Mineral transformations by mycorrhizal fungi

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Mineral Transformations by Mycorrhizal Fungi

Elena Martino & Silvia Perotto
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Abstract

This review addresses the significance and the mechanisms of mineral weathering by mycorrhizal fungi, and the role of this process in plant nutrition and protection from metal toxicity. The fact that mycorrhizal mycelia may actively release nutrients from mineral particles through weathering is raising an increasing interest and the uptake of mineral-derived nutrients by the host plants has been reported. Both chemical dissolution (protonation, chelation) and physical mechanisms (high hyphal pressures) are involved in the weathering process. Mineral solubilization can result in the release of the associated toxic metals. Organic acid exudation and metal complexation may represent a host plant protection mechanism.

Keywords: metal toxicity, mineral weathering, mycorrhizal fungi.

WEATHERING BY MYCORRHIZAL FUNGI: GENERAL INTRODUCTION

About a decade ago, Jongmans et al. (1997) found tunnels inside mineral grains that were likely formed by hyphae of ectomycorrhizal (ECM) fungi. This observation implied that mycorrhizal fungi were able to dissolve mineral grains. This finding raised several questions on the ecology of these microorganisms that started to be called “rock-eating” fungi (Van Schöll et al. 2008). Although it is well accepted that mycorrhiza assist plants in the acquisition of mineral nutrients already in the soil solution, the fact 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 is raising increasing interest (Landeweert et al. 2001). Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. "Mineral dissolution by ectomycorrhiza”. In Fungi in biogeochemical cycles, Edited by: Gadd, G M. 681–717. Cambridge: Cambridge University Press. ; Finlay and Rosling 2006 Finlay, R D and Rosling, A. 2006. “Integrated nutrient cycles in forest ecosystems, the role of ectomycorrhizal fungi”. In Fungi in biogeochemical cycles, Edited by: Gadd, G M. 28–50. Cambridge: Cambridge University Press. ; Wallander 2006 Wallander, H. 2006. Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical mycelium. J Exp Bot, 59: 1115–1126. ).

Fungi play a central role in many microbiological and ecological processes, influencing soil fertility, cycling of minerals and organic matter, as well as plant health and nutrition (Finlay 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. )

Seven different types of mycorrhizal symbioses have been distinguished on the basis of morphological characteristics and of the fungal and plant species involved (Finlay 2008 Finlay, RD. 2008. Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional

. Fungi are heterotrophs and require external sources of organic carbon for energy and cellular synthesis. They have adopted three different trophic strategies to obtain this carbon, occurring as saprotrrophs, necrotrophs, and biotrophs. Mycorrhizal symbiosis is the most ancient and widespread form of fungal symbiosis with plant roots (Smith and Read 2008 Smith, S E and Read, D J. 2008. Mycorrhizal symbiosis, 3rd edn, Academic Press.). More than 80% of plant roots form mycorrhiza with soil fungi, and in boreal and temperate regions, as much as 90% of the woody tree root tips are covered by ectomycorrhizal fungal sheaths (as much as 600 km of fungal mycelium per kg of soil) (Ek 1997 Ek, H. 1997. The influence of nitrogen fertilization on the carbon economy of Paxillus involutus in ectomycorrhizal association with Betula pendula. New Phytol, 135: 133–142.; Read and Perez-Moreno 2003 Read, D J and Perez-Moreno, J. 2003. Mycorrhizas and nutrient cycling in ecosystems—A journey towards relevance?. New Phytol, 157: 475–492.). Thus, virtually all nutrients taken up by trees pass through these fungi, and in return, the fungi receive 20%–30% of the carbon fixed during photosynthesis by the host plants (Högberg and Högberg 2002 Högberg, M N and Högberg, P. 2002. Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. New Phytol, 154: 791–795.).

*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 Redecker, D, Kodner, R and Graham, L E. 2000. Glomalean fungi from the Ordovician. *Science*, 289: 1920–1921. ). *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-impoverished areas, 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 (i.e., *Rhizoscyphus ericae*, *Oidiodendron maius*), which penetrate the cell walls of roots and form coiled structures within each cell without penetrating the host plasma membrane (Finlay 2008 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.

Recent evidence suggests that basidiomycetes belonging to clade B Sebacinales are also common ericoid mycorrhizal fungi (Selosse et al. 2007 Selosse, M-A, Setaro, S, Glatard, F, Richard, F, Urcelay, C and Weiss, M. 2007. Sebacinales are common mycorrhizal associates of Ericaceae. *New Phytol*, 174: 864–878. ). Many long-lived herbaceous and woody plants 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 Taylor, A FS and Alexander, I. 2005. The ectomycorrhizal symbiosis: life in the real world. *Mycologist*, 19: 102–112. ). Although this represents only a small fraction of the total number of terrestrial plants, these species often form the dominant components of forest ecosystems and occupy 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 Caesalpinioideae in tropical forests. The fungi do not penetrate the host cells, and the symbiosis is characterized by the presence of a fungal mantle 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 host plant. 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 (Finlay 2008 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. ). 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 Wallander, H, Nilsson, L O, Hagerberg, D and Bååth, E. 2001. Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. *New Phytol*, 151: 752–760. ).

The hyphae that grow outward from the mantle into the surrounding soil are very efficient nutrient scavengers, owing to their high surface area:mass ratio and their ability to penetrate microsites that are inaccessible to plant roots. The expanding mycorrhizal mycelium exploits a larger soil volume than do roots alone (Landeweert et al. 2001 Landeweert, R, Hoffland, E, Finlay, R D, Kuypers, T W and Van Breemen, N. 2001. Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. *Trends Ecol Evol*, 16: 248–254. ). Four other types of mycorrhiza can be recognized: the *orchid mycorrhiza* (Bidartondo et al. 2002 Bidartondo, M I, Redecker, D, Hijri, I, Wiemken, A.

