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Microbial characteristics of ectomycorrhizal mat communities in Oregon and California*

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Summary. Specialized ectomycorrhizal fungi form dense mats in forest soils that have different enzyme levels, higher respiration rates, more biomass, different soil fauna, and different soil chemistry compared with adjacent soils not obviously colonized by these mats. In this study, mats formed by two genera of fungi collected in three locations were compared with a wide range of measurements. Per cent moisture, pH, chloroform fumigation-flush C, anaerobic N mineralization, exchangeable ammonium, and respiration, N_2 fixation, and denitrification rates were compared between soils or litter colonized by ectomycorrhizal mat-forming fungi and adjacent non-mat material. Significant differences were observed between the two genera of mat-forming fungi and also between mats formed primarily in mineral soil and those formed in litter. These differences suggest that different mat-forming fungi perform different functions in forest soils and that these fungi function differently in mineral soil compared with litter.

Key words: Ectomycorrhizae – Microbial activity – Nitrogen cycle – Mat communities

It has been generally accepted that the primary role of mycorrhizal fungi is to transport inorganic P and N and possibly moisture from the soil to the plant roots. Recent studies have shown that this may be a simplistic view of how mycorrhizal fungi function. For example, Read and coworkers (Stribley and Read 1980; Bajwa and Read 1985; Abuzinadah et al. 1986) have shown that mycorrhizal fungi can use organic sources of N.

We have been studying ectomycorrhizal mat communities in Douglas-fir ecosystems of the Pacific Northwest. The mat communities are perennial features in these forests and are easily detected by the presence of high concentrations of rhizomorph material in the mineral soil (Griffiths et al. 1991). These mycorrhizal mat communities provide an excellent opportunity to study, in the field, their function as tree symbionts. Initial studies have suggested that the mat communities are capable of degrading complex organic materials (Griffiths et al. 1990). In this way, organic N and P from both litter and soil organic matter may become available to mycorrhizal fungi (Caldwell 1990, unpublished data). Ratios of chloroform fumigation-flush C to anaerobic N mineralization ($C_{fum}:N_{min}$) are consistently higher in mat soils compared to non-mat soils, suggesting either that differences occur in the C:N ratios of the microfauna or that labile N is reduced in the mats (Griffiths et al. 1990). Comparisons of denitrification and acetylene reduction rates suggest that compared to non-mat soil, the ectomycorrhizal mat communities may act to accumulate fixed N_2 (Griffiths et al. 1990).

During comparisons of mat soils and soils not obviously colonized by mat-forming mycorrhizal fungi, a number of additional differences have been observed. Respiration rates and levels of microbial biomass as measured by chloroform fumigation-flush C were significantly higher in mat soils (Griffiths et al. 1990). In addition, differences in extractable cation chemistry (Rose et al. 1990), greater concentrations of oxalate (Cromack et al. 1979; Sollins et al. 1981), and oxalate-degrading bacteria (Knutson et al. 1980) and qualitative differences in protozoa and microarthropod populations (Cromack et al. 1988) have also been reported.

These observations were all made on the ectomycorrhizal fungus *Hysterangium setchellii* growing at one location in the Oregon Coast Ranges. The objective of the present study was to expand these observations to other species of the genus *Hysterangium* and to the ectomycorrhizal fungus *Gautieria monticola*. In addition, we wanted to compare mat-forming mycorrhizal fungi that colonize litter with those colonizing mineral soil, and to study in greater detail the composition of the microflora present.

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Methods and materials

Site description and sample preparation

Three sites were sampled. Site one was in the Oregon Coast Ranges (Woods Creek on Mary's Peak) at approximately 460 m elevation, which is dominated by a 75 to 80-year-old stand of Douglas-fir. The soil at this site is a gravelly loam derived from a colluvium of weathered basalt and sandstone. This site has been described in detail by Fogel (1976), Cromack et al. (1979), and Hunt and Trappe (1987). Site two was in the Oregon Cascade Mountains in the H. J. Andrews Experimental Forest at approximately 625 m elevation and is dominated by a 42-year-old Douglas-fir stand that had been precommercially thinned 10 years previously. The soil at this site is another gravelly loam derived from a colluvium of Mazama ash where the bedrock is primarily pyroclastic. Site three was located 9 miles south of Albion on the northern California coast at 50 m elevation. This 25-ha site was planted with *Eucalyptus globulus* 25 years ago. The soil at this site is sand. At each site and sampling time, five samples were taken from different mat soils and adjacent non-mat soils using a trowel.

