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Spatial distribution of ectomycorrhizal mats in coniferous forests of the Pacific Northwest, USA

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Abstract

Ectomycorrhizal mats in forest soils have a wide global distribution and have been noted as potentially important elements in forest soil nutrient cycling. To elucidate the relationship between ectomycorrhizal mats and their environment, we undertook field studies and spatial analyses of mat distributions at different spatial scales.

We used two experimental approaches to study mat-forming ectomycorrhizal fungi in coniferous forests of the Pacific Northwest in the United States. In the first approach, ectomycorrhizal mats and other forest floor features were mapped in 2 × 10 m plots and digitized into a geographical information system (GIS) for spatial pattern analysis. In order to examine larger-scale phenomena, a second approach involving other sites was taken; soil cores were taken along 30-m transects, and distance to the closest living potential host tree was calculated for each core.

Mat patterns were studied at two scales: (1) within-stand level (i.e. variability attributed to distribution of other mat species, forest floor attributes, and understory vegetation); and (2) stand level (i.e. variability expressed along a successional gradient). Mat distribution was influenced by: (1) the proximity of one mat to another; (2) the distance from the mat to the closest living tree; (3) the density of living trees in a stand; and (4) the successional stage of the stand.

Although GIS analysis indicated that mats of different morphologies did not physically overlap, there was a tendency for clustering of mats. No apparent correlations were observed between forest floor features and mats located within the 2 × 10 m grids. On the scale of tens of meters, mats decreased with distance from the closest potential host tree. Spatial patterns of mat distributions in harvested sites suggest that these mats may persist at least 2 years after their host trees have been cut. For *Gautieria* mats, total mat area, size, and frequency differed with stand age.

This study has demonstrated the importance of both spatial scaling and forest stand age when the natural distribution of mycorrhizal fungi is examined. Results suggest the need for mat research directed at higher-order scales (e.g. stand and watershed) that will provide accurate information for managing forests to ensure their survival and normal function.

Introduction

Ectomycorrhizal fungi play an important role in preserving species diversity by providing host trees with necessary nutrients from mineral soil and soil organic matter (Read, 1993). Some ectomycorrhizal fungi form dense, visible mats commonly found in the litter

layers and upper soil horizons of forest soils throughout the world (Castellano, 1988). This study examines mat-forming ectomycorrhizal fungi such as those in the genera *Gautieria* and *Hysterangium*, which produce hypogeous sporocarps (truffle fruiting bodies). These mats alter the chemical and physical properties of forest soil, producing localized habitats for unique assemblages of soil organisms (Cromack et

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al., 1988; Griffiths et al., 1994; Neal et al., 1964). They increase nutrient availability to their host trees by weathering mineral soils and decomposing forest floor and soil organic matter (Griffiths et al., 1991a, 1994) and enhance survival of Douglas-fir seedlings under enclosed canopies (Griffiths et al., 1991b). Ectomycorrhizal mats occur in high concentrations (Cromack et al., 1979) and have an essentially global distribution, from boreal to semi-tropical forests (Castellano, 1988). Thus, these fungi appear to play an important role in forest ecosystems.

Ectomycorrhizal mats are excellent systems for studying ectomycorrhizal-soil interactions because their hyphae form bundles that develop into rhizomorphs. In fungal mats, the rhizomorphs can be present in high numbers, so that up to 50% of the dry weight of mat soils can be made up of these rhizomorphs (Ingham et al., 1991). By comparing chemical and biological characteristics of soils with high concentrations of rhizomorphs (mat soils) with adjacent soils with no obvious mat structure, we have been able to determine the roles these fungi may play in forest soils (Griffiths et al., 1990; Griffiths and Caldwell, 1992). In particular, we intensively studied mats produced by two genera of ectomycorrhizal fungi, *Gautieria* and *Hysterangium*. These studies have been conducted in several physiographies: the coniferous forests of the Pacific Northwest region, a eucalyptus forest in Northern California, a deciduous forest in the southwestern US, and a mixed conifer-hardwood stand in Alaska (Griffiths et al., 1991a).

Our previous studies suggest that fungi in these two genera have different and distinct functions in forest ecosystems (Griffiths and Caldwell, 1992). Fungi of the genus *Gautieria* weather soil minerals, resulting in the release of nutrients for possible use by the host tree (Griffiths et al., 1994). In contrast, fungi of the genus *Hysterangium* seem best adapted to decomposing organic matter releasing organic nitrogen and phosphorus for use by the host. Within the coniferous forests examined in this study in Oregon's central Cascades (USA)-*Gautieria* and *Hysterangium* mats are found on the roots of Douglas-fir (*Pseudotsuga menziesii*), in some cases growing adjacent to each other on the same root (Griffiths et al., 1991b). In all of these studies, mats were identified to species by the use of sporocarp morphology (Griffiths et al., 1991b).

Little is known about the factors influencing mat distribution at any spatial scale. Although significant efforts have been directed at characterizing above-ground forest systems at the landscape scale, little

research has been conducted on belowground systems (G Bradshaw, D Perry and T Bell, unpub. results). This study is the first that attempts to identify the distribution of mat-forming mycorrhizal fungi in a spatially explicit manner using a geographical information system (GIS) for the analysis.

To date, the only direct studies of ectomycorrhizal mat distribution have been at the 5 × 5 m plot scale. The few stand-level sporocarp distribution studies (Luoma et al., 1991) have not included estimations of mat distribution patterns in their design. Unfortunately, defining mat distributions by the sporocarp approach has drawbacks. Although sporocarp presence is a positive identifying feature of a given ectomycorrhizal fungus, it gives little information about the quantitative extent of mats, and, for several reasons, sporocarp absence does not prove mats are not present (Luoma et al., 1991).

Although there have been no direct observations of mat distribution on either a regional or a watershed scale, studies suggest that mycorrhizal mat distribution may be influenced by factors at higher-order scales, such as: (1) vegetation succession (Last et al., 1987; Read, 1993); (2) the distribution of specific plant species (Molina et al., 1992); (3) soil type (Read, 1993); and (4) the availability of propagules. At these larger scales, mat distribution patterns are most likely to be influenced by factors affecting vegetation distribution patterns, such as climate, disturbance type, and disturbance patterns.

Somewhat more information is available on mat distribution patterns at the stand level, but again, it is based on the collection of sporocarps produced by mat-forming fungi. These studies have shown that the distribution of mat-forming fungi can be influenced by stand age and soil moisture (Luoma et al., 1991) and local climate (Hunt and Trappe, 1987). These results suggest that at this scale, and presumably at the watershed level, mat distribution may be affected by microclimate, as influenced by slope, aspect, and elevation.

Somewhat more is known about factors influencing mat distribution patterns at the individual plot scale. While studying ectomycorrhizal colonization of seedling roots, Harvey et al. (1987) found a direct correlation between ectomycorrhizal fungal establishment and the organic content of the soil. Fogel (1976), who studied hypogeous sporocarps in a Douglas-fir stand, found a relationship between sporocarp presence and distance to the nearest live Douglas-fir stem, with maximum concentrations at about 160 cm from the nearest tree.

At this scale there have been several direct studies of ectomycorrhizal mat distribution patterns. Some of the earliest work showed that fungal mats (presumed to be mycorrhizal) covered up to 25% of the forest floor in a Finnish coniferous forest (Hintikka and Naykki, 1967). However, this study did not mention spatial pattern relative to other forest floor features except