The ability of some ericoid mycorrhizal fungi (mycorrhizal endophytes of Woolsia pungens (Epacridaceae), Hymenoscyphus ericae and Oidiodendron maius) to dissolve hydroxyapatite, and Zn oxide and phosphate have also been reported (Van Leerdam et al. 2001 Van Leerdam, D M, Williams, P A and Cairney, J WG. 2001. Phosphate-solubilising abilities of ericoid mycorrhizal endophytes of Woolsia pungens (Epacridaceae). Austr J Bot, 49: 75–80.; Martino et al. 2003a Martino, E, Perotto, S, Parsons, R and Gadd, G M. 2003a. Solubilization of insoluble inorganic zinc compounds by ericoid mycorrhizal fungi derived from heavy metal polluted sites. Soil Biol Biochem, 35: 131–141.). For dissolution of Ca sulphate (gypsum) and different forms of Ca phosphate, it was found that solubilization was significantly affected by the supply of the supplied N.

**THE MECHANISMS INVOLVED IN WEATHERING BY MYCORRHIZAL FUNGI**


Mycorrhizal fungi, as well as other fungi, can dissolve minerals in the course of the so-called “heterotrophic leaching” by employing several mechanisms, including protonation (acidolysis), chelation (complexolysis) and metal accumulation, where the biomass functions as a metal sink.
Chemical Dissolution Mechanisms


Podzols are characterised by four distinct soil horizons: a dark-coloured organic (O) horizon underlain by a white/ash-coloured eluvial (E) horizon, overlying a usually dark-coloured illuvial (B) horizon on top of the unaltered parent (C) material. These tunnels had smooth and parallel-oriented walls with a constant diameter (3–10 μm) and rounded ends, which distinguished them from (coalesced) etch pits and cracks caused by abiotic weathering processes known so far (Hoffland et al. 2002 Hoffland, E, Giesler, R, Jongmans, T and van Breemen, N. 2002. Increasing feldspar tunneling by fungi across a North Sweden podzol chronosequence. *Ecosystems*, 5: 11–22.).

Because (1) the size and shape of the tunnels perfectly fitted hyphae, (2) some tunnels were actually colonised by hyphae and (3) hyphae were seen to penetrate mineral grains, a fungal role for rock weathering seemed likely (Van Schöll et al. 2008 Van Schöll, L, Kuyper, T W, Smits, M M, Landeweert, R, Hoffland, E and van Breemen, N. 2008. Rock-eating mycorrhizas: their role in plant nutrition and biogeochemical cycles. *Plant Soil*, 303: 35–47.). Jongmans, A G, van Breemen, N, Lundström, U S, van Hees, P AW, Finlay, R D, Srinivasan, M, Unestam, T, Giesler, R, Melkerud, P-A and Olsson, M. 1997. Rock-eating fungi. *Nature*, 389: 682–683. further hypothesised that such tunnels were formed through LMWOAs exuded at hyphal tips. The term rock-eating fungi therefore refers to fungi that have the capacity to exude LMWOAs to an extent that mineral weathering rates are significantly increased. 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 Schöll et al. 2008 Van Schöll, L, Kuyper, T W, Smits, M M, Landeweert, R, Hoffland, E and van Breemen, N. 2008. Rock-eating mycorrhizas: their role in plant nutrition and biogeochemical cycles. *Plant Soil*, 303: 35–47.).

nutrition?}. Biogeochemistry, 49: 53–67. also hypothesize that these pores were formed by complex-forming LMWOAs exuded by or formed in association with mycorrhizal fungi. They provided direct evidence that the mycelium is able to penetrate, and most probably create, microsites which are inaccessible to plant roots and isolated from bulk soil solution phenomena. Moreover, Van Breemen et al. (2000b) Van Breemen, N, Lundström, U S and Jongmans, A G. 2000b. Do plants drive podzolization via rock-eating mycorrhizal fungi?. Geoderma, 94: 163–171. presented evidence that such rock-eating mycorrhizal fungi help to mobilize Al and Si from weatherable minerals of the E horizon, and transport these elements into the O horizon from where they may percolate downwards.

They hypothesized that weathering products mobilized by ectomycorrhizal fungai in the E horizon are transported through hyphae towards the hyphal mantles of mycorrhizal roots, most of which are probably in the O horizon. Most of the P and an appreciable part of other nutrients derived by mineral weathering (notably K, Mg and Ca) are probably transferred to the plant, bypassing the soil solution with often toxic concentration of Al\(^{3+}\) from acid rain, and bypassing competition for nutrient uptake by other organisms. It is highly unlikely, however, that much of the Si and the (organically complexed) Al and Fe is taken up by the tree roots. These elements will therefore be either exuded from the hypha near the root, or stored inside the hypha, to be released when the hypha die. Part of the soluble complexes may percolate downward, causing relatively high fluxes of Al, Fe and Si from the O into the E horizon. Mean annual fluxes of Al, Fe and Si at the O/E boundary and the E/B boundary, estimated from hydrological data and soil solution concentrations (Giesler et al. 2000 Giesler, R, Ilvesniemi, H, Nyberg, L, Van Hees, P AW, Starr, M, Bishop, K, Kareinen, T and Lundström, U S. 2000. Distribution and mobilization of Al, Fe and Si in three podzolic soil profiles in relation to the humus layer. Geoderma, 94: 249–263. ) confirm this hypothesis.

In this hypothesis, the release of dissolved Si and (organically complexed) Al in the O horizon is an integral part of the process of podzolization itself, which in this case appears to be driven by plant-ectomycorrhizal associations in search of nutrients (Van Breemen et al. 2000b Van Breemen, N, Lundström, U S and Jongmans, A G. 2000b. Do plants drive podzolization via rock-eating mycorrhizal fungi?. Geoderma, 94: 163–171. ).


It is not clear if ericoid endomycorrhiza play a role in the podzolization commonly found under ericaceous plants. Ericoid fungi can also produce high amounts of LMWOAs (Martino et al. 2003a Martino, E, Perotto, S, Parsons, R and Gadd, G M. 2003a. Solubilization of insoluble inorganic zinc compounds by ericoid mycorrhizal fungi derived from heavy metal polluted sites. Soil Biol
Biochem, 35: 133–141.), and may thereby contribute to tunnel formation. It seems unlikely, however, that ericoid mycorrhizal fungi are (solely) responsible for tunnel formation, as tunnels were found in sites with no ericoid mycorrhizal plants, and where they are unlikely to have grown, considering the rapid establishment of the productivity gradient following deglaciation (Giesler et al. 1998 Giesler, R, Högberg, M and Högberg, P. 1998. Soil chemistry and plants in Fennoscandian boreal forest as exemplified by a local gradient. Ecology, 79: 119–137.). ECM fungi could therefore have been responsible or co-responsible for tunnel formation.

