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## Technical Focus

# Approaches to modelling mineral weathering by fungi

Anna ROSLING<sup>a,\*</sup>, Tiina ROOSE<sup>b</sup>, Anke M. HERRMANN<sup>c</sup>, Fordyce A. DAVIDSON<sup>d</sup>,  
Roger D. FINLAY<sup>a</sup>, Geoffrey M. GADD<sup>e</sup>

<sup>a</sup>Department of Forest Mycology and Pathology, Uppsala BioCenter, SLU, Box 7026, 750 07 Uppsala, Sweden

<sup>b</sup>School of Mathematics, University of Southampton, University Road, Southampton SO17 1BJ, UK

<sup>c</sup>Department of Chemistry, Uppsala BioCenter, SLU, Box 7015, 750 07 Uppsala, Sweden

<sup>d</sup>Division of Mathematics, University of Dundee, Dundee DD1 5EH, Scotland, UK

<sup>e</sup>Division of Molecular Microbiology, College of Life Sciences, University of Dundee, Dundee DD1 5EH, Scotland, UK

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### ABSTRACT

Fungi are agents of geochemical change in the environment and play important roles in the soil, the plant-root zone, and in rock and mineral habitats. Modelling may serve as a tool to quantify fungal weathering under natural conditions. This paper provides a review of existing mycelial growth models and examines how these can be adapted to describe weathering by ectomycorrhizal and other fungi in mineral soil.

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## 1. Introduction

The term geomycology, by definition an interdisciplinary research topic, has been coined for the study of the role fungi play in biogeochemical processes including mineral weathering in terrestrial ecosystems (Burford *et al.*, 2003; Gadd, 2007). Because of the complexity of biotic and abiotic interactions that can occur, it is challenging to study these interactions using experimental methods alone. A combined mathematical modelling and experimental approach can be useful to provide greater insight into the problem (Davidson, 2007a,b). Most fungal growth models are based on

observations of free-living fungi (Davidson, 2007a,b), but recently modellers have also started assessing the importance of fungus–plant interactions on nutrient uptake by plants (Schnepf and Roose, 2006; Schnepf *et al.*, 2008a,b).

Ectomycorrhizal fungi are symbiotic colonizers of woody roots (Fig 1) and are ubiquitous in boreal forest soils. Vertically stratified Podzol soils are common in boreal forests throughout Fennoscandia and the majority of ectomycorrhizal root tips may occur in the mineral horizons (Rosling *et al.*, 2003). In mineral soil, mycorrhizal fungi have been found to dominate the total fungal community (Lindahl *et al.*, 2007). Together these observations indicate that mineral soil is an

\* Corresponding author. Tel.: +46 18 67 18 64; fax: +46 18 67 35 99.

E-mail address: [anna.rosling@mykopat.slu.se](mailto:anna.rosling@mykopat.slu.se) (A. Rosling).