At site one in the Coast Ranges, we studied two ectomycorrhizal mat communities; *H. setchellii* and *G. monticola*. The mat communities were located in the mineral soil with little or no visible evidence that their rhizomorphs penetrated the litter-moss layer. However, there was extensive rhizomorph development in the top 10 cm of the mineral soil. These mats were most often found under a continuous bryophyte layer. At site two in the Cascade Mountains, *H. setchellii* mats were scarce; therefore, we sampled two closely related mat-forming ectomycorrhizal species, *H. coriaceum* and *H. crassirhachis*, both occurring primarily in mineral soil, as well as *G. monticola* which was found exclusively in mineral soil. At site three, in northern California, the dominant mat-forming ectomycorrhizal fungus was *H. gardneri* which is associated exclusively with *Eucalyptus* litter. At this site, we compared mat and non-mat litter rather than mat and non-mat soil, as was done in sites one and two.

Each site was sampled at least once during each major season, although site three was sampled four times instead of five. In previous work (Griffiths et al. 1990), we had determined that there were four times of year during which distinctive physiological changes occurred in the ectomycorrhizal mat community: (1) in late summer when soils were dry and warm, (2) in fall with initiation of the rainy season while the ground was still relatively warm, (3) in the wet and cold winter, and (4) in the moist and warm mid- to late spring. After samples had been collected at each site, the soils or litter were placed in plastic bags and transported to our laboratory in ice chests for initial processing. Rocks, stems, small branches, and roots were removed from the samples by hand.

Assays

The methods used to assay soil moisture, extractable ammonium, N mineralization, respiration rates, chloroform fumigation-flush, and N_2 fixation and denitrification rates were the same as those described by Griffiths et al. (1990). The ammonia-sequestering capacity of California litter was measured by adding 5 g field-moist litter to 30 ml of 0.1 *M* NH_4Cl and shaking the mixture for 30 min at 22 °C. Samples were filtered through a Whatman no. 1 filter, and the litter caught by the filter was washed three times with 30 ml deionized water. The filter with litter was added to 50 ml 2 ml 2 *M* KCl and shaken for 1 h, and the ammonia concentration measured as above. Filter paper without litter was run as a control.

Measurements of all variables except chloroform fumigation-flush C were made using duplicate subsamples. Triplicate subsamples were analyzed for chloroform fumigation-flush C. Three-way analyses of variance using SPSS (Nie et al. 1975) was performed using season (spring, summer, fall, and winter), site (Mary's Peak, Andrews, and California) and mat type (*Hysterangium, Gautieria,* and non-mat) as main effects. The data were analyzed in three ways, mat and non-mat soils in Oregon, *Hysterangium* and non-mat soils in Oregon and California, and *Hysterangium* and non-mat soils in California. The mat/non-mat comparisons were made using the separate Oregon and California analyses and the combined Oregon and California analysis was used to compare the significance of difference by site. Least significant differences (Fisher-protected LSD) were calculated for all values only when F was significant at $P \leq 0.05$.

Results

Abiotic variables

The pH was significantly higher in non-mat mineral soils and litter than in mat soils and litter at all three sites (Table 1). Mineral soils colonized by *G. monticola* were significantly drier than the non-mat soils at both Oregon sites (Table 2). There was no significant difference in moisture between mat and non-mat litter from the California site where all mats were *Hysterangium gardneri*, nor between *Hysterangium* mat soil and non-mat soil in the Oregon sites. Extractable ammonium levels associated with litter in the California site were significantly greater than levels observed in the Oregon mineral soil samples (Table 3). In addition, the ammonium concentrations were significantly greater in California mats than in non-mat litter, extractable ammonium being 14.1 ± SD 10.3 and 45.7 ± SD 43.3 $\mu g\ g^{-1}$ dry weight, respectively, for non-mat and mat litter. In Oregon, when data were summed over all dates and both sites, ammonium levels in the mat and non-mat mineral soils did not differ significantly. There was no significant difference between the ammonium-sequestering capacity of five California non-mat litter samples (462 ± SD 86 $\mu g\ NH_4^+$-N sequestered g^{-1} dry weight) compared with five mat litter samples (453 ± SD 52 $\mu m\ NH_4^+$-N sequestered g^{-1} weight).

