Feldspar Tunneling by Fungi along Natural Productivity Gradients

Ellis Hoffland,[1]* Reiner Giesler,[2] Antoine G. Jongmans,[1] and
Nico van Breemen[1]

[1]Laboratory of Soil Science and Geology, Wageningen University, P.O. Box 37, 6700 AA Wageningen, The Netherlands;
[2]Department of Forest Ecology, Swedish University of Agricultural Science, 901 83 Umeå, Sweden

ABSTRACT

Recently, it was hypothesized that ectomycorrhizas hyphae are involved in mineral tunneling. We evaluated the role of ectomycorrhizas in mineral weathering and the ecosystem influx of basic cations by correlating mineral tunnel density to ectomycorrhizas density in two forest productivity gradients. The gradients, two gentle slopes in northern Sweden, are the result of groundwater movement and are characterized by reduced productivity upslope due to lower nitrogen availability. As expected, ectomycorrhizas density in the O horizon was higher upslope, where nitrogen availability was lower and where the vegetation was dominated by ectomycorrhizas plant species. We consistently found that tunnel formation in mineral grains was more intense in nutrient-poor sites, indicating a higher contribution of fungi to ecosystem influx of potassium and calcium. ectomycorrhizas density was positively correlated with feldspar tunnel density in the upper 2 cm of the E horizon. This suggests that ectomycorrhizas are involved in mineral tunneling. We discuss the possible involvement of ericoid mycorrhizas and saprotrophic fungi in feldspar tunneling and the role of the weathering status of mineral grains as additional factors controlling mineral funneling.

Key words: boreal forest; ectomycorrhiza; ericoid mycorrhiza; feldspar tunneling; productivity gradient; weathering.

INTRODUCTION

Jongmans and others (1997) were the first to describe tunnels inside mineral grains taken from podzolic soils under coniferous forests. Several observations led to the hypothesis that these tunnels were formed by ectomycorrhizas (EcM) hyphae exuding mineral-dissolving organic anions. The size and shape of the tunnels perfectly matched those of the fungal hyphae, and some tunnels were colonized by fungal hyphae (Jongmans and others 1997). Furthermore, EcM fungi prevailed in all ecosystems where tunnels were found. EcM hyphae are known to exude organic anions, such as oxalate

and citrate, which can weather feldspar minerals (Cumming and others 2001; Landeweert and others 2001), and they are known to dissolve minerals and mobilize the nutrients contained by them (Landeweert and others 2001; Leyval and Berthelin 1993; Olsson and Wallander 1998; Wallander 2000a, 2000b; Wallander and Wickman 1999). The tunneling of feldspar minerals by EcM hyphae would offer the plant a monopoly for a specific source of mineral nutrients (Van Breemen and others 2000a) and possibly of nitrogen (N) (Hoffland and others 2001; Thompson and others 2001). Ectomycorrhizae would thereby contribute to ecosystem influx of these elements (Hoffland and others 2002) and could contribute to soil formation (Van Breemen and others 2000b).

Although there is little doubt that the tunnels are created by fungal hyphae, no direct evidence has been presented so far that EcM hyphae are exclusively responsible for tunnel formation. Arbuscular

mycorrhizae (AM) are unlikely candidates because they are not known to produce organic acids (Allen and others 1996) or any other weathering agent. Moreover, their hyphae are nonseptate, whereas tunnel-colonizing hyphae clearly show septae (Hoffland and others 2002). Ericoid plants are unavoidably present in the ecosystems considered, and ericoid mycorrhizal fungi could also be responsible. No records are available on the production of weathering agents by these fungi (mainly Ascomycota and Basidiomycota). However, the exudation of organic anions is a common feature among septate fungi. Saprotrophic Ascomycota and Basidiomycota are also known to exude organic anions with weathering potential, such as oxalate (Dutton and Evans 1996; Gadd 1999).