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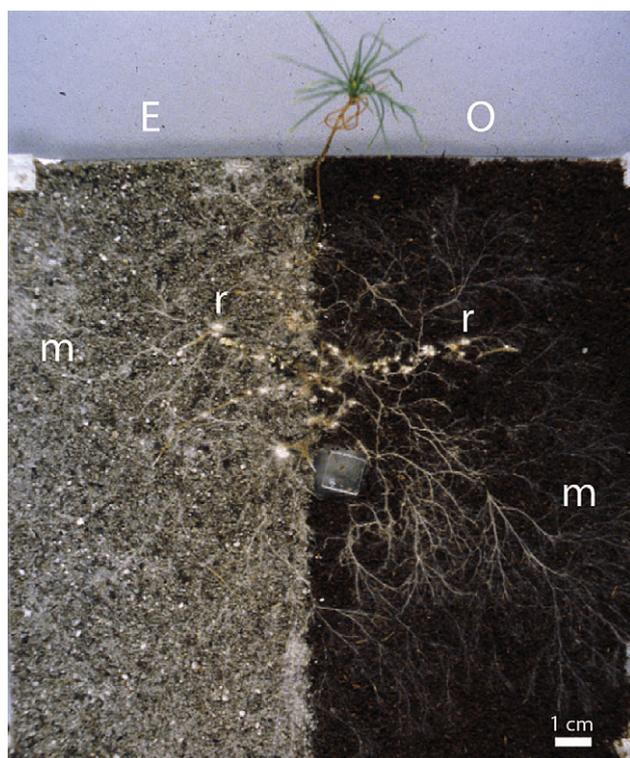
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important growth substrate for ectomycorrhizal fungi. Their high abundance in boreal forest soils (350–650 m of fungal hyphae per gram of mineral soil in a forest podzol; Söderström, 1979) provides great potential for interactions between fungal hyphae and mineral surfaces. The extensive growth of their mycelia enables the fungi to colonize and exploit nutrient-rich substrates, and to assimilate and translocate (reallocate) nutrients and carbon in soils (Ritz, 2006). *In vitro* experiments using pine seedlings inoculated with two different ectomycorrhizal fungi have demonstrated selective colonization and intense carbon allocation to patches of nutrient-rich potassium feldspar in comparison with patches of nutrient-poor quartz (Rosling et al., 2004a). The extramatrix mycelia of ectomycorrhizal fungi may thus provide a direct link between photosynthetically-assimilated carbon from trees and weathering of soil minerals (Fig 1). Weathering of minerals by fungi forming symbiotic associations with photobiotrophs in lichens is well established as a model system (Banfield et al., 1999). The potential for weathering interactions in ectomycorrhizal symbioses is even greater since these fungi are connected to plants, which represent a much larger sink for nutrients and are able to supply the fungi with much larger amounts of photosynthetically fixed carbon.

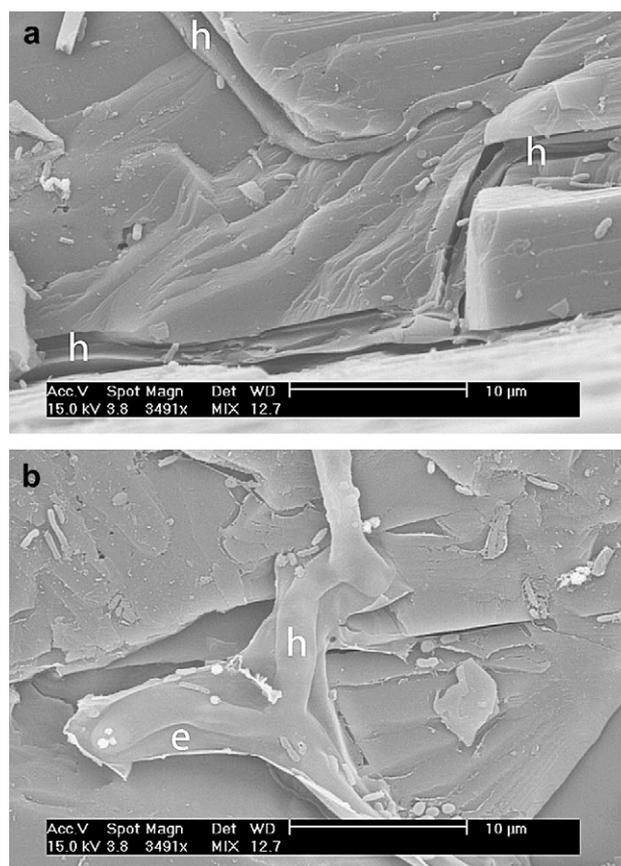
Hyphal tip growth is principally driven by internal pressure and the growing tip may thus exert considerable pressure at the micrometre scale upon interaction with surfaces (Money, 2008). This phenomenon has been modelled (Gierz and

