



Ecological significance of mineral weathering in ectomycorrhizal and arbuscular mycorrhizal ecosystems from a field-based comparison



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ABSTRACT

Plants forming symbioses with ectomycorrhizal fungi dominate ecosystems worldwide, yet the advantage of ectomycorrhizal symbiosis compared with symbioses with arbuscular mycorrhizal fungi remains unknown. One hypothesis is that only ectomycorrhizal fungi have direct access to mineral phosphorus (P) in soils. ‘Tunnel’ features have been found in soil minerals under ectomycorrhizal forests and these ‘tunnels’ have been attributed to mineral weathering by ectomycorrhizal fungi to obtain mineral P for the host plant. To compare ecosystems we established 24 paired field plots in New Zealand’s South Island, one of each pair was in an arbuscular mycorrhizal forest where ectomycorrhizal vegetation had been absent since the last glacial maximum and the other was in an ectomycorrhizal forest. We investigated the occurrence of ‘tunnels’ under both forest types, and incubated quartz and apatite in mesh bags in soil to test whether ectomycorrhizal and arbuscular mycorrhizal roots have access to mineral-derived P, which was assessed by measuring rare earth element uptake in roots. With the same mesh bags we used pyrosequencing to study fungal community composition. We found mineral weathering ‘tunnels’ under both arbuscular and ectomycorrhizal forests; and both arbuscular and ectomycorrhizal roots showed uptake of rare earth elements from apatite signifying access to mineral P in apatite. Fungal community composition differed between arbuscular and ectomycorrhizal forests, but not between types of incubated minerals. Ectomycorrhizal DNA found in samples from forest sites with only arbuscular mycorrhizal trees did not imply the presence of active ectomycorrhizal communities and should serve as a caution for interpretation of high-throughput environmental sequencing. We suggest that mineral weathering is caused by acidification of the rhizosphere by mycorrhizal fungi, saprotrophic fungi and bacteria. The acidification and weathering in the rhizosphere creates different weathering features in mineral grains, and makes mineral nutrients available for both arbuscular and ectomycorrhizal plants.

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1. Introduction

Virtually all trees acquire nutrients through symbiotic mycorrhizal fungi, but different trees associate with different types of mycorrhizas, and in particular either arbuscular mycorrhizas or ectomycorrhizas (Brundrett, 2009). Arbuscular mycorrhizas are the ancestral associates of all land-plants (Schüßler et al., 2001) and are formed by more than 70% of plant species (Brundrett, 2009), including all trees in the Podocarpaceae, Cupressaceae and Magnoliaceae families, and most in the Rosaceae family (Koele et al.,

2012). Ectomycorrhizas, in contrast, are only formed by around 2% of all plant species. However, this group includes the dominant tree species of most temperate and boreal forests (e.g. all species in Pinaceae, Fagales, Salicaceae and some Myrtaceae) and some dominant forest types in tropical forests (e.g. all Dipterocarpaceae and some Caesalpinioideae species). This raises the key question of how such a relatively small number of tree species have become overwhelmingly dominant in forests worldwide.

Several studies have suggested that ectomycorrhizal fungi are exclusively able to dissolve minerals in order to obtain nutrients (Jongmans et al., 1997; van Breemen et al., 2000a; Blum et al., 2002; Hoffland et al., 2005) including the essential nutrient phosphorus (P) from the mineral apatite. Jongmans et al. (1997) observed ‘tunnels’ in mineral grains, presumably formed by the excretion of organic acids by ectomycorrhizal fungi, dissolving the mineral

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structure and taking up nutrients (van Breemen et al., 2000a; Landeweert et al., 2001; Hoffland et al., 2003; Smits, 2006; van Schöll et al., 2006). Indeed several studies have shown initial ‘tunnel’ formation in minerals under the influence of ectomycorrhizal hyphae (Leake et al., 2008; Bonneville et al., 2009) as well as direct nutrient uptake by ectomycorrhizal roots from rock-forming minerals (e.g. Leyval and Berthelin, 1989; Paris et al., 1996; Wallander et al., 1997; Glowa et al., 2003). This raises the possibility that a direct effect of ectomycorrhizal mineral dissolution might contribute to the worldwide success of ectomycorrhizal trees.

Despite the evidence for mineral dissolution under ectomycorrhizal vegetation, other evidence suggests that the mineral dissolution trait cannot be exclusively ascribed to ectomycorrhizal fungi. Smits et al. (2010) found that mineral P dissolution occurred at similar rates in both ectomycorrhizal ecosystems and those where ectomycorrhizal fungi were absent; other organisms or abiotic processes appeared to be responsible for the release of mineral P in the non-ectomycorrhizal ecosystem. Sanz-Montero and Rodríguez-Aranda (2012) provided fossil evidence for mineral weathering by arbuscular mycorrhizal fungi in the Miocene, and Arocena et al. (2012) found mineral weathering by arbuscular mycorrhizal plant roots in a potted-plant experiment. Mineral weathering by both arbuscular mycorrhizal fungi and non-symbiotic rhizosphere bacteria supplied *Zea mays* with nutrients in an experiment by Berthelin and Leyval (1982). Quirk et al. (2012) also showed mineral weathering and trenching by both arbuscular and ectomycorrhizal fungi, although they calculated that arbuscular mycorrhizal fungi facilitate slower weathering rates than ectomycorrhizal fungi. Mineral strontium uptake by a wood-rot fungus was shown by Connolly et al. (1999), and suggests that non-mycorrhizal saprotrophic fungi may play a role in forest nutrient cycling via biological weathering.