Because mineral tunneling is a slow process (Van Breemen and others 2000a; Hoffland and others 2002), it may be impossible to prove experimentally whether saprotrophic, arbuscular, or ericoid mycorrhizal, or EcM, or all four types of fungi are involved in feldspar tunneling. We therefore tried to solve this question indirectly by relating EcM density to tunnel frequency in selected field sites where we expected a gradient in EcM density and activity.

We selected two previously described forest productivity gradients, Betsele and Varjisån in northern Sweden (Giesler and others 1998, 2002). The gradients reflect the variations in pH, N supply, and vegetation that are usually observed in a larger, regional perspective. They consist of a toposequence with a groundwater recharge area upslope, blending into a groundwater discharge area downslope. Soils of the groundwater discharge area downslope have a higher pH and more available N (Nordin and others 2001). This higher pH is most likely caused by the discharge of highly alkaline groundwater and accumulated weathering products because no differences in mineralogy have been found. The higher N availability may be caused by (a) a supply of N via the groundwater, (b) higher N_2 fixation and mineralization rates due to a more favorable pH, and (c) less N loss due to fire because of the prevailing wet conditions (Högberg 2001).

The Varjisån gradient is similar to the Betsele gradient, for which the species composition has been described in detail (Giesler and others 1998). Upslope, an ericaceous dwarf shrub forest type is found, with EcM and ericoid mycorrhizal plants. Farther downslope, a short-herb forest type is found; plant species consist of a mixture of EcM trees, ericoid mycorrhizal dwarf shrubs, and potentially arbuscular mycorrhizal herbs. Downslope, the forest consists of tall-herb types, and the field layer is dominated by potentially arbuscular mycorrhizal herbs.

Using analyses of specific fatty acids, Nilsson and others (2001) showed that arbuscular mycorrhizal mycelium production decreases upslope along the two gradients. Due to the changes in plant species composition related to nutrient availability, we expected the reverse for EcM density. If ectomycorrhizae are responsible for mineral tunneling, we also expected a positive correlation between EcM density and tunnel frequency. This study was done to determine if such a correlation indeed exists.

MATERIALS AND METHODS

Study Sites

Two transects were used, both located in northern Sweden, about 150 km apart.

Betsele   The Betsele gradient has been described in detail before (Giesler and others 1998). It is 90 m long and located at the bottom of the Umeå River Valley, northwest of Betsele (64°39'N, 18°30'E, 235 m a.s.l.). Mean annual temperature and precipitation are 1.0°C and 570 mm, respectively. The gradient has a constant slope of about 2%. The nutrient-poor upper end (0–40 m) is a dwarf shrub forest type dominated by *Pinus sylvestris;* the field layer is dominated by *Vaccinium myrtillus* and *V. vitis-idaea.* The nutrient-rich lower end (90 m) is a tall-herb forest type dominated by *Picea abies;* the field layer is dominated by *Rubus ideaeus, Actaea spicata,* and *Aconitum septentrionale.* In between these two ends (50–80 m), the forest is a short-herb type (Giesler and others 1998).

Soils along the gradient are loamy, sandy tills with many boulders, classified as Typic Haplocryods in the recharge and as Aquic or Oxyaquic Haplocryods in the groundwater discharge areas (Giesler and others 1998; Soil Survey Staff 1998). They were deglaciated about 9200 years ago. The E horizon is about 0.05 m thick throughout the gradient.