Bartniki-Garcia, 2001; Goriely and Tabor, 2008) but such single hyphal models are not considered in detail in this review because of the difficulty of translating small-scale findings to the soil, plant, tree and forest scale. We focus on hyphal and colony scale phenomena in this review. Contact guidance (thigmotropism) (Bowen et al., 2007a,b) enables hyphae to orientate their growth in relation to substrate topography and this appears to be important in the spatial exploration and colonization of soil, rocks and minerals (Fig 2a). In addition, ectomycorrhizal fungi have the ability to modify their chemical environment through local acidification around the hyphae and by exuding metal-complexing weathering agents such as organic acids (Rosling, 2009) and siderophores (Winkelmann, 2007). Due to their wide array of biogeochemical and biomechanical interactions, ectomycorrhizal fungi have been suggested to play a central role in mineral weathering in boreal forest soils (Landeweert et al., 2001).

The aim of this review is to (i) outline available models of fungal mycelial growth and function, and (ii) discuss how



**Fig. 1** – Pine seedling grown in symbiosis with the ectomycorrhizal fungus *Suillus bovinus*. The fungal mycelia (m) extends from the colonized root tips (r) into the soil substrate, organic soil (O) and podzol E horizon soil (E). A 1 cm scale is given at the bottom of the image.



**Fig. 2** – Scanning electron microscopy (SEM) image of hyphae (h) of the ectomycorrhizal fungus *Heboloma velutipes* on a surface of potassium feldspar. The fungus was grown in symbiosis with a pine seedling and allowed to colonize the mineral particle for 7 months. a) Contact guidance (thigmotropism) enables hyphae to orientate their growth in relation to substrate topography. b) In the process of sample preparation, extracellular polymeric substances (e) have dried and shrunk around the hyphae.

these models can be developed to describe mineral weathering by symbiotic ectomycorrhizal fungi in boreal forest soils.

## 2. Modelling of fungal mycelium growth and function

Mathematical modelling has played a significant role in the development of our understanding of the growth and function of the fungal mycelium (Edelstein, 1982; Prosser, 1995; Davidson, 2007a,b; Schnepf and Roose, 2006; Schnepf et al., 2008a,b). This includes complex interactions within their environment, such as “real-time” descriptions of the colonization of soil-like structures, acidification of the fungal microenvironment and translocation phenomena (Boswell et al., 2002; 2003a,b, 2007; Jolicoeur et al., 2003; Tlalka et al., 2003; Darrah et al., 2006; Schnepf and Roose, 2006; Boswell, 2008; Jager et al., 2008; Schnepf et al., 2008a,b). The choice of scale is one of the main challenges with any mathematical modelling approach. Full investigation of fungal growth and function requires the consideration of scales ranging from the molecular, through nano- and micro-scale, to the kilometre scale and above, especially where global biogeochemical phenomena are being considered. Ultimately, modelling frameworks need to link environmental conditions to community structure, biotic interactions and function (Falconer et al., 2007, 2008). As yet, models have not successfully captured interactions across such extremes of scale, but focusing on selected ranges has rendered significant progress (Davidson, 2007a; Schnepf and Roose, 2006; Schnepf et al., 2008a,b). The main focus at the macro-scale is the interactions of fungi with the environment. Lamour et al. (2000, 2002) modelled the production of fungal biomass by consumption of growth-limiting substrates (carbon and nitrogen sources) and the accumulation of these elements by the developing mycelium. At the molecular, nano- and micro-scale, much modelling work has been devoted to the development of hyphal tips, branching and anastomosis (see for example the recent special issue: Hyphal tip growth, *Fungal Biology Reviews*, 22, 2008).