Chloroform fumigation-flush C and N mineralization measurements

With few exceptions, there were significant differences between chloroform fumigation-flush C (C_{fum}) in both

Table 1. Soil pH in each ecosystem over a 1-year period for mat and non-mat soils or litter

Location	Month	Non-mat	*Hysterangium* mat	*Gautieria* mat
Mary's Peak, Oregon	May	5.10^A	4.77^B	4.63^C
	Jun	5.67^A	4.77^B	4.84^C
	Aug	5.16^A	4.78^C	4.91^B
	Nov	5.39^A	4.75^C	4.85^B
	Mar	5.12^A	4.88^B	5.07^A
H. J. Andrews, Oregon	May	5.61^A	5.51^B	5.28^C
	Aug	5.27^A	4.78^C	5.04^B
	Nov	5.73^A	5.37^B	5.43^B
	Apr	5.35^A	4.94^C	5.09^A
California	Mar	5.45^A	5.14^B	*
	Jun	4.71^A	4.54^A	*
	Sep	5.44^A	4.73^B	*
	Dec	5.12^A	4.79^B	*
	Mar	5.20^A	5.03^A	*

Values followed by different letters are significantly different at $P \leq 0.05$; least significant differences (LSD) were 0.098 (Oregon) and 0.284 (California) for mat/non-mat comparisons

*No *Gautieria* mats found in California litter

Table 2. Soil per cent moisture

Location	Month	Non-mat	*Hysterangium* mat	*Gautieria* mat
Mary's Peak, Oregon	May	62.4^{A}	42.2^{B}	66.7^{A}
	Jun	59.8^{A}	68.2^{A}	40.8^{B}
	Aug	27.5^{A}	24.5^{A}	24.0^{A}
	Nov	49.7^{A}	36.2^{A}	28.7^{B}
	Mar	51.4^{A}	52.2^{A}	38.5^{B}
H.J. Andrews, Oregon	May	49.9^{A}	58.0^{A}	34.5^{B}
	Aug	16.9^{A}	27.6^{A}	17.6^{A}
	Nov	65.7^{A}	60.8^{A}	51.4^{B}
	Apr	75.5^{B}	101.3^{A}	48.8^{C}
California	Mar	25.9	35.1	*
	Jun	38.1	25.5	*
	Sep	17.8	23.4	*
	Dec	58.0	48.2	*
	Mar	114.4	138.2	*

LSD = 13.6 for Oregon mat/non-mat comparisons. For other explanations, see Table 1

Table 3. Soil-extractable ammonia using 2.0 *M* KCl

Location	Month	Non-mat	*Hysterangium* mat	*Gautieria* mat
Mary's Peak, Oregon	May	14.3^{A}	5.12^{B}	4.15^{B}
	Jun	2.07^{B}	5.24^{A}	2.07^{B}
	Aug	2.31^{B}	7.44^{A}	4.71^{B}
	Nov	1.63^{A}	2.83^{A}	3.13^{A}
	Mar	1.84^{A}	1.30^{A}	1.48^{A}
H.J. Andrews, Oregon	May	1.06^{A}	1.57^{A}	1.14^{A}
	Aug	2.49^{A}	1.72^{A}	3.72^{A}
	Nov	1.01^{A}	0.89^{A}	0.86^{A}
	Apr	0.56^{A}	1.85^{A}	0.70^{A}
California	Mar	8.69^{B}	70.9^{A}	*
	Jun	7.63^{B}	29.4^{A}	*
	Sep	16.2^{B}	25.2^{A}	*
	Dec	16.2^{A}	20.4^{A}	*
	Mar	9.5^{B}	45.1^{A}	*

Values are μg ammonium-N g^{-1} dry weight soil or litter; LSD = 2.7 (Oregon) and 7.6 (California) for all mat/non-mat comparisons; for other explanations, see Table 1

Table 4. Fumigation flush C

Location	Month	Non-mat	*Hysterangium* mat	*Gautieria* mat
Mary's Peak, Oregon	May	145^{C}	702^{A}	351^{B}
	Jun	161^{B}	525^{A}	361^{A}
	Aug	70^{C}	898^{A}	304^{B}
	Nov	160^{C}	989^{A}	404^{B}
	Mar	153^{C}	956^{A}	390^{B}
H.J. Andrews, Oregon	May	204^{C}	921^{A}	447^{B}
	Aug	96^{B}	602^{A}	418^{A}
	Nov	209^{C}	1099^{A}	633^{B}
	Apr	148^{C}	861^{A}	597^{B}
California	Jun	423	362	*
	Sep	353	380	*
	Dec	590	984	*
	Mar	967	653	*

