

Mycorrhizal fungi and their multifunctional roles

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The effects of mycorrhizal fungi have traditionally been considered within the rather narrow perspective of their effects on the mineral nutrition of individual plants. Most biologists are familiar with the idea that these symbiotic fungi may improve plant uptake of dissolved mineral nutrients. What other effects do these symbionts have? Research during the past 20 years has increasingly viewed symbiotic mycorrhizal associations between plants and fungi within a wider, multifunctional perspective. New molecular methods have been applied to investigate mycorrhizal fungal communities (Bruns & Bidartondo, 2002) and greater attention has been paid to their possible effects at the level of the plant community. As we have acquired greater knowledge about fungal species diversity, so we have become more aware of the potential functional diversity of mycorrhizal fungi. The new multifunctional perspective includes mobilisation of N and P from organic polymers, possible 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 microorganisms.

Keywords: Microbial interactions, mycorrhizal fungi, nutrient cycling, plant communities, weathering, stress

Introduction

Symbiotic mycorrhizal fungi influence the terrestrial environment in different ways, either through direct interactions with the mineral or organic substrates that they colonise, or indirectly, via interactions with their host plants or other organisms. Traditionally, research has been dominated by studies of the effects of mycorrhizal fungi on the growth and nutrient status of individual plants, mostly concentrating on the uptake of mineral nutrients. More recently there has been increased focus on the ways in which mycorrhizal fungi affect the functioning of plant communities and ecosystems, and greater attention has been paid to the role of the fungi in releasing plant growth limiting nutrients such as N and P from organic polymers. This research is leading to a better awareness of the ways in which different types of mycorrhizal fungi contribute to the development and dominance of distinctive plant communities at different spatial scales. The current 'multifunctional' perspective of mycorrhizal symbiosis also takes account of the ways in which mycorrhizal fungi influence carbon partitioning and cycling within plant ecosystems, as well as the different ways in which the symbiosis may influence plant responses to stress

factors such as drought, soil acidification, toxic metals and plant pathogens. There is also increasing recognition of the possible ways in which mycorrhizal fungi interact with other groups of microorganisms and so influence nutrient cycling. These different environmental effects are outlined in Fig 1 and discussed in greater detail below.

Mobilisation and uptake of mineral nutrients

The effects of mycorrhizal mycelia on the uptake of dissolved mineral nutrients are well documented (Smith & Read, 1997). In ectomycorrhizal and arbuscular-mycorrhizal associations at least, the mycorrhizal mycelium provides an increased surface area for nutrient uptake and improves the nutrient acquisition of the host plants. The hyphae are also able to penetrate small microsites that are inaccessible to the much coarser plant roots. Active uptake of poorly mobile nutrients such as phosphorus leads to the formation of nutrient-depleted volumes of soil around roots, which the mycorrhizal hyphae are able to bridge, supplying nutrients from more distant soil. In some ectomycorrhizal fungal species, differentiated structures such as fungal rhizomorphs facilitate translocation of nutrients over long distances.