N is probably the growth-limiting nutrient in the major part of the gradient (0–80 m). Plant production and foliar N concentrations increase gradually downslope, which is in line with increasing soil solution concentrations of NO_3^- and NH_4^+ (Giesler and others 1998; Nordin and others 2001). Ratios of potassium (K) to N, Calcium (Ca) to N, and magnesium (Mg) to N in leaves and needles support sufficient supply of K, Ca, and Mg relative to N throughout the toposequence. At the nutrient-rich lower end (90 m), phosphorus (P) is probably the plant growth-limiting factor (Giesler and others 2002). Soil solution pH of the lower half of the O

Table 1. Characteristics of the Two Forest Productivity Gradients

Gradient	Position (m)	Relative Altitude	Relative Productivity	Forest Type[1]	pH Lower O Horizon[1]	Weathering Status E Horizon[2]	Grain Size Distribution E horizon (w/w)[3]		
							< 50 μm	50–600 μm	> 600 μm
Betsele	0	High	Low	Dwarf shrub	3.5	M/H; H; H	0.24[a]	0.47[a]	0.29[a]
	45			Short herb	4.0	M/H; M/H; M/H	0.21[a]	0.43[a]	0.37[a]
	65			Short herb	4.5	H; H; M	0.24[a]	0.37[a]	0.39[a]
	90	Low	High	Tall herb	6.4	L/M; L/M; L/M	0.24[a]	0.35[a]	0.41[a]
Varjisån	0	High	Low	Dwarf shrub	4.1	H; H; H	0.22[a]	0.53[a]	0.25[a]
	40			Spruce/blueberry	4.7	M; M; M	0.12[b]	0.50[a]	0.37[b]
	55	Low	High	Tall herb	6.0	L; L; M	0.15[b]	0.30[b]	0.54[c]

[1]*Giesler and others (1998, 2002)*
[2]*Classes considered, depending on the percentage of feldspar grains that show weathering features other than tunnels, such as etch pits and cracks: Low, < 25%; Moderate, 25–50%; High, > 50%. Results of three replicates are given.*
[3]*Means (n = 8) with the same letter are not significantly different (Tukey test; comparisons for each gradient separately).*

horizon ranges from about 3.5 at the nutrient-poor end (0 m) to about 6.4 at the nutrient-rich lower end (90 m) of the gradient (Giesler and others 1998) (Table 1).

Varjisån The second gradient, Varjisån, has also been described before (Giesler and others 2002) and is similar to the Betsele gradient. It is located farther north (66°03'N, 19°38'E), and the mean annual temperature (-1°C) is lower. The altitude is similar (230 m a.s.l.), indicating that the age of the soils is highly similar. Soil types and soil pH (Table 1) are also similar. The dominant tall-herb species in the nutrient-rich end (55 m) are somewhat different. Varjisån is dominated, among others, by *Actaea spicata, Geranium sylvaticum,* and *Paris quadrifolia.*

Soil Sampling

Soil samples from the O and E horizons were taken at four (Betsele) or three (Varjisån) positions within the gradients in September 2000. Samples of the O horizon, from top to bottom, were taken with an auger (Ø, 0.07 m). Within 0.1 m distance of each O horizon sample, two samples from the uppermost 2 cm of the E horizon were taken with a smaller auger (Ø, 0.02 m) and combined into one sample. Within each position, this procedure was repeated eight times, so that 32 and 24 samples were available from the O and E horizons in Betsele and Varjisån, respectively.

Ectomycorrhizal Density and Root Length

To estimate the density of EcM root tips and root length per m² soil surface area, O horizon samples were washed and sieved (2 mm). The remainder of the sample was spread out in a container (0.40 ×

0.30 m) with a grid on the bottom. The number of EcM root tips was counted, and the total root length was determined using the cross-section method (Newman 1966).

Mineralogy and Texture

The mineralogical composition of E horizon samples was analyzed by x-ray diffraction. Previously, organic matter was removed from samples with H_2O_2. Guinier exposures were made from grains less than 2 mm, ground to a powder, and mixed with glycerol (Van Doesburg 1996). Texture was determined by sieving after sonication.