The fact that some ectomycorrhizal fungi have been shown to weather minerals and increase nutrient uptake of the host plant (Paris et al., 1996; Wallander et al., 1997; Arocena and Glowa, 2000) does not prove ectomycorrhizal weathering to be a widespread phenomenon. Berner et al. (2012) found no effect of mineral amendment on fungal community structure, indicating that no fungi in that experiment had specific mineral dissolution traits. Nevertheless Berner et al. (2012) did note larger fungal biomass with mineral amendment, which they suggest may have been due to increased carbohydrate rewards from the host trees for ectomycorrhizal nutrient uptake from the mineral source. The ecological significance of ‘rock-eating’ ectomycorrhizal fungi remains elusive. In particular, there are no direct field-based comparisons of ecosystems dominated by trees with ectomycorrhizas versus ecosystems without ectomycorrhizas.

In New Zealand unique biogeographic features provide an ideal field comparison of arbuscular mycorrhizal and ectomycorrhizal forest ecosystems growing under otherwise constant environmental conditions, most notably highly P-deficient soils (McLaren and Cameron, 1996). We used this as a natural experiment to test the ecological significance of ectomycorrhizal mineral dissolution in three ways:

1. Mineral grains from ectomycorrhizal *Nothofagus* and arbuscular mycorrhizal podocarp-dominated ecosystems were investigated for the presence of ‘tunnel’ features to test whether these features are restricted to ectomycorrhizal soils;
2. Substrate bags were incubated in paired sites of ectomycorrhizal and arbuscular mycorrhizal forests to test whether ectomycorrhizal fungi are better at colonising and using P-bearing mineral grains in forest soils than arbuscular mycorrhizal hyphae;

3. Finally we explored whether specific ectomycorrhizal species colonise P-bearing mineral grains, and whether specific species of saprotrophic fungi play a similar role in the absence of ectomycorrhizal fungi.

2. Methods

2.1. Field sites

We established 24 paired field sites of which 12 were dominated by ectomycorrhizal *Nothofagus menziesii* (Hook.f.) Oerst. trees (with arbuscular mycorrhizal vegetation also present) and 12 consisted of arbuscular mycorrhizal plant species dominated by *Dacrydium cupressinum* Lamb., with no ectomycorrhizal vegetation present. The arbuscular mycorrhizal Podocarpaceae forests of New Zealand contrast perfectly with ectomycorrhizal forests known for mineral ‘tunnel’ formation, as the New Zealand Podocarpaceae have many traits similar to ectomycorrhizal forests: Podocarpaceae are long-lived, have been established since the last glaciation, have recalcitrant litter, and form the same podzolic soils characterised by organic matter accumulation and low pH (Wardle et al., 2008).

Each ectomycorrhizal site was paired with an arbuscular mycorrhizal site that shared the same parent material (i.e. 4 pairs (8 sites) on each of granite, schist, or glacial till). All sites were glaciated during the last glacial maximum (Suggate et al., 1978) so that soil development is approximately 18,000 years at each site. The sites received an average 3644 mm year⁻¹ precipitation during the observation period 1980–2012 (NIWA, 2013). All sites are on conservation land (administered by the Department of Conservation) and have never been logged. The soil type at all sites is podzol formation of an iron pan at ca. 30 cm depth, which inhibits drainage such that all sites have relatively poor drainage despite having (coarse) sandy texture (Gibbs, 1980). Sites were at least 100 m from roads and tracks. Within each site we established three 20 × 20 m plots ca. 100 m apart (pooled into a single replicate for analysis). Plots were chosen around mature large *N. menziesii* or *D. cupressinum* trees for ectomycorrhizal and arbuscular mycorrhizal sites, respectively.

2.2. Thin sections

We took undisturbed samples of the vertical face of 0–10 cm mineral soil intervals at each site, with Kubiëna tins of 5 × 7 × 3 cm. The samples in the tins were first impregnated with water-based acrylic varnish (Estopol) to replace water and ensure cohesion of the samples upon further handling. After drying of the varnish the samples were re-impregnated with polyester resin under vacuum, left to cure for 6 weeks and cut and mounted on glass slides (for polarised light microscopy). Bulk soil samples, unsieved, were taken from mineral soil layers at 10–30 cm and 30–50 cm depth, air dried and impregnated with polyester resin in aluminium foil shaped to 2 × 7 × 3 cm, and cut and mounted on glass slides as for the undisturbed samples. Polished sections of selected samples were prepared for scanning electron microscope (SEM) observation. We identified ‘tunnels’ by smooth sides, constant diameter, and rounded ends as opposed to square or lens-shaped etch pits and cracks (Fig. 1) as described by Hoffland et al. (2002).

2.3. Substrate bags

Fungal in-growth bags were constructed of nylon mesh (8 × 8 cm, 50-µm mesh size) by melting the edges, interfaced with a 4-mm-wide strip of PVC-film (flagging tape), with a heat sealer (the tape was necessary to achieve a strong bond). This nylon mesh size excludes roots, but allows hyphae to enter. Each nylon bag was

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