The contribution of ECM mineral tunnelling to total weathering was quantified via image analysis in soil thin sections (Smits et al. 2005 Smits, M M, Hoffland, E and Van Breemen, N. 2005. Contribution of mineral tunneling to total feldspar weathering. Geoderma, 125: 59–69.) which were taken from a North Michigan dune chronosequence. Although it was initially postulated that mineral tunnelling by fungal hyphae might contribute substantially to weathering, measurements by Smits and colleagues (2005) Smits, M M, Hoffland, E and Van Breemen, N. 2005. Contribution of mineral tunneling to total feldspar weathering. Geoderma, 125: 59–69. showed that the contribution to total feldspar weathering is less than 1%, suggesting that the weathering of mineral surfaces is quantitatively more important. Output from an improved version of the model (Smits et al. 2008 Smits, M M, Bonneville, S, Haward, S and Leake, J R. 2008. Ectomycorrhizal weathering, a matter of scale?. Mineral Magaz, 72: 131–134.) indicated that surface weathering is an order of magnitude higher than weathering through tunnelling.


Their mycelial networks strongly attach to mineral surfaces, and weathering processes are likely to be initiated and to proceed directly at the mineral-fungal interface. This interface may therefore play a far greater role in initiating and controlling the weathering rates than previously thought. There is clearly a large potential for interaction between mycorrhizal hyphae and mineral surfaces and researches by Rosling et al. (2003) Rosling, A, Landeweert, R, Lindahl, B, Larsson, K H, Kuyper, T W, Taylor, A FS and Finlay, R. 2003. Vertical distribution of ectomycorrhizal root tips in a podzol soil profile. New Phytol, 159: 775–783. 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. In a soil column study by van Hees et al. (2004) Van Hees, P AW, Jones, D L, Jentschke, G and Godbold, D L. 2004. Mobilization of aluminium, iron and silicon by Picea abies and ectomycorrhizas in a forest soil. Eur J Soil Sci, 55: 101–111., the presence of young Picea abies trees and the ectomycorrhizal fungus P. involutus increased Al and Si mobilization 1.5–2 times as compared to non-planted

       Reduced availability of K, Ca and Mg in mineral tunnelling by ECM fungi could lead to increased Al and Si mobilization.
controls, despite similar pH values. The possible enhancement of Al and Si mobilization by hyphae was mainly attributed to surface dissolution.


The fungal species used were P. involutus, which is commonly associated with organic soil horizons; Piloderma croceum (also known as Piloderma fallax), which has been found in both organic and mineral horizons; and Hebeloma longicaudum which has been found in the mineral horizon (Laiho 1970 Laiho, O. 1970. Paxillus involutus as a mycorrhizal symbiont of forest trees. Acta For Fenn, 106: 5–72.; Landeweert et al. 2003 Landeweert, R, Leeflang, P, Kuyper, T W.
Hoffland, E, Rosling, A, Wernars, K and Smit, E. 2003. Molecular identification of ectomycorrhizal mycelium in soil horizons. *Appl Environ Microbiol*, 69: 327–333. Concentrations of all dicarboxylic LMWOA in the rooting medium were measured. Nonmycorrhizal seedlings released predominantly malonate. Colonization with *Hebeloma longicaudum* decreased the amount of organic anions exuded, whereas *P. involutus* and *P. croceum* increased the concentration of oxalate but not the total amount of LMWOA. Phosphorus deficiency increased the concentration of LMWOA by nonmycorrhizal and ECM seedlings. Magnesium deficiency increased the concentration of oxalate by nonmycorrhizal and ECM seedlings, but not the concentration of total LMWOA. K limitation did not influence the exudation of LMWOAs by nonmycorrhizal and ECM seedlings.

The authors concluded that ectomycorrhizal fungi did not increase the total concentration of LMWOA compared with nonmycorrhizal seedlings but, depending on the fungal species, they affected the type of LMWOA found. The fact that P limitation significantly increased the total concentrations of LMWOAs is in contrast with the results reported by Van Hees et al. (2003) Van Hees, P AW, Godbold, D L, Jentschke, G and Jones, D L. 2003. Impact of ectomycorrhizas on the concentration and biodegradation of simple organic acids in a forest soil. *Eur J Soil Sci*, 54: 697–706. who did not find any effect of omitting P from the nutrient solution. In the latter study anyway there was a very high turnover of organic anions, as evidenced from the low concentrations found, and this may have obscured treatment effects.

Van Schöll et al. (2006a) Van Schöll, L, Hoffland, E and Van Breemen, N. 2006a. Organic anion exudation by ectomycorrhizal fungi and *Pinus sylvestris* in response to nutrient deficiencies. *New Phytol*, 170: 153–163. also showed that *P. involutus* grown in pure culture responded differently to low nutrient supply compared with symbiotic growth. Under P deficiency, the concentration of malonate, but not oxalate, exuded by *P. involutus* in pure culture was significantly increased compared with complete nutrition or limited N, Mg or K. Also, acidification was stronger with low P supply than with low N, Mg K or complete nutrient supply. These findings can explain the high phosphate-solubilizing activity of *P. involutus* found by Lapeyrie et al. (1991) Lapeyrie, F, Ranger, J and Vairelles, D. 1991. Phosphate-solubilizing activity of ectomycorrhizal fungi in vitro. *Can J Bot*, 69: 342–346.

These results show the potential of trees and ECM fungi to manipulate their environment and to respond to nutrient deficiencies by increasing the exudation of LMWOAs with high weathering ability.