Micromorphology: Tunneling and Weathering Status

For analyses of tunnel frequency and weathering status of mineral grains, the 50–600-μm fractions of E horizon samples were impregnated with polyester resin (Synolyte 544-A-4). Only the 50–600-μm fraction was used, because grains smaller than 50 μm are too small to detect tunnels and the presence of grains larger than 600 μm in a field of view would increase the variation between samples dramatically. Thin sections (1.4 × 1.4 cm) were made according to FitzPatrick (1970) and examined with a petrographic light microscope (Zeiss Axioskop) in cross-polarized light. Thin sections were described according to Bullock and others (1985).

Weathering phenomena designated as tunnels had to meet the following criteria: (a) The diameter varies between 3 and 10 μm but is constant for each individual tunnel, (b) the walls are smooth and parallel, and (c) the end is rounded. This is to distinguish tunnels from other weathering features

such as etch pits and cracks, as illustrated photographically by Hoffland and others (2002). Digital images were made with a CoolSNAP microscope camera (RS Photometrics), and the images were used to measure tunnel length (at magnification ×200) and surface area (×100) of all cross-sectioned minerals in a field of view. The images were analyzed using the Image-Pro Plus software package (Media Cybernetics). Tunnel length was expressed as μm tunnel mm^{-2} mineral surface examined. Per sample, about six fields of view were analyzed, yielding a total surface of cross-sectioned minerals of at least 2.5 mm^2.

The weathering status of feldspar grains was assessed by estimating the percentage of grains that show weathering features other than tunnels, such as etch pits and cracks. The following classes were distinguished: low, less than 25%; moderate, 25%–50%; high, more than 50% of the grains show weathering features. Three replicate samples were considered for each position within both gradients.

Statistics

For statistical comparison between positions along the gradient, one-way analysis of variance (ANOVA) was performed with position as a fixed factor. Multiple comparisons in variance analyses were performed with Tukey's test.

For statistical correlation between tunnel density and EcM density, we used linear regression analysis with site as a dummy variable, including interaction between the two independent variables (site and EcM density). The EcM density was used as independent variable because we hypothesized that there was a causal relationship between tunnel formation and the hyphal activity of EcM. We used the mean values of these two parameters for each position within the gradient because the individual replicates were not taken randomly along the gradient but were spread around selected positions. Moreover, the individual tunnel and EcM densities of each replicate are not necessarily coupled for the following reasons: (a) EcM densities vary strongly in time (Söderström 1979). The densities we found in September are random indications and are probably different from the ones to be found in spring. However, we expect the trends along the gradient to be similar throughout the year. (b) Mineral tunneling is the result of a process that takes thousands of years (Hoffland and others 2002), during which time EcM densities have probably varied widely in space (Bååth and Söderström 1982). Thus, in terms of spatial distribution, our data are random indications, but they are still indicative of EcM distributions within the gradients during the time they have existed.

Analyses of variance and linear regression analyses were done with SPSS software (SPSS, Chicago, IL, USA). Transformations were performed if necessary to meet the criterion of homogeneity of variances. Significant differences refer to $P < 0.05$.

RESULTS

Tunnel Formation and Weathering along the Gradients

The number of tunnels per cross-sectioned mineral surface area (Table 2) differed significantly within both the Betsele ($P = 0.02$) and Varjisån ($P = 0.03$) gradients. The fewest tunnels were found at the lower, nutrient-rich ends of both gradients (90 and 55 m, respectively). There was also a tendency for decreased tunnel density toward the lower ends of the slopes in both Betsele and Varjisån (Table 2). Tunnel density in Betsele varied from 200 to 40 μm tunnel per cm^2 mineral surface area, whereas tunnel densities were generally lower at Varjisån (Table 2). Due to large within-site variation, differences were not statistically significant. Tunnels were found exclusively in feldspar grains. Mean tunnel length showed no trend with the position in the gradient (Table 2). In Betsele, the length of the tunnels varied (not statistically significant) but showed no consistent pattern with forest productivity. In Varjisån, individual tunnel lengths were similar along the slope.