Values are mc C 100 g^{-1} dry weight; LSD = 190 for Oregon mat/non-mat comparisons; for other explanations, see Table 1

Table 5. Mineralizable N

Location	Month	Non-mat	*Hysterangium* mat	*Gautieria* mat
Mary's Peak, Oregon	May	255^{B}	199^{B}	134^{C}
	Jun	207^{B}	268^{A}	126^{C}
	Aug	219^{B}	269^{A}	153^{C}
	Nov	118^{B}	184^{A}	159^{A}
	Mar	69^{B}	118^{A}	55^{B}
H.J. Andrews, Oregon	May	98^{B}	218^{A}	109^{B}
	Aug	203^{B}	445^{A}	144^{C}
	Nov	86^{B}	139^{A}	138^{A}
	Apr	90^{B}	220^{A}	79^{B}
California	Mar	166	446	*
	Jun	402	556	*
	Sep	875	472	*
	Dec	380	352	*
	Mar	412	618	*

Values are μg N g^{-1} dry weight soil; LSD = 21 for all Oregon mat/non-mat comparisons; for other explanations, see Table 1

Table 6. Ratio of C from chloroform-fumigation flush CO_2 to mineralizable N

Location	Month	Non-mat	*Hysterangium* mat	*Gautieria* mat
Mary's Peak, Oregon	May	6.11^{B}	35.9^{A}	28.2^{A}
	Jun	8.37^{B}	22.5^{A}	31.1^{A}
	Aug	3.90^{B}	33.3^{A}	20.3^{A}
	Nov	10.3^{B}	54.0^{A}	27.3^{B}
	Mar	23.6^{C}	118^{A}	77.3^{B}
H.J. Andrews, Oregon	May	24.2^{B}	45.2^{A}	47.5^{A}
	Aug	5.69^{B}	13.9^{B}	38.2^{A}
	Nov	26.7^{C}	95.6^{A}	49.3^{B}
	Apr	25.7^{C}	96.4^{A}	53.2^{B}
California	Jun	12.8	9.77	*
	Sep	2.81	11.54	*
	Dec	15.6	29.5	*
	Mar	23.5	10.8	*

LSD = 20.2 for all Oregon mat/non-mat comparisons; for other explanations, see Table 1

H. setchellii and *G. monticola* mats compared to non-mat soils at the two Oregon sites throughout the year (Table 4). The highest flush C values occurred in *H. setchellii* mats, with intermediate values in *G. monticola* mats and the lowest values in non-mat soils. There was no significant difference between flush C in mat and non-mat litter samples from the *Eucalyptus* stand in northern California. In June and March, flush C was greater in the California non-mat litter samples than in the mat litter.

N mineralization (N_{min}) was significantly higher in a number of mat/non-mat comparisons at all sites, as indicated in Table 5. When N mineralization was used to generate C_{fum} : N_{min} ratios, some interesting trends were observed (Table 6). There was a significant difference between both *Hysterangium* sp. and *G. monticola* mat soils compared with non-mat Oregon soils from both sites. There was no significant difference between the C_{fum} : N_{min} ratios in mat and non-mat litter in the California samples.

Respiration, N fixation, and denitrification rates

Respiration rates were significantly greater in mat soils or their litter than in non-mat soils or the corresponding litter at all locations during most of the sampling periods (Table 7), and respiration rates in non-mat samples from California were significantly greater than those from the Oregon sites. In California, the only time when respiration rates were greater in non-mat litter than in mat litter was in September, when the litter was driest.

There was no significant difference between denitrification rates compared across mat, site, or date, primarily due to wide variations in the data (Table 8). The mean denitrification rates observed in mat litter were greater than those in non-mat litter in the California samples for four of the five months tested, although these differences were not statistically significant. There was also no significant difference between the N_2-fixation rates in mat and non-mat samples by site (Table 9); however, N_2-fixation rates were greater in mat litter in the first three sampling periods at the California site.