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

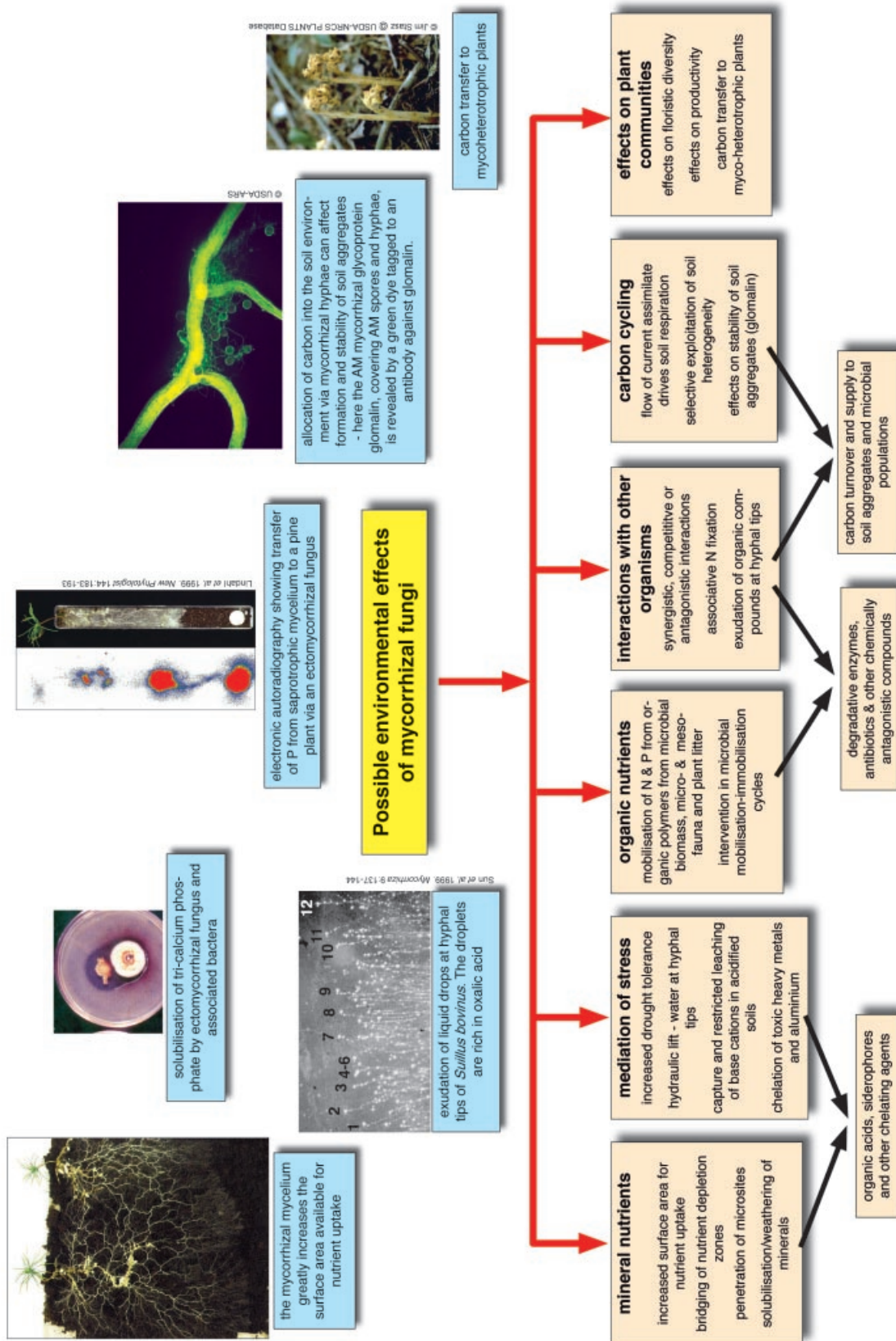


Fig 1 Possible environmental effects of mycorrhizal fungi include effects on mineral nutrient uptake and availability, mediation of different types of plant stress, mobilisation of organic nutrients, interactions with other organisms, effects on carbon cycling and effects on plant communities. These are illustrated by examples, but each effect does not necessarily apply to all types of mycorrhizal fungi (Figures from *Mycorrhiza* and *New Phytologist* appear courtesy of Springer and Blackwell respectively).

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). 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-solubilising microorganisms (see interactions with other organisms – below). 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-Jonnarth *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. Irrespective of whether these pores are actually formed by mycorrhizal hyphae or not, 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 is 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.*, 2004) 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 mobilise significant amounts of P and K from the minerals apatite and biotite and probably plays a significant role in transporting these to trees.

Nutrient mobilisation from organic substrates

During recent years increasing emphasis has been placed upon the ability of mycorrhizal fungi to mobilise N and P from organic polymers (Read, 1991). The idea that the supply of N and P to plants is totally dependent on the nutrient mobilising activities of decomposers has been increasingly challenged by observations of the ability of mycorrhizal fungi to sequester N and P from a range of biologically relevant substrates such as pollen, dead nematodes and soil micro-arthropods as well as saprotrophic mycelia (Lindahl *et al.*, 1999; Read & Perez-Moreno, 2003). Intervention by different groups of mycorrhizal fungi in microbial mobilisation-immobilisation cycles, resulting in mobilisation of N and P from microbial, micro-faunal, meso-faunal and plant litter, has thus enabled the development of distinctive plant communities along altitudinal or latitudinal gradients. This is particularly evident in the ericoid mycorrhizal fungi colonising heathland ecosystems and in ectomycorrhizal fungi colonising 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. 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. 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 mobilise 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 microorganisms.

Effects on carbon cycling

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 & 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 Högberg *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 solubilisation of mineral substrates 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 microorganisms associated with the arbuscular mycorrhizal mycelium (Johansson *et al.*, 2004) (see - Interactions with other organisms). Although allocation of carbon may be increased in ectomycorrhizal mycelia colonising patches of decomposing plant litter, Leake *et al.* (2001) showed that allocation of carbon to 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 & Fitter, 1999) question the significance of the process, or advocate a more mycogenic viewpoint (Fitter *et al.*, 2000). Finlay & 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 Högberg *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 - Effects on plant communities and ecosystems).

Effects on plant communities and ecosystems

The floristic diversity and productivity of re-constructed 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 belowground 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 addition of new fungal species leads to increases in the survival and vigour of more plant species that are responsive to mycorrhizal colonisation then there may be a positive feedback on the mycorrhizal fungi, leading to more efficient resource utilisation and increases in overall productivity. The ecological significance of the possible transfer of photosynthetically derived carbon between different plant species is still questioned by some scientists (Robinson & Fitter, 1999) 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 & Bruns, 1997; McKendrick *et al.*, 2000).

Mediation of plant responses to stress

Although mycorrhizal fungi are themselves affected by environmental perturbations, they also have the ability to mediate the responses of plants to different types of environmental stress. 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). The effects of mycorrhizal fungi on plant responses to drought stress have been discussed by a number of authors (Smith & Read, 1997) 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. Recent experiments by Quiereta *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 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.

Interactions with other microorganisms

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 microorganisms, 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. Bacteria with potential to fix nitrogen have been discovered growing endosymbiotically within arbuscular mycorrhizal hyphae, as well as in association with tuberculate roots of ectomycorrhizal plants. Obviously such tripartite symbioses would be of significance in nitrogen-limited environments. Exudation and re-absorption 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 exchange of nutrients and carbon compounds with the adjacent soil environment and its other microorganisms. The extent to which interactions between mycorrhizal mycelia and other microorganisms 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 mobilised by the activities of other organisms.

Conclusions

The role of symbiotic mycorrhizal fungi in shaping terrestrial ecosystems is fundamental. Many of the characteristic plant communities that dominate the major terrestrial biomes of the world do so today because selection has favoured different types of symbiotic associations that are adapted to the prevailing suites of soil, vegetation and climatic conditions characterising these different environments. As we learn more about the diversity of the fungi involved and the specificity of their relationships with different plants, so we improve our understanding of the functional diversity of mycorrhizal symbioses. Old models, based solely on the mineral nutrition of individual plants, are giving way to new models 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 pre-requisite for future, sustainable management of terrestrial ecosystems.

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