Growth and function of the fungal mycelium have been examined by three main modelling approaches: (i) continuous, (ii) discrete and (iii) hybrid discrete-continuum automaton modelling. Homogeneous growth conditions, including carbon availability e.g. in agar plates, are the simplest environments in which growth of mycelial fungi can be examined. There is a significant body of qualitative and quantitative data on biomass densities, structural properties (e.g. the fractal dimension of the mycelium) and metabolic activities, e.g. acid production, in such conditions (see, for example, Ritz and Crawford, 1990; Sayer et al., 1995; van Hees et al., 2006; Boswell et al., 2003a, 2007). A common approach to modelling medium-scale spatio-temporal properties of fungal mycelia growing in homogeneous environments has been to model the fungus and growth-promoting substrates as continuous variables so that the model comprises a system of (non-linear) partial differential equations (PDEs) (e.g. Edelstein, 1982; Davidson, 1998; Boswell et al., 2002, 2003a; Schnepf and Roose, 2006; Schnepf et al., 2008a,b). Boswell et al. (2003a) modelled the dynamics of substrate-limited fungal growth. Their model

was found to be in good agreement with observed behaviour of growth of dense mycelia and provided insight into the action of translocation (internal distribution of nutrients). The interaction of fungal colonies has also been studied using these techniques (Falconer et al., 2008). Using a similar model to Boswell et al. (2003a), Schnepf and Roose (2006) and Schnepf et al. (2008a,b) investigated phosphate uptake in a symbiotic fungal – plant interaction and found that overall phosphate uptake was dominated by the fungus.

When growth is sparse as in nutrient-poor conditions or in structurally heterogeneous environments, such as soil, then a discrete modelling approach is more appropriate, in which individual hyphae are identified. Such discrete models usually take the form of computer simulations derived from the statistical properties of the investigated experimental system (e.g. Bell, 1986; Kotov and Reshetnikov, 1990; Ermentrout and Edelstein-Keshet, 1993; Soddell et al., 1995; Regalado et al., 1996; Meskauskas et al., 2004a,b). These models often yield images that are almost indistinguishable from real fungi grown in uniform conditions. However, because non-mechanistic rules are used to generate hyphal tip extension and hyphal branching such models must be reformulated or at least re-calibrated to describe growth under different conditions or of a different species. Furthermore, these models typically neglect anastomosis and, because of the computational difficulties, have neglected translocation, a process crucial in hyphal tip extension and colonization of heterogeneous environments (Jacobs et al., 2004).

The third approach indicated above was introduced by Boswell et al. (2007), who developed a multi-scale hybrid site-jump cellular automaton model of mycelial growth to investigate the development of mycelial networks in growth matrixes of different complexity, including homogeneous conditions, heterogeneous conditions with spatial and temporal nutritional heterogeneity, and soil-like structures. Their model explicitly includes both passive and active translocation and was able to capture experimental observations of colony expansion rate, biomass distribution and fractal dimension (Ritz and Crawford, 1990) and make predictions regarding acidification of the local environment (Sayer et al., 1995; Jacobs et al., 2002a,b; Fomina et al., 2003). A computational-lattice-free version of this model has been recently constructed (Carver and Boswell, 2008), which will allow for a wider range of applications.

In contrast to free-living fungi, mycorrhizal fungi are connected to a stable carbon supply and a large nutrient sink through their symbiotic association with a host plant. Mycelial growth models have been adjusted to describe symbiotic growth of vesicular-arbuscular mycorrhizal fungi (VAM) and fungal influence on phosphate uptake (Schnepf and Roose, 2006; Schnepf et al., 2008a,b). Here, the model boundary is the colonized root surface from where new hyphae may emerge into the soil substrate. Schnepf and Roose (2006) and Schnepf et al. (2008a,b) found that most of the phosphate was removed from the soil by the mycorrhiza indicating that the plant relied almost entirely on the fungus for its phosphate supply. Schnepf and Roose (2006) also found that translocation of phosphate within the fungal mycelia is so fast that any phosphate taken up by the fungus can be considered to be almost instantaneously available to plants. While the models

by Schnepf and Roose (2006) and Schnepf et al. (2008a,b) were developed with the specific aim of estimating phosphate uptake, they could be extended to deal with other nutrients such as nitrogen sources or potassium. However, one would need to use a rigorous multi-scale modelling approach to derive a correct model for nutrient uptake and translocation within the fungus. While the model derived for phosphate might be applicable to other nutrients that are strongly bound in the soil, it may not be applicable to highly mobile nutrients like certain nitrogen sources or potassium. Therefore, new models to deal with weakly adsorbed nutrients must be developed. In addition, the models developed for VAM are probably applicable to model the external hyphae of ectomycorrhizas. However, the boundary conditions representing the root infection and carbon source need to be amended to take into account specific effects characteristic to ectomycorrhizas.