Discussion

Differences between mat types

In a previous study, soils associated with *H. setchellii* and *G. monticola* mat soils had significantly different levels of soil enzymes, suggesting that different mat-forming mycorrhizal fungi may play different roles in plant nutrition (Caldwell 1990, unpublished data). Enzymes that break down plant structural polymers were found at significantly higher levels in *H. setchellii* mat soils than in *G. monticola* mat soils. Since *G. monticola* as higher concentrations of calcium oxalate than *H. setchellii* (Sollins et al. 1981), it is likely that of the two extomycorrhizal fungi, *G. monticola* is better suited for extracting plant nutrients by weathering minerals, since oxalic acid is known to have mineral-soil weathering properties (Robert and Berthelin 1986; Tan 1986). *H. setchellii,* however, has elevated hydrolase activities relative to *G. monticola,* suggesting that of the two, *H. setchellii* should be better suited to breaking down organic matter.

In this study, additional differences were observed between soils colonized by *G. monticola* and *Hysterangium* spp. Chloroform fumigation-flush C was significantly greater in samples collected from *Hysterangium* spp. mats than *G. monticola* mats, both of which produced significantly greater C_{fum} than non-mat soil (Table 4), supporting previous findings of greater microbial biomass, and C levels, in mat-dominated soils (Cromack et al. 1988). Of the two fungi, *G. monticola* formed significantly drier mat soil compared with the adjacent non-mat soils (Table 2). The dryness associated with *G. monticola* is an interesting feature of these mats. A recent study of soil hydrophobicity showed that *G. monticola* mats are extremely hydrophobic, with negligible water penetration after 24 h (K. Anderson 1989, personal communication). This concurs with informal field observations that *G. monticola* mats appear much drier than adjacent soils during much of the year. In contrast,

Table 7. Respiration rates

Location	Month	Non-mat	*Hysterangium* mat	*Gautieria* mat
Mary's Peak, Oregon	May	0.299^{B}	1.247^{A}	0.910^{A}
	Jun	0.224^{B}	1.172^{A}	1.031^{A}
	Aug	0.140^{C}	0.905^{B}	1.217^{A}
	Nov	0.145^{C}	0.966^{B}	1.033^{A}
	Mar	0.136^{C}	0.619^{B}	1.183^{BA}
H. J. Andrews, Oregon	May	0.356^{B}	1.032^{A}	1.201^{A}
	Aug	0.253^{B}	1.236^{A}	1.111^{A}
	Nov	0.128^{B}	0.786^{A}	0.833^{A}
	Apr	0.121^{C}	0.835^{A}	0.466^{B}
California	Mar	0.813^{B}	1.809^{A}	*
	Jun	0.625^{B}	1.476^{A}	*
	Sep	0.745^{A}	0.418^{A}	*
	Dec	0.575^{B}	1.705^{A}	*
	Mar	0.820^{B}	1.596^{A}	*

Values are μmol CO_2 g^{-1} dry weight h^{-1}; LSD = 0.34 (Oregon) and 0.43 (California) for mat/non-mat comparisons; for other explanations, see Table 1

Table 8. Denitrification rates

Location	Month	Non-mat	*Hysterangium* mat	*Gautieria* mat
Mary's Peak, Oregon	May	32,2	20.0	12.1
	Jun	31.7	42.7	7.9
	Aug	19.9	12.3	36.5
	Nov	ND	ND	ND
	Mar	1.26	0	8.1
H. J. Andrews, Oregon	May	79.7	86.2	63.6
	Aug	51.1	0	23.0
	Nov	ND	ND	ND
	Apr	0	0	0
California	Mar	37.0	125	*
	Jun	36.3	72.7	*
	Sep	0.9	14.3	*
	Dec	177	24.3	*
	Mar	103	608	*

Values are pmol NO g^{-1} dry weight soil d^{-1}; ND, not determined; for other explanations, see Table 1

Table 9. N_2 fixation rates

Location	Month	Non-mat	*Hysterangium* mat	*Gautieria* mat
Mary's Peak, Oregon	May	15.9	38.1	76.4
	Jun	32.0	78.8	107
	Aug	12.3	110	53.6
	Nov	0	0	0
	Mar	0	0	0
H. J. Andrews, Oregon	May	3.42	3.29	15.0
	Aug	0	92.8	79.0
	Apr	0	0	0
California	Mar	121	229	*
	Jun	72.7	314	*
	Sep	0	10.3	*
	Dec	780	612	*
	Mar	607	0	*

Values are pmol ethylene g^{-1} dry weight soil d^{-1}; for other explanations, see Table 1

Hysterangium spp. mats wet up soon after the onset of fall rains.