The thin sections allowed easy distinction be-

Table 2. Feldspar Tunneling in the Uppermost 2 cm of the E Horizon across Two Forest Productivity Gradients

Gradient	Position (m)	Number of Tunnels[1] (cm^{-2})	Tunnel Density[1] (μm cm^{-2})	Mean Tunnel Length (μm)
Betsele	0	15.2[a]	165[a]	15[a]
	45	9.5[ab]	204[a]	21[a]
	65	2.8[b]	79[a]	32[a]
	90	2.6[b]	39[a]	16[a]
Varjisån	0	4.9[a]	106[a]	23[a]
	40	4.8[a]	128[a]	25[a]
	55	1.0[b]	25[a]	23[a]

Means (n = 8) with the same letter are not significantly different (Tukey test; comparisons per gradient).
[1]*Number of tunnels and tunnel density are expressed per cross-sectioned mineral surface area considered.*

Table 3. Ectomycorrhizal Root Tips (EcM) in the O Horizon of Two Forest Productivity Gradients

Gradient	Position (m)	O Horizon Thickness (cm)	EcM per Soil Surface Area (cm^{-2})	EcM per Root Length (m^{-1})
Betsele	0	5.9[a]	170[a]	65[a]
	45	6.6[a]	151[a]	55[a]
	65	5.3[a]	77[b]	46[a]
	90	3.1[b]	20[c]	13[b]
Varjisån	0	3.6[a]	180[ab]	53[ab]
	40	3.8[a]	226[a]	66[a]
	55	4.8[a]	71[b]	25[b]

Means (n = 8) with the same letter are not significantly different (Tukey test; comparisons for each gradient separately).

tween tunnels and other, non–fungus-mediated weathering features, such as etch pits and cracks. In both gradients, the feldspar grains had fewer etch pits and cracks in the nutrient-rich lower end of the slope (90 and 55 m, respectively). (Table 1). A pronounced gradient in weathering status was found in Varjisån. This was less obvious in Betsele.

No differences in mineralogy were found among the samples, or among the different positions within a gradient, or between the two gradients. All samples contained mainly quartz (60%–70%) and about 20%–30% feldspars. The remainder of the minerals (about 10%) were amphiboles. Among the feldspars, the major part (about 70%) was plagioclase, which were further identified as oligoclase ($(NaAlSi_3O_8)_{90-70}(CaAl_2Si_2O_8)_{10-30}$). About 30% of the feldspars were K feldspars ($KAlSi_3O_8$), which could not be further identified as orthoclase or microcline.

Soil texture was similar in the two gradients. In the Varjisån gradient, the finer fractions increased significantly toward the higher, nutrient-poor end (0 m) of the toposequence (Table 1). Within the Betsele gradient, the E horizon also tended to be finer-textured toward the higher end (0 m) of the slope.

Ectomycorrhizal Density

There was a strong gradient in EcM root tip density across the two gradients (Table 3). Generally, the density of the EcM root tips was lower in the nutrient-rich lower end of the gradient (90 and 55 m, respectively). In both Betsele ($P < 0.0001$) and Varjisån ($P = 0.02$), there was a significant effect of position along the gradient on EcM root density,
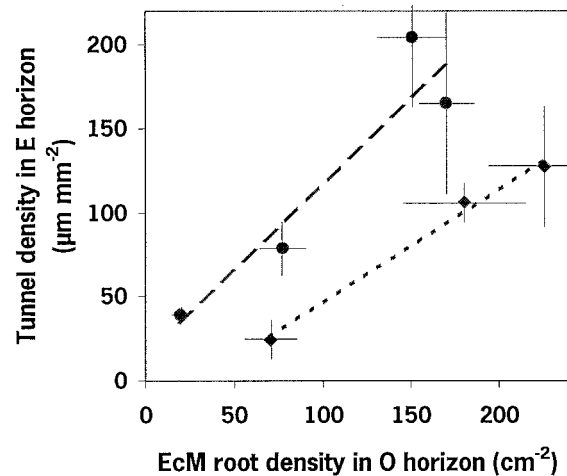
Figure 1. Correlation of ectomycorrhizas (EcM) root tip density in the O horizon and feldspar tunnel density in the uppermost 2 cm of the E horizon in two forest productivity gradients (●, Beetsle; ⋄, Varjisån). Data points are means of eight replicates, both for x and y values, as given in Table 3 and 2, respectively. The bars represent SEs. The lines (*dashed* for Betsele; *dotted* for Varjisån) are based on regression analysis.