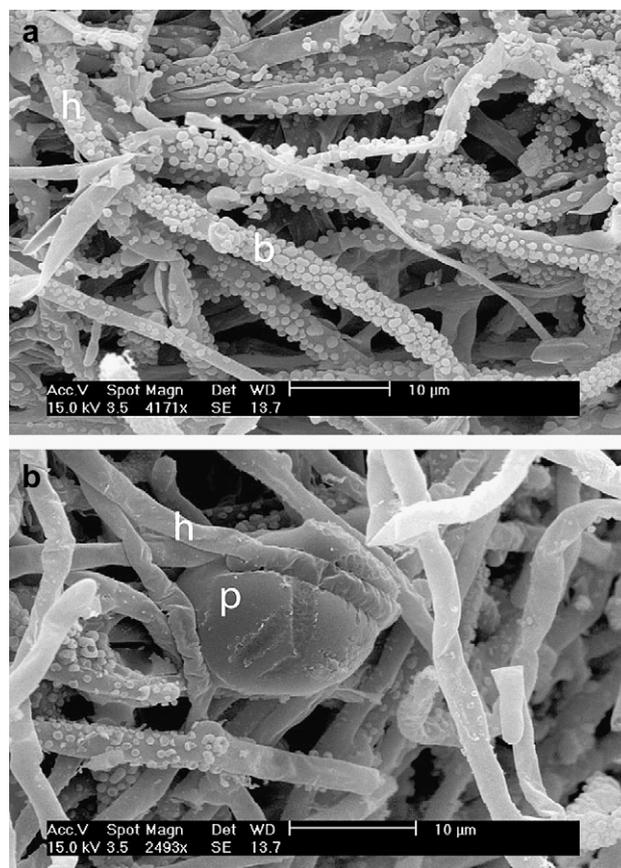
### 3. Modelling of mineral weathering by symbiotic ectomycorrhizal fungi in soils

Any mycorrhizal modelling exercise needs to first define the spatial and temporal scale that is of interest since the processes involved are inherently multi-scale, i.e., there are hyphal, colonial, single root, root system, plant and forest scales. While in principle one could model from small to large scale using the homogenisation theory, it is often more effective to start modelling at a scale where most of the experimental data is available.

There are important morphological differences in the symbiotic interface of arbuscular and ectomycorrhizal fungi. In ectomycorrhizal fungi, the functional unit of the symbiosis is the colonized root tip (Fig 1) where transfer of carbon to the fungus, and nutrients to the plant, occurs (Smith and Read, 1997). For the purpose of modelling mycelial growth in ectomycorrhizal fungi, we propose that the root system is defined as the model boundary from which newly colonized root tips may emerge. In field studies, the number of root tips colonized by different fungal species is used as a quantitative measurement of the degree of colonization as well as the relative abundance of different species (Taylor, 2002). Such data may provide valuable insights for defining the boundary of models dealing with mineral weathering by ectomycorrhizal fungi. Ultimately, carbon is the driver of ectomycorrhizal weathering activity. In the colonized root tip, carbon is transferred from the host tree to the fungus. Since we propose that the colonized mycorrhizal root tip is the model boundary, carbon allocation from the host tree would be included in the model as the number of emerging root tips. In stratified soil the distribution of root tips between different soil horizons would obviously be important (Rosling et al., 2003).

In biotic weathering models developed for rock inhabiting lichens, the symbiotic fungal partner mediates weathering through colonization and chemical activity driven by carbon from the host (Banfield et al., 1999). In the zone of mineral-microbial contact, mineral dissolution, precipitation and clay mineral formation is influenced by the presence of the microbial cells and organic compounds produced by them. Below the contact zone, weathering is still influenced by organic compounds produced by the fungi (Banfield et al., 1999).