The significance of the shifts in C:N ratios

In a previous seasonal study of *H. setchellii* mat soils, the ratio of $C_{fum}:N_{min}$ was greater in mat soils than in non-mat soils (Griffiths et al. 1990). The results from the current study confirm this observation in both Oregon locations. Ratios of chloroform fumigation-flush C to N mineralization were significantly higher in *Hysterangium* spp. and *G. monticola* mats than in non-mat soils (Table 6). This pattern might be expected if significant differences occur in the microbial populations of mat and non-mat soils. For example, it is known that the C:N ratio of fungi is generally much greater than of bacteria, with C:N ratios of 4.5 to 15 common for active fungal hyphae (40–100 for inactive hyphae but 3–5 common for bacteria; Paul and Clark 1989). Protozoa and nematodes may also constitute a significant fraction of "microbial" biomass (Ingham and Horton 1987), and their C:N ratios are approximately 10–40 for protozoa and 40–80 for nematodes (Paul and Clark 1989). If it is true, as hypothesized by Myrold (1987), that both chloroform fumigation-flush C and N mineralization are indices of microbial biomass, then it seems logical that mats would have higher $C_{fum}:N_{min}$ ratios if there were a higher fungal than bacterial biomass in mat soils compared to non-mat soils.

Direct counts in both mat and non-mat soils reveal, however, that although the total microbial biomass is greater in mat soils, the ratio fungi:bacteria:protozoa:nematodes was not significantly different in mat soils compared to non-mat soils (Cromack et al. 1988; Ingham et al. 1991). From this we conclude that shifts in $C_{fum}:N_{min}$ ratios represented more than a shift in the qualitative characteristics of the microbial assemblages present. It is likely that these shifts represent differences in the relative concentrations of labile C and N in these soils.

There is evidence that the chloroform-fumigation technique exposes soil organic materials to microbial degradation that does not occur in soil that has not been fumigated with chloroform (Voroney and Paul 1984; Brookes et al. 1985; Azam et al. 1989). If this is the case, estimates of microbial biomass by flush C or N mineralization may overestimate the concentration of microorganisms present. Conversely, if there is a large segment of the microbial population that is not degraded following chloroform fumigation, flush C will underestimate microbial biomass (Ingham and Horton 1987). Similar arguments could also be applied to the 7-day anaerobic incubation period at 40 °C used to determine mineralizable N.

If mineralizable N reflects the labile N component of soil organic matter (including microbial biomass) rather than just microbial biomass, it appears that the ratio of labile N to labile C was lower in mat soil than in non-mat soil. This is the condition we would expect if mat fungi were removing labile organic N from the system in preference to labile C. This observation therefore supports the contention that mycorrhizal fungi, or at least the mat community as a whole, is capable of "mining" organic N from soil.

Increased ammonium concentrations in California mat samples

Extractable ammonium was significantly greater in mat than in non-mat litter from the California sample site (Table 3) but not different in the Oregon mat and non-mat soils. The Oregon results were the same as those observed in a previous study (Griffiths et al. 1990). There are at least three plausible explanations for the differences seen in the California samples: (1) The ectomycorrhizal fungus increased the rate of litter decomposition; (2) the fungus increased the ammonium-sequestering capability of the litter; or (3) the fungus in some way enhances N_2-fixation rates in mat litter. Samples of mat and non-mat litter were treated with elevated concentrations of ammonium (10^{-2} *M*), washed, and then extracted. There was no significant difference between the mat and non-mat litter, suggesting that either the fungal mat does not sequester ammonium or that all sites of ammonium attachment were already occupied with ammonium ions. The mean N_2-fixation values were greater in mat than in non-mat litter for three out of five sampling periods, but these differences were not statistically significant, suggesting that the third explanation is not attractive.

If decomposition rates were significantly greater in mat litter, we would expect elevated respiration rates in these samples and, with the exception of the samples collected at the driest time of the year, this was true (Table 3). However, why was there no difference in $C_{fum}:N_{min}$ ratios between mat and non-mat litter in the California system while there were significant differences between the Oregon mat and non-mat soils, and why was there a significant sequestering of ammonium in the California mat litter and not in the Oregon mat soils? The answer may lay in the temporal characteristics of the Oregon soil versus California litter systems. Mycorrhizal mats collected in Oregon are perennial features, similar to those reported by Hintikka and Naykki (1967). The mats in litter in the California eucalyptus grove appear to be a more seasonal feature. These mats occupied nearly 100% of the litter during the moist months of the year, but occurred only in isolated patches during the dry periods.