All plants except the grasses use the Strategy I response to solubilize and transport iron into roots when iron is limiting: a proton pump acidifies the rhizosphere, a ferric chelate reductase converts Fe(III)-chelates to Fe(II) and a Fe(II) transporter moves iron into cells. Grasses produce small molecules with high affinity for ferric iron called phytosiderophores (PSs): PS are secreted into the
rhizosphere where they chelate and help to solubilize Fe(III). The Fe(III)–PS complex is then taken up into root cells through the action of Yellow Stripe1 (YS1) proteins (Walker and Connolly 2008). To have access to the soil iron reservoir, also ECM fungi produce siderophore (Landeweert et al. 2001). Linking plants to rocks: ectomycorrhizal fungi mobilize nutrients from minerals. (Walker, E L and Connolly, E L. 2008. Time to pump iron: iron-deficiency-signaling mechanisms of higher plants. Current Op Pl Biol., 11: 530–535.).

Ericoid mycorrhizal fungi release ferricrocin or fusigen as the main siderophores. Ferricrocin was also shown to be produced by the ectomycorrhizal fungi Cenococcum geophilum and Hebeloma crustuliniforme. Arbuscular mycorrhizal fungi are reported to enhance Fe-uptake rates of associated host plants, which can be taken as an indication that mycorrhizal siderophores of a yet unknown structure may be involved.

Mycorrhizal fungi of orchids were shown to produce as the main siderophores, both well known ferrichrome-type siderophores or the novel linear trishydroxamate basidiochrome (Haselwandter 2008). Physical Disintegration Mechanisms

A very interesting work was recently published by Bonneville and collaborators (2009) Bonneville, S, Smits, M M, Brown, A, Harrington, J, Leake, J R, Brydson, R and Benning, L G. 2009. Plant-driven fungal weathering: Early stages of mineral alteration at the nanometer scale. Geology, 37: 615–618. Their findings indicate that fungal weathering is predominantly occurring at the hypha-mineral interface with an early mechanical forcing acting in concert with later chemical alteration of micaceous minerals. They reported for the first time, in situ observations at the nanometer scale of the early stages of weathering of biotite by an ectomycorrhizal fungus, P. involutus, grown under axenic and controlled temperature, humidity, and photoperiod conditions in symbiosis with a boreal pine tree, P. sylvestris.

This approach recreates the essential symbiotic relationship between the tree and the mycorrhizal fungus under the typical unsaturated conditions found in soils, while excluding all other potential weathering pathways (i.e., soil pore water and other soil microorganisms). Ultramicroscopic and spectroscopic analysis of the fungus-biotite interfaces revealed intimate fungal-mineral attachment, biomechanical forcing, altered interlayer spacings, substantial depletion of potassium (~50 nm depth), oxidation of the biotite Fe(II), and the formation of vermiculite and clusters of Fe(III) oxides. The study by Bonneville and collaborators (2009) Bonneville, S, Smits, M M, Brown, A, Harrington, J, Leake, J R, Brydson, R and Benning, L G. 2009. Plant-driven fungal weathering: Early stages of mineral alteration at the nanometer scale. Geology, 37: 615–618. demonstrated the biomechanical-chemical alteration interplay at the fungus-biotite interface at the nanometer scale.

They specifically observed that the weathering process was initiated by physical distortion of the lattice structure of biotite within 1 μm of the attached fungal hypha. Only subsequently did the distorted volume become chemically altered through dissolution and oxidation reactions that lead to mineral neoformation. The lattice distortion at the hyphae-biotite contact was likely a consequence of fungal attachment and growth across the biotite surface. Fungal attachment to mineral surfaces usually occurs via class I hydrophobins, which are ubiquitous hyphal surface proteins of basidiomycete fungi (Wosten et al. 1993; Wosten, H AB, De Vries, O MH and Wessels, J GH. 1993. Interfacial self-assembly of a fungal hydrophobin into a hydrophobic rodlet layer. The Plant Cell, 5: 1059–1070.);


Cation uptake by fungi is usually achieved by proton pumps, which acidify their near environment (Lian et al. 2007 Lian, B, Wang, B, Pan, M, Liu, C and Teng, H H. 2007. Microbial release of potassium from K-bearing minerals by thermophilic fungus Aspergillus fumigatus. Geoch Cosmoch Acta, 72: 87–98.). Protons diffusing into the biotite substitute the potassium in the interlayer and ultimately cause the partial transformation of biotite into potassium-free vermiculite adjacent to the hypha. The role of the fungi in the oxidation of Fe(II), and especially whether this is an active biological process or a secondary effect of the fungal weathering of biotite, is unclear. Microcavities formed during the very early stages of contact may facilitate the penetration of oxidizing compounds or exudates into the biotite structure, possibly causing Fe(II) oxidation. The formation of vermiculite and/or Fe(III) oxide subdomains is commonly reported to be the first step in biotite weathering under abiotic acidic conditions in liquid media (Murakami et al. 2003 Murakami, T, Utsunomiya, S, Yokoyama, T and Kasama, T. 2003. Biotite dissolution processes and mechanisms in the laboratory and in nature: Early stage weathering environment and vermiculitization. Am Mineral, 88: 377–386.).

liquid-free medium, that such secondary minerals can also be formed in relatively short periods at the interface between living fungal hyphae and biotite. The mechanism documented in their study is a significant advance on previous simplistic concepts of biotic weathering relying solely on the effects of fungal exudates (i.e., organic acids, ligands, and siderophores) released into the soil pore water. Those exudates are thought to consist of aqueous ligands for elements of biological interest, for example oxalic acid, which strongly binds iron in solution; hence, thermodynamically favoring the dissolution of iron-bearing minerals.

Through weakening of the biotite lattice structure and the formation of microcavities (increase of mineral surface area), the mechanical forcing of the mineral surface by the hypha greatly enhances the chemical weathering rates, which in turn will promote further physical breakdown of the mineral. This mechanical-chemical weathering interplay at the hypha-mineral interface therefore provides the ECM fungus with a hitherto unsuspected means to weather rocks and to actively acquire essential nutrients for plant growth in return for photosynthate carbon. Ultimately these processes form soils. Given the ubiquitous occurrence of ECM fungi in symbiotic association in boreal and temperate forests, these findings have major implications for our understanding of the link between biologically induced rock weathering and the carbon cycle at the global scale (Bonneville et al. 2009 Bonneville, S, Smits, M M, Brown, A, Harrington, J, Leake, J R, Brydson, R and Benning, L G. 2009. Plant-driven fungal weathering: Early stages of mineral alteration at the nanometer scale. Geology, 37: 615–618.).