expressed as number of EcM root tips either per unit of soil surface area or per unit root length. Arbuscular mycorrhizas were found only in samples from the richer ends of both gradients (90 and 55 m, respectively).

Relationship of Ectomycorrhizas Density to Tunnel Density

Ectomycorrhizal and tunnel densities were linearly positively related (Figure 1). The linear regression model with EcM density and site as independent variables explained 84% (adjusted R^2) of the variation in tunnel density ($P = 0.03$, $n = 7$). The interaction between EcM density and site was not significant ($P = 0.35$).

DISCUSSION

This study clearly shows that feldspar tunneling (a) differs in a landscape perspective (Table 2) and (b) is positively related with EcM root density (Figure 1).

Tunnel Formation and Weathering along Productivity Gradients

Our data show that both tunnel formation in mineral grains and surface weathering in the E horizon is more intense in nutrient-poor sites along natural productivity gradients (Tables 1 and 2). These gradients represent the variation in plant community

composition, soil chemistry, and N availability frequently found in Fennoscandian boreal forests on a larger, regional scale (Högberg 2001). Soil solution pH was lower at the nutrient-poor sites along the gradients (Giesler and others 1998, 2002) and probably explains the higher frequency of feldspar grains with etch pits (Blum and Stillings 1995) (Table 1). Etch pits are easily distinguishable from fungal tunnel formation in thin sections (Hoffland and others 2002). Increased tunneling implies a higher contribution of fungi to weathering and ecosystem influx of K and Ca at nutrient-poor sites. It could not be explained by differences in mineralogy because none were observed. Textural differences were relatively small or nonexistent (Table 1) and are thus not likely to explain the differences in tunnel formation along the gradients either.

The increased density of feldspar tunnels is caused by an increase in the number of tunnels and not by an increase in individual tunnel length (Table 2). This could mean that a tunnel is formed by one single hypha instead of several generations and that the formation of a single tunnel is not as prolonged a process as has been assumed to date (Van Breemen and others 2000a).

Previously, we hypothesized that the onset of tunneling was related to the presence of etch pits on mineral surfaces (Hoffland and others 2002). Surface roughnesses could slow down the diffusion of the compounds exuded by hyphal tips into the bulk solution. This could accelerate tunneling. Our data are in line with this hypothesis: The more feldspar grains show signs of weathering other than tunneling (Table 1), the more tunnels are found inside the grains (Table 2). It seems likely that tunnel formation depends on the chance that a hypha hits an etch pit or crack on a feldspar grain surface, making both the density of etch pits and cracks and the density of hyphae equally important factors.

Relationship between Ectomycorrhizas Density and Tunnel Formation

In line with our expectations, we found higher EcM densities in the poorer ends (0 m) of both gradients (Table 3). This can be explained by the higher density of EcM plant species that has developed at the nutrient-poor sites as a result of environmental conditions (Giesler and others 1998, 2002). The positive regression between EcM root density in the O horizon and tunnel density in the E horizon (Figure 1) supports the hypothesis that EcM fungi are involved in feldspar tunneling.