Similarly, the weathering activity of ectomycorrhizal fungi has been separated into two major effects, the effect of mycelial soil colonization and the effect of chemical activity of the mycelia (Wallander et al., 1997). The chemical activity of the mycelia includes acidification around the growing hyphae due to release of respired CO<sub>2</sub>, proton efflux, the presence of acidic extracellular polymeric substances (EPS, Fig 2b), release of low molecular weight organic acids (LMWOAs) and precipitation of biominerals (Fig 3a) (Burford et al., 2003; Gadd, 1999, 2007). As in the lichen model discussed above, the zone of influence is larger for the chemical effect compared to colonization alone. For modelling of fungal weathering in mineral soil systems, the principal parameters to quantify are A the fungal-mineral contact interface and B the total area of mineral surface influenced by compounds produced by the fungi, which includes A as well as the additional internal surface area and intra-mineral voids not directly colonized by the fungi but still influenced by their chemical products. Secondly the chemical activity in these two zones has to be defined, including the parameters (i) uptake (zone A), (ii) transport (zone B), (iii) pH and (iv) the composition and



**Fig. 3 – SEM image of mycelia of the ectomycorrhizal fungus *Hebeloma velutipes* growing in mineral soil from a Podzol E horizon. The fungus was grown in symbiosis with a pine seedling. a) Biominerals (b) precipitated on fungal hyphae (h) growing in mineral soil. b) Alteration of the surface of a mineral soil particle (p) after colonization by fungal hyphae (h).**

concentration of organic compounds, which are relevant in both zones A and B.

The fungal–mineral contact area (Fig 3b) in a given soil volume will be influenced by the total fungal mycelial surface area, the total area of mineral surfaces, and the proportion of the mycelium that is in direct contact with the minerals. Fungal tunnelling as a mean of weathering (Jongmans *et al.*, 1997) does not need to be considered explicitly. The phenomena has been demonstrated to comprise less than 1% of the total soil weathering (Smits *et al.*, 2005) and can thus be included within the context of zones A and B. Fungal biomass can be quantified in various ways, including measurements of carbon allocation (Rosling *et al.*, 2004a), ergosterol (Wallander *et al.*, 1997; Hagerberg *et al.*, 2003), fungal specific PLFAs (Wilson *et al.*, 2008) or direct counts of hyphal length (Söderström, 1979). As yet there are few detailed studies relating total fungal biomass to mycelial surface area, but for modelling purposes, simple assumptions about particle size- and hyphal diameter size distributions can be made. Microscopic examination of thin soil sections or fresh samples provides a possibility for direct quantification of the fungal–mineral interaction in soil samples (Schack-Kirchner *et al.*, 2000; Smits, *this issue*). This might be necessary for accurate calibration of model parameters.

Chemical activity is directly dependent on the presence of growing mycelium, but the relative activity per unit mycelium may vary substantially with species and conditions. Of the macronutrients occurring in mineral forms, experimental studies using ectomycorrhizal fungi have examined growth and weathering activity, mainly in relation to P, K and Mg (Fomina *et al.*, 2004, 2006; Rosling, 2009). So far no universal driver of fungal weathering has been postulated but there is an indication that K and Mg-limiting growth conditions result in increased exudation of LMWOAs and siderophores and that P-limiting conditions result in increased substrate acidification (Rosling, 2009). To reflect the complexity of the below ground ectomycorrhizal community an ultimate model would include different activities and degrees of mineral colonization for the different fungal species involved. The differential sensitivity of different minerals to weathering agents and the different particle size distributions of these minerals would also need to be included.