MYCORRHIZAL FUNGAL WEATHERING AND PLANT NUTRITION


*Phosphorus* is an essential element for plant and microbial nutrition and can only be assimilated as soluble phosphate species. However, in the soil, a large proportion of the phosphorus pool is poorly soluble, which means that the mechanisms by which fungi and plants obtain phosphate are of major significance. Plants have evolved a range of adaptive morphological, biochemical and symbiotic strategies that increase the acquisition of Pi and/or improve the efficiency of internal utilization of Pi. Among these adaptations is an increase of root hair formation and the formation of cluster roots by some species (López-Bucio et al. 2003 López-Bucio, J, Cruz-Ramírez, A and Herrera-Estrella, L. 2003. The role of nutrient availability in regulating root architecture. *Current Op Pl Biol*, 6: 280–287.). Cluster roots comprise bottlebrush-like clusters of rootlets of determinate development arising along the lateral roots. They have been found in a range of plant species adapted to habitats of extremely low soil fertility (members of the Proteaceae, Cyperaceae and Restionaceae families).

These combine a high density of determinate lateral roots in a localised soil volume for gathering Pi, with a synchronised release of organic acids and acid phosphatases that increase the availability of Pi in the immediate vicinity of these roots. Most agricultural, heath and forest species that form cluster roots do not appear to become colonised by mycorrhizal fungi. Formation of cluster roots or mycorrhizal colonisation therefore appears to be alternative strategies for improving Pi acquisition in most species (López-Bucio et al. 2003 López-Bucio, J, Cruz-Ramírez, A and Herrera-Estrella, L. 2003. The role of nutrient availability in regulating root architecture. *Current Op Pl Biol*, 6: 280–


Most forest ecosystems are considered to be N-limited. For a wide range of fungi, oxalate production is stimulated by low N availability (Dutton and Evans 1996 Dutton, M V and Evans, C S. 1996. Oxalate production by fungi: Its role in pathogenicity and ecology in the soil environment. Can J Microbio, 42: 881–895.). P. involutus increased the concentration of oxalate in response to N
limitation when grown in pure culture (Van Schöll et al. 2006a Van Schöll, L, Hoffland, E and Van Breemen, N. 2006a. Organic anion exudation by ectomycorrhizal fungi and Pinus sylvestris in response to nutrient deficiencies. New Phytol, 170: 153–163. ). On the other hand, in areas with high levels of N deposition, Mg, K and P can become limiting (Tamm et al. 1999 Tamm, C O, Aronsson, A, Popovic, B and Flower Ellis, J. 1999. Optimum nutrition and nitrogen saturation in Scots pine stands. Studia Forest Sue, 1999: 1–126. ), and enhanced weathering of mineral grains by increased exudation of LMWOAs can become an important mechanism for nutrient supply and forest growth. It is broadly held that mycorrhizas are relatively unimportant in disturbed and N-limited soils dominated by fast-growing species (e.g., many species belonging to Brassicaceae and Chenopodiaceae), which flourish on disturbed sites and complete their life cycle rapidly; these species exhibit no special strategies other than rapid growth of roots, and formation of root hairs (Lambers et al. 2008 Lambers, H, Raven, J A, Shaver, G R and Smith, S E. 2008. Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol, 23: 95–103. ).

Although phosphorus becomes increasingly limiting in ancient soils, as it gradually disappears through leaching and erosion, nitrogen tends to limit plant productivity on young soils. As already discussed, adaptations to N- and P-limited conditions include mycorrhizas and cluster roots. Mycorrhizas ‘scavenge’ P from solution or ‘mine’ insoluble organic N. Cluster roots function in severely P-impoverished landscapes, ‘mining’ P fixed as insoluble inorganic phosphates. The ‘scavenging’ and ‘mining’ strategies of mycorrhizal species without and non-mycorrhizal species with cluster roots, respectively, allow functioning on soils that differ markedly in P availability (Lambers et al. 2008 Lambers, H, Raven, J A, Shaver, G R and Smith, S E. 2008. Plant nutrient-acquisition strategies change with soil age. Trends Ecol Evol, 23: 95–103. ). Anyway, the cluster root strategy is not restricted to ancient landscapes, but also occurs in many species in North America and Europe, where it tends to increase in importance in either relatively acidic or calcareous soils, where P is immobilized. There are thus many ecosystems where plants with all the possible N- and P-acquisition strategies coexist.


Van Schöll et al. (2006b) Van Schöll, L, Smits, M M and Hoffland, E. 2006b. Ectomycorrhizal weathering of the soil minerals muscovite and hornblende. New Phytol, 171: 805–814. determined the effect of ECM fungi on K and Mg availability through mineral weathering. Non-mycorrhizal and ECM tree seedlings were grown in pots with muscovite as the only K source or hornblende as
the only Mg source. Weathering of muscovite was increased by tree seedlings by a factor 1.7, and was increased even further to a factor of 3.3 when tree seedlings were colonised by *P. involutus*. However, colonisation of the tree seedlings by the ECM fungi *Suillus bovinus* or *P. croceum* did not have an additional effect. Only seedlings colonised by *P. involutus* significantly increased oxalate exudation under K deficiency.

This K deficiency-induced oxalate exudation could explain the enhanced weathering of muscovite. Therefore, the increased ECM mineral weathering in response to nutrient deficiency could be a species specific response. The *P. involutus*-mediated mobilization of K from muscovite resulted in increased K content of root plus adhering hyphae, but not of shoots. Under natural conditions, ectomycorrhizal fungi generally enhance shoot growth of their host tree, and it may be expected that mobilized K will be transported to the shoot. By retaining K in the hyphae, the K is protected against leaching (Van Schöll et al. 2006b).