We took the density of EcM root tips in the organic horizon as an indication that EcM hyphae were active in the upper 2 cm of the E horizon. We

did so because tunnel frequency is highest in this upper part of the E horizon (Hoffland and others 2002), suggesting that feldspar tunneling is related to biological activity in the O horizon. We assume that EcM hyphae from O horizon root tips penetrate into the uppermost part of the E horizon. EcM hyphal tips are the parts of the ectomycorrhizas expected to be involved in mineral tunneling. So far, EcM root density is the only parameter to estimate activity of EcM hyphae. There are, however, strong indications that EcM hyphal density is strongly and positively correlated to EcM root density in the two productivity gradients. Studies with mesh bags filled with mineral grains, from which saprotrophic hyphae were excluded, that were buried at different positions along the two gradients have shown that EcM mycelium production decreases downslope of the gradients (Nilsson and others 2001).

A significant regression between EcM root density and mineral tunneling does not prove a causal relationship. Therefore, the possible involvement of other fungi in mineral tunneling along the two productivity gradients has to be evaluated carefully. We confirmed that AM fungi are unlikely candidates because we found the highest tunnel densities at the nutrient-poorends of the gradients (0 m) (Table 2), where both AM mycorrhizal plant species (Giesler and others 1998) and AM mycelium production (Nilsson and others 2001) are absent.

It is unlikely that ericoid mycorrhizal fungi are solely responsible for mineral tunneling. Based on plant species composition, we expected ericoid mycorrhizal density to be positively correlated to mineral tunnel density. However, we did find tunnels in the lower ends of the two gradients (90 and 55 m, respectively), where no ericoid plant species are found (Giesler and others 1998). It is unlikely that during the period of soil formation ($\pm$ 9500 years ago), ericoid plant species have grown in these lower ends because the presence of the productivity gradient and the related gradient in plant species composition is due to topography and must therefore have been established quickly after deglaciation.

The involvement of saprotrophic fungi in mineral tunneling cannot be excluded. It is likely that saprotrophic fungal density increases together with EcM densities downslope of the gradients, but less strongly so. Future studies similar to this one will benefit from newly developed tools to distinguish densities of EcM mycelium from other mycelium in field samples (Landweweert and others 2003a, 2003b). All current markers to quantify fungal biomass are aspecific and could not distinguish be-

tween ectomycorrhizas and saprotrophic and ericoid mycorrhizal fungi (Wallander and others 2001). In the best attempt so far, L. O. Nilsson and H. Wallander (unpublished) found more biomass of EcM than of saprotrophic fungi in the O horizon at the top of the gradients (0 m), whereas the opposite was true at the lower ends of the gradients. The biomass of both EcM and saprotrophic fungi decreased toward the nutrient-rich end of the slopes; however, the decrease of saprotrophic biomass was less strong. These estimates were based on the assumption that phospholipid fatty acid biomarkers of EcM origin degraded after incubation of soil for 3 months, whereas those of saprotrophic origin remained constant during the incubation. This may have caused an overestimation of saprotrophic biomass at the nutrient-poor end (0 m), where EcM biomass densities were higher. The correlation between saprotroph density in the O horizon and mineral tunneling is therefore likely to be less strong than the one between EcM density and tunneling. No data are available for the E horizon, where fungal tunnels are concentrated.

CONCLUSIONS

In conclusion, we found that feldspar tunneling is more intense in sites with lower nutrient availability. We found a significant positive correlation between EcM root tip density and feldspar tunnel density. This is in line with the hypothesis that EcM hyphae play a role in this type of mineral weathering, thereby contributing to ecosystem influx of K and Ca. This contribution is higher in areas of reduced N availability. Mineral tunneling seems to be accelerated by prior chemical weathering (etch pit formation).

We confirmed that AM fungi are unlikely to be involved in mineral tunneling. Although EcM are most likely responsible for mineral tunneling, we cannot definitively exclude the involvement of ericoid mycorrhizae and saprotrophic fungi. New tools need to be developed that can determine the hyphal densities of these different functional types of fungi and to provide definitive answers to questions concerning involvement of different types of fungi in feldspar tunneling.

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