudomonads individually and under associative conditions. *Journal of Applied Microbiology* **86**, 817–826.
- Sarand I, Timonen S, Nurmiaho Lassil EL, Koivula T, Haahtela K, Romantschuk M, Sen R. 1998. Microbial biofilms and catabolic plasmid harbouring degradative fluorescent pseudomonads in Scots pine mycorrhizospheres developed on petroleum contaminated soil. *FEMS Microbiology Ecology* **27**, 115–126.
- Schützendübel A, Polle A. 2002. Plant responses to abiotic stresses: heavy metal-induced oxidative stress and protection by mycorrhization. *Journal of Experimental Botany* **53**, 1351–1365.
- Selosse M-A, Setaro S, Glatard F, Richard F, Urcelay C, Weiss M. 2007. Sebaciales are common mycorrhizal associates of Ericaceae. *New Phytologist* **174**, 864–878.
- Simard SW, Perry DA, Jones MD, Myrold DD, Durall DM, Molina R. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. *Nature* **388**, 579–582.
- Singh BK, Naoise N, Ridgway KP, McNicol J, Young JPW, Daniell TJ, Prosser JL, Millard P. 2008. Relationship between assemblages of mycorrhizal fungi and bacteria on grass roots. *Environmental Microbiology* **10**, 534–541.
- Smith SE, Read DJ. 2008. *Mycorrhizal symbiosis*. 3rd edn. Academic Press.
- Smits MM, Hoffland E, Jongmans AG, van Breemen N. 2005. Contribution of mineral tunneling to total feldspar weathering. *Geoderma* **125**, 59–69.
- Sun Y-P, Unestam T, Lucas SD, Johanson KJ, Kenne L, Finlay RD. 1999. Exudation–reabsorption in mycorrhizal fungi, the dynamic interface for interaction with soil and other microorganisms. *Mycorrhiza* **9**, 137–144.

- Taylor AFS, Alexander I.** 2005. The ectomycorrhizal symbiosis: life in the real world. *Mycologist* **19**, 102–112.
- Taylor DL, Bruns TD.** 1997. Independent, specialized invasions of ectomycorrhizal mutualism by two nonphotosynthetic orchids. *Proceedings of the National Academy of Sciences, USA* **94**, 4510–4515.
- Toljander JF, Artursson V, Paul LR, Jansson JK, Finlay RD.** 2006. Attachment of different soil bacteria to arbuscular mycorrhizal fungi is determined by hyphal vitality and fungal species. *FEMS Microbiology Letters* **254**, 34–40.
- Toljander JF, Paul L, Lindahl BD, Elfstrand M, Finlay RD.** 2007. Influence of AM fungal exudates on bacterial community structure. *FEMS Microbiology Ecology* **61**, 295–304.
- van Breemen N, Finlay RD, Lundström U, Jongmans AG, Giesler R, Olsson M.** 2000. Mycorrhizal weathering: a true case of mineral nutrition? *Biogeochemistry* **49**, 53–67.
- van der Heijden MGA, Klironomos JN, Ursic M, Moutoglou 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 der Heijden MGA, Scheublin TR.** 2007. Functional traits in mycorrhizal ecology: their use for predicting the impact of arbuscular mycorrhizal fungal communities on plant growth and ecosystem functioning. *New Phytologist* **174**, 244–250.
- Vandenkoornhuyse P, Mahé S, Ineson P, Staddon P, Ostle N, Cliquet J-B, Francez A-J, Fitter AH, Young JPW.** 2007. Active root-inhabiting microbes identified by rapid incorporation of plant-derived carbon into RNA. *Proceedings of the National Academy of Sciences, USA* **104**, 16970–16975.
- van Hees PAW, Jones DL, Finlay RD, Godbold DL, Lundström US.** 2005. The carbon we do not see, Do low molecular weight compounds have a significant impact on carbon dynamics and respiration in forest soils? *Soil Biology and Biochemistry* **37**, 1–13.
- Vogelsang KM, Reynolds HL, Bever JD.** 2006. Mycorrhizal fungal identity and richness determine the diversity and productivity of a tallgrass prairie system. *New Phytologist* **172**, 554–562.
- Wallander H.** 2006. Mineral dissolution by ectomycorrhizal fungi. In: Gadd GM, ed. *Fungi in biogeochemical cycles*. Cambridge, UK: Cambridge University Press, 28–50.
- Wallander H, Johansson L, Pallon J.** 2002. PIXE analysis to estimate the elemental composition of ectomycorrhizal rhizomorphs grown in contact with different minerals in forest soil. *FEMS Microbiology Ecology* **39**, 147–156.
- Wallander H, Nilsson LO, Hagerberg D, Bååth E.** 2001. Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. *New Phytologist* **151**, 752–760.