Decreased leaching of K and other base cations under ectomycorrhizal seedlings compared with nonmycorrhizal seedlings has been shown by Jonnarth et al. (2003). After decomposition, the K retained in the roots and hyphae will become available for uptake. The ecosystem influx of bioavailable K will be especially important in forests where K is growth-limiting, because of a combination of high biomass removal and decreasing concentrations of K in the soil solution as a result of continuous acidification and leaching (Übel and Heinsdorf 1997 übel, E and Heinsdorf, D. 1997. Results of long-term K and Mg fertilizer experiments in afforestation. For Ecol Manag, 91: 47–52. ; Jönsson et al. 2003 Jönsson, U, Rosengren, U, Thelin, G and Nihlgard, B. 2003. Acidification-induced chemical changes in coniferous forest soils in southern Sweden 1988–99. Environ Poll, 123: 75–83. ).

The depletion of calcium in forest ecosystems is thought to be a consequence of acidic deposition and to be at present restricting the recovery of forest and aquatic systems (Huntington 2000 Huntington, TG. 2000. The potential for calcium depletion in forest ecosystems of southeastern United States: Review and analysis. Glob Biogeochem Cycles, 14: 623–638. ) now that acidic deposition itself is declining (Blum et al. 2002 Blum, J D, Klaue, A, Nezat, C A, Driscoll, C T, Johnson, C E, Siccama, T G, Eagar, C, Fahey, T J and Likens, G E. 2002. Mycorrhizal weathering of apatite as important calcium source in base-poor forest ecosystems. Nature, 417: 729–731. ). This depletion of calcium has been inferred from studies (Likens et al. 1996 Likens, G E, Driscoll, C T and Buso, D C. 1996. Long-term effects of acid rain: Response and recovery of a forest ecosystem. Science, 272: 244–246. ) showing that sources of calcium in forest ecosystems—namely, atmospheric deposition and mineral weathering of silicate rocks such as plagioclase, a calcium-sodium silicate—do not match calcium outputs observed in forest streams. It is therefore thought that calcium is being lost from exchangeable and organically bound calcium in forest soils (Blum et al. 2002).

Blum et al. (2002) Blum, J D, Klaue, A, Nezat, C A, Driscoll, C T, Johnson, C E, Siccama, T G, Eagar, C, Fahey, T J and Likens, G E. 2002. Mycorrhizal weathering of apatite as important calcium source in base-poor forest ecosystems. *Nature*, 417: 729–731. showed that the dissolution of apatite (calcium phosphate) represents a source of calcium that is comparable in size to known inputs from atmospheric sources and silicate weathering. Moreover, apatite-derived calcium was utilized largely by ECM tree species, suggesting that mycorrhiza may weather apatite and absorb the released ions directly, without the ions entering the exchangeable soil pool. Therefore, it seems that apatite weathering can compensate for some of the calcium lost from base-poor ecosystems, and should be considered when estimating soil acidification impacts and calcium cycling (Blum et al. 2002 Blum, J D, Klaue, A, Nezat, C A, Driscoll, C T, Johnson, C E, Siccama, T G, Eagar, C,

It remains, however, uncertain if this response is regulated by plant exudation or by fungal exudation when both organisms are grown in symbiosis. The exudation of oxalate and malonate by \textit{P. sylvestris} seedlings and \textit{P. involutus} in response to nutrient deficiencies differed strongly when grown either in pure culture or in symbiosis (Van Schöll et al. 2006a Van Schöll, L, Hoffland, E and Van Breemen, N. 2006a. Organic anion exudation by ectomycorrhizal fungi and \textit{Pinus sylvestris} in response to nutrient deficiencies. \textit{New Phytol}, 170: 153–163. ). Therefore only experiments with both symbiotic partners can yield ecological realism (Van Schöll et al. 2008).

**ECOLOGICAL IMPORTANCE OF WEATHERING BY MYCORRHIZAL FUNGI: WEATHERING IN THE MYCORRHIZOSPHERE**

Symbiotic mycorrhizal associations between plants and fungi occur, almost ubiquitously, in a wide range of terrestrial ecosystems (Finlay 2008 Finlay, RD. 2008. Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical mycelium. \textit{J Exp Bot}, 59: 1115–1126. ). 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 well accepted that mycorrhizal fungi 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 (Smith and Read 2008 Smith, S E and Read, D J. 2008. \textit{Mycorrhizal symbiosis}, 3rd edn, Academic Press. ).

By virtue of their small diameter the hyphae are also able to penetrate soil microsites which are inaccessible to plant roots. Examples of improved vegetative growth and nutrient status of individual plants following mycorrhizal inoculation abound (Smith and Read 2008 Smith, S E and Read, D J. 2008. \textit{Mycorrhizal symbiosis}, 3rd edn, Academic Press. ), 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 (Finlay 2008 Finlay, RD. 2008. Ecological aspects of mycorrhizal symbiosis: with special emphasis on the functional diversity of interactions involving the extraradical mycelium. \textit{J Exp Bot}, 59: 1115–1126. ).


Interactions of fungi with toxic metals and radionuclides is of economic and environmental significance (metals can be considered conservative because they are not decomposed in the environment. Organic contaminants and even short-lived radionuclides that can become less toxic over time, like degradable and radionuclides that can be complexed with soil organic materials, or precipitated as pure or mixed solids, can be considered conservative because they are not decomposed in the environment. The influence of microbiological processes on contamination of the environment by toxic metals and radionuclides is of economic and environmental significance (Gadd 1993). Interactions of fungi with toxic metals. New Phytol, 124: 25–60.


MYCORRHIZAL FUNGAL WEATHERING AND METAL CONTAMINATION


MYCORRHIZAL FUNGAL WEATHERING AND METAL CONTAMINATION


However, the potential of microbial processes for bioremediation may be dependent on the physical and chemical nature of the site which influences the form in which metals occur. Furthermore, mineral components contain considerable quantities of metals which are biologically unavailable. Certain microbial processes dissolve metal minerals thereby increasing metal bioavailability and potential toxicity, whereas others immobilize them and reduce bioavailability (Fomina et al. 2005 Fomina, M, Alexander, I J, Colpaert, J V and Gadd, G M. 2005. Solubilization of toxic metal minerals and metal tolerance of mycorrhizal fungi. Soil Biol Biochem, 37: 857–866. ).