In a growing mycelium, carbon is partitioned between biomass production, respiration and exudation of organic compounds. These three carbon sinks reflect the weathering effects of mycelial soil colonization and chemical activity and we propose that carbon partitioning is a key parameter to include as a regulatory element in models that seek to examine weathering activity of ectomycorrhizal fungi. In a model that predicts how environmental structure can influence the growth of fungal mycelia, Boswell (2008) demonstrated that changes in hyphal extension and branching rates associated with explorative/exploitative growth could be controlled simply by the redistribution of internal substrate, i.e. translocation. Adding carbon partitioning to this model could potentially provide a feasible approach to model mineral soil colonization by ectomycorrhizal fungi and their effect on soil mineral weathering. Species-specific patterns of carbon partitioning have been demonstrated in relation to nitrogen availability (Fransson *et al.*, 2007). In

relation to mineral weathering, fungal responses to phosphorus, potassium and magnesium limitation are of primary interest. Complete carbon partitioning studies are not available for these elements, but species-specific patterns of substrate acidification in relation to mycelial density has been demonstrated for a number of ectomycorrhizal fungi (Rosling *et al.*, 2004b). Conditions that influence the regulation of organic acid excretion in fungi are reviewed in this issue (Fransson and Plassard, *this issue*).

The low molecular mass (<1kDa, LMM) fraction of soil solution dissolved organic carbon plays an important role in mineral weathering and element mobility leading to soil development in podzol soils (Vestin *et al.*, 2008). LMM carbon compounds originate mainly from metabolic pathways in plants and microorganism but bulk concentrations in soil solution are usually low due to high mineralization rates, adsorption, precipitation and spatial heterogeneous concentrations (Jones *et al.*, 2003). Smits (*this issue*) examines the scale of chemical influence using oxalate and feldspar as a model weathering system. An overall pathway of induced weathering in response to phosphorus availability has not been identified in ectomycorrhizal fungi (Rosling, 2009). Lowering of substrate pH under P limiting conditions appears to be a possible mechanism of induced P mineral dissolution in ectomycorrhizal fungi (Arvieu *et al.*, 2003). Dissolution of primary P minerals, such as apatite, is strongly pH-dependent within the range of pH 2–5, with higher dissolution at lower pH values (Guidry and Mackenzie, 2003). However, the rate of apatite dissolution is sufficiently high to buffer P concentrations at the solution interface (Oelkers *et al.*, 2008), possibly making P uptake the main biotic mechanism of weathering of primary P minerals. Intense mycelial colonization of apatite has been observed in field experiments (Hagerberg *et al.*, 2003). Available models of phosphate uptake (Schnepf and Roose, 2006; Schnepf *et al.*, 2008a,b) could easily be adapted to model weathering of primary P minerals.

#### 4. Conclusions

Existing models of fungal growth and function can be adapted to examine weathering of minerals by ectomycorrhizal fungi. The first step is to define the model boundary as the colonized mycorrhizal root tip from which mycelia extend into the soil. The mycelial expansion from the root will depend on the colonizing fungal species. By defining root tip properties, such as functional characteristics of the colonizing fungi, models can be developed to encompass the functional diversity of ectomycorrhizal fungi. The spatial distribution of roots within stratified soils and specific substrate colonization by the mycelium in relation to different minerals provides input to determine the size of the fungal–mineral interface in soil.

Mineralogical properties of the soil, such as surface area, element composition and weathering rates of different minerals, can be included in the model. Defining the chemical conditions in the fungal–mineral interface and in influenced mineral pore spaces, is possibly the main challenge of developing a realistic model. Available data on fungal exudation, acidification and uptake from experimental studies has to be adapted to field conditions where the fungal mycelium

co-exists with other fungi, bacteria and micro-fauna. Fungal exudates are an important energy source for associated bacteria and decomposition of exuded organic compounds prevents accumulation of high concentrations in the field.

Including differences among fungal species and soil layers provides a model framework to extrapolate predictions from small-scale interactions with the substrate to examine the effect of fungal weathering at catchment levels. Modelling of weathering by ectomycorrhizal fungi provides an opportunity to examine the quantitative contribution of this process in relation to total nutrient budgets including cycling of decomposed material within the ecosystem.

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