The perennial mats sampled in Oregon may be adapted to using any litter that falls onto the ground rather than gaining access to new material through rapid outward expansion. Preliminary data indicate that the metabolic activity in the edges of the mat is not significantly different from that in the center (1989, unpublished data). In the Oregon mats, both rapid decomposition and recovery of organic nutrients from soil organic matter may occur as the result of ectomycorrhizal fungal colonization. In the California litter system, however, it is possible that the ectomycorrhizal fungus decomposes the litter, as the litter is invaded during the moist season. In the litter-mat system, the ability of the fungus to take up and transport organic N and P released during decomposition

may not be as fully developed as in the perennial mats found in Oregon coniferous forests.

The role of mycorrhizal fungi in promoting soil heterogeneity

In addition to their possible role in promoting organic matter degradation, fungal mat communities increase soil heterogeneity, thereby providing habitats different from those in both the bulk soil and the non-mycorrhizal rhizosphere. As mentioned above, compared to non-mat soils, mat soils may be more hydrophobic, have a lower pH, and higher levels of oxalic acid (Cromack et al. 1979, 1988). The elevated concentrations of oxalic acid in mat soils are thought to be primarily responsible for the significantly altered soil chemistry (Rose et al. 1991) and the elevated concentrations of oxalic acid-using bacteria (Knutson et al. 1980). All of these observations taken together strongly suggest that mycorrhizal mat communities may provide a distinct habitat within forest soil that may increase soil species diversity. In addition, these mat communities may increase host plant survival by increasing rhizosphere heterogeneity.

There should also be qualitative differences in the organic material available for use by heterotrophs. Mycorrhizal plants are known to allocate greater portions of total photosynthate production to the rhizosphere compared to non-mycorrhizal plants (Bevege et al. 1975; Pang and Paul 1980; Reid et al. 1983). The increase in photosynthates and the action of the mycorrhizal fungus can alter the composition of organic substances released into the mycorrhizosphere (Meyer 1974; Bevege et al. 1975). It is likely that these differences will influence the characteristics of microbial populations and the belowground foodweb. Indeed, this was the finding in a preliminary study of protozoa, nematodes, and microarthropod populations in mat and non-mat soils (Cromack et al. 1988). Other studies have also shown qualitative and quantitative differences in bacterial populations associated with mycorrhizal plants (Meyer and Linderman 1986; Knutson et al. 1980).

In addition to differences in microflora and fauna, mycorrhizal mat communities are thought to alter plant community composition as well. Early studies of presumed mycorrhizal mats in subarctic forests have shown that plants growing in soils colonized by perennial fungal mats were different from those growing in non-mat soil. These plants were typical of those growing on soils depleted of nutrients (Hintikka and Naykki 1967).

During the course of our field studies on mycorrhizal mat communities, we discovered that under the enclosed canopy of a mature Douglas-fir forest, Douglas-fir seedlings are found exclusively in either *Hysterangium* or *Gautieria* mats (Griffiths et al. 1991). This suggests that mat soils may act as a nursery for seedling establishment under conditions that normally would not allow seedling survival. The mechanism that allows this to occur is not known at this time, but the mat community may enable the seedling to tap into the resources of the overstory tree, which would include a potential pool of photosynthates, inorganic nutrients, and/or water (Read et al. 1985). The mat community may also act to reduce the seedling's susceptibility to attack by root pathogens (Marx 1972).

Conclusions

A comparative study of forest soil and litter colonized with mat-forming mycorrhizal fungi in Oregon and California was conducted in which per cent moisture, pH, chloroform fumigation-flush C, N mineralization, exchangeable ammonium, and respiration, N_2-fixation and denitrification rates were measured. The data suggest that: (1) different mat-forming mycorrhizal fungi may play different functional roles in forest soils, (2) mat-forming mycorrhizal fungi increase the heterogeneity of forest soils, thereby increasing the potential for increased species diversity, and (3) based on shifts in C_{fum} : N_{min} ratios, fungal mats may be capable of preferentially removing labile organic N from mineral soils.

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