Of special interest are the mechanisms by which fungi and plants obtain phosphate since solubilization of inorganic phosphates can result in release of the associated toxic metals (Gadd 1986, Gadd, GM. 1986. “Fungal responses towards heavy metals”. In Microbes in Extreme Environments, Edited by: Herbert, R A and Codd, G A. 83–110. London: Academic Press. ). Conversely, formation of insoluble metal phosphates will reduce both metal and phosphate bioavailability. For other insoluble metal compounds and minerals (e.g. various sulphates, oxides, carbonates), solubilization can also result in release of anionic species.


Metal tolerance and solubilizing ability varied widely between different mineral and fungal species, and strains derived from sites differing in the degrees of metal pollution. Zinc phosphate exhibited the least toxicity and was the easiest to solubilize by the majority of tested fungal isolates.

Solubilization of toxic metal minerals was connected with both the pH of the medium and growth and tolerance of fungi and it seemed that acidification of the medium was the main mechanism of mineral dissolution for most of the mycorrhizal fungi studied. A very strong lethal effect was observed for ECM isolates in the presence of Pb phosphate, carbonate, sulphide and tetraoxide. In contrast, ericoid mycorrhizal isolates were able to grow on Pb-mineral-amended media.

A significant proportion of ericoid mycorrhizal cultures solubilized Cd and Cu phosphates and cuprite. None of the ericoid mycorrhizal and ECM fungi were able to produce a clear zone in Pb mineral-containing agar. However, many fungi were able to accumulate mobilized Pb in their mycelia. Differences in toxic metal mineral tolerance, mineral solubilization and metal uptake between populations isolated from metal-polluted and uncontaminated sites were related to the toxic metal which was the main pollutant in the original contaminated environment. In general, metal-
tolerant fungi grew and solubilized toxic metal minerals better than non-tolerant isolates (Fomina et al. 2005).

Martino et al. (2003a) Martino, E, Perotto, S, Parsons, R and Gadd, G M. 2003a. Solubilization of insoluble inorganic zinc compounds by ericoid mycorrhizal fungi derived from heavy metal polluted sites. *Soil Biol Biochem*, 35: 133–141. demonstrated that ericoid fungal strains belonging to the species *Oidiodendron maius* and derived from polluted and unpolluted soils mobilize insoluble inorganic zinc compounds to different extents. They found that strains from polluted soils showed little ability to solubilize Zn from both ZnO and Zn$_3$(PO$_4$)$_2$, whereas strains from unpolluted soils showed a higher solubilization potential. Martino and colleagues (2003a) Martino, E, Perotto, S, Parsons, R and Gadd, G M. 2003a. Solubilization of insoluble inorganic zinc compounds by ericoid mycorrhizal fungi derived from heavy metal polluted sites. *Soil Biol Biochem*, 35: 133–141. speculated that this may reflect specific strategies to maintain homeostasis of essential metals under different soil conditions. Induction of organic acids (malate and citrate) by the metal compounds was shown to be at least in part responsible for metal solubilization. Zinc precipitation was demonstrated for one of the ericoid strains tested by Martino et al. (2003a) Martino, E, Perotto, S, Parsons, R and Gadd, G M. 2003a. Solubilization of insoluble inorganic zinc compounds by ericoid mycorrhizal fungi derived from heavy metal polluted sites. *Soil Biol Biochem*, 35: 133–141. who observed zinc crystals formation underneath the fungal colony after growing in the presence of insoluble zinc oxide. The insoluble metal compounds was firstly solubilized by the ericoid strain and then precipitated in an insoluble form (Figures 1 and 2).

**FIG 1** Crystals formed by *Oidiodendron maius* in the agar medium underneath the fungal colony. (a) Solubilization activity on solid 2% (w/v) malt medium containing 0.12% (w/v) ZnO. The photograph shows the clear zone of solubilization halo around the colony of an *Oidiodendron maius* strain from unpolluted soils. The photograph was taken after 30 d incubation at 25°C. (b) A SEM micrograph showing the morphology of the crystals formed in the medium in correspondence to the solubilization halo. Bar is 20 μm. When these crystals were purified and analysed by SEM and X-ray microanalysis, a strong Zn peak was identified, indicating that they actually represent a form of metal insolubilization (see Martino et al. 2003a Martino, E, Perotto, S, Parsons, R and Gadd, G M. 2003a. Solubilization of insoluble inorganic zinc compounds by ericoid mycorrhizal fungi derived from heavy metal polluted sites. *Soil Biol Biochem*, 35: 133–141.)
Ericoid fungi were also shown to be able to solubilize iron from a very particular substrate, asbestos fibres (Figure 3) (Martino et al. 2003b Martino, E, Prandi, L, Fenoglio, I, Bonfante, P, Perotto, S and Fubini, B. 2003b. Soil fungal hyphae bind and attack asbestos fibres. Angewandte Chemie-International Edition, 42: 219–222., 2004 Martino, E, Cerminara, S, Prandi, L, Fubini, B and Perotto, S. 2004. Physical and biochemical interactions of soil fungi with asbestos fibers. Environ Toxicol Chem, 23: 938–944.). Iron, a structural component of most asbestos, is thought to play a crucial role in asbestos toxicity. Surface iron favors fibres uptake by mammalian cells and promotes the generation of free radicals with consequent DNA and lipid damage. In some cases, chemical removal of iron from asbestos fibres has reduced several cellular responses to asbestos. As previously mentioned, microorganisms have developed mechanisms to scavenge iron from poorly soluble forms (Haselwandter et al. 2008).

FIG 3 Effects of an ericoid strain on a suspension of asbestos fibres. (a) Oidiodendron maius control culture, without asbestos fibres. (c) Fine asbestos fibres (1.5–4 μm mean diameter) form a turbid suspension when dispersed in the Czapek glucose medium. (b) When the fungal mycelium was grown in the medium containing asbestos fibres, it removed the fibres from the suspension, thus leaving a clear supernatant. This phenomenon indicates that the fungal hyphae can bind or entrap the asbestos material. (d) Scanning electron micrograph showing the fungal hyphae of O. maius (arrow) intertwined with asbestos fibres. A large fibre is clearly visible in the center of the photograph (arrowhead), whereas smaller fibres (double arrowhead) can be found associated with the surface of the fungal hyphae (scale bar corresponds to 50 μm). A large fibre is clearly visible in the center of the inset photograph surrounded by fungal hyphae. Scale bar is 20 μm. (e) A specific plate assays shows the release of siderophores by O. maius, detected as a clear halo. Highly
solubilizing fungal strains produced significantly higher amounts of siderophores than less solubilizing fungi, so siderophores might be partly responsible for the iron extraction from fibres (see Martino et al. 2004 Martino, E, Cerminara, S, Prandi, L, Fubini, B and Perotto, S. 2004. Physical and biochemical interactions of soil fungi with asbestos fibers. Environ Toxicol Chem, 23: 938–944 ).

Martino and collaborators (2003b Martino, E, Prandi, L, Fenoglio, I, Bonfante, P, Perotto, S and Fubini, B. 2003b. Soil fungal hyphae bind and attack asbestos fibres. Angewandte Chemie-International Edition, 42: 219–222. , 2004 Martino, E, Cerminara, S, Prandi, L, Fubini, B and Perotto, S. 2004. Physical and biochemical interactions of soil fungi with asbestos fibers. Environ Toxicol Chem, 23: 938–944. ) investigated the ability of some soil fungi to produce iron chelators capable of extracting iron from crocidolite (blue asbestos). Among the species/isolates investigated, also some ericoid mycorrhizal strains could remove iron from crocidolite fibres. A tight interaction between the fungus and the fibres was observed using the scanning electron microscope (SEM) (Figure 3). By binding the fibres and depriving them of iron, selected species/strains of soil fungi might represent interesting tools for the bioremediation of asbestos-contaminated soils.

Processes of toxic metal mineral solubilization by mycorrhizal fungi should therefore be considered in connection with the metal tolerance of these organisms but experiments should also be performed in association with the host plant. Interestingly, Fomina et al. (2006) Fomina, M, Charnock, J M, Hillier, S, Alexander, I J and Gadd, G M. 2006. Zinc phosphate transformations by the Paxillus involutus/pine ectomycorrhizal association. Microb Ecol, 52: 322–333. investigated zinc phosphate transformations by Paxillus involutus/pine ectomycorrhizas using zinc-resistant and zinc-sensitive strains of the ectomycorrhizal fungus under high- and low-phosphorus conditions to further understand fungal roles in the transformation of toxic metal minerals in the mycorrhizosphere. In

The role of ECM fungi in the uptake of Ca and Mg under Al toxicity is especially of interest as Al$^{3+}$ specifically inhibits the uptake of Ca and Mg by kinetic processes at the root cell wall, thereby inducing plant deficiencies of Ca and Mg. ECM fungi ensheathe the root apices, which are the main sites for Al toxicity and uptake of Ca and Mg, and it seems likely that ECM fungi affect the uptake Ca and Mg at the root tips (Finlay 1995 Finlay, RD. 1995. Interactions between soil acidification, plant growth and nutrient uptake in ectomycorrhizal associations of forest trees. Ecol Bull, 44: 197–214.). Under conditions of sufficient nutrient supply, which avoids differences in growth and biomass between non-mycorrhizal and ECM seedlings (Hobbie 2006 Hobbie, EA. 2006. Carbon allocation to ectomycorrhizal fungi correlates with belowground allocation in culture studies. Ecology, 87: 563–569.), uptake of Ca and Mg under Al toxicity was not affected by ECM colonisation (Van Schöll et al. 2005 Van Schöll, L. Keltjens, W G, Hoffland, E and van Breemen, N. 2005. Effect of ectomycorrhizal colonization on the uptake of Ca, Mg and Al by Pinus sylvestris under aluminium toxicity. For Ecol Manag, 215: 352–360.).

Increased exudation of oxalate by tree seedlings under Al toxicity has been shown by Ahonen et al. (2000) Ahonen Jonnarth, U, Van Hees, PAW, Lundstrom, U S and Finlay, R D. 2000. Organic acids produced by mycorrhizal Pinus sylvestris exposed to elevated aluminium and heavy metal concentrations. New Phytol, 146: 557–567., and in several cases this was increased further by ECM fungi. Van Schöll (2006a) Van Schöll, L, Hoffland, E and Van Breemen, N. 2006a. Organic anion exudation by ectomycorrhizal fungi and Pinus sylvestris in response to nutrient deficiencies. New Phytol, 170: 153–163. demonstrated that oxalate exudation by ECM fungi was induced by Al, and exudation was further enhanced by simultaneous Al toxicity and Mg and P deficiency. Arbuscular mycorrhizal fungi can also protect their host plants from Al toxicity. In the eastern United States, broomsedge (Andropogon virginicus L.) is found growing on abandoned coal mined lands that have extremely acidic soils with high residual aluminium (Al) concentrations. Broomsedge may be inherently metal-resistant and nutrient-efficient or may rely on the arbuscular mycorrhizal fungal association to overcome limitations on such sites. Cumming and Ning 2003 Cumming, J R and Ning, J. 2003. Arbuscular mycorrhizal fungi enhance aluminium resistance of broomsedge (Andropogon virginicus L.). J Exp Bot, 54: 1447–1459. showed that an AM fungal consortium conferred Al resistance to broomsedge. They demonstrated that arbuscular mycorrhizal fungi reduced Al uptake and translocation in host plants, potentially reflecting measured reductions in inorganic Al availability in the rhizosphere of mycorrhizal plants.

CONCLUSIONS

and then remove any useful chemical elements to pass on to their host tree. During the process, the rocks change their chemistry, lose their strength and in the long-run become soil. Different types of mycorrhizal symbioses play fundamental roles in shaping terrestrial ecosystems and the characteristic plant communities that dominate the major terrestrial biomes of the world today do so because selection has favoured symbiotic association functionally adapted to the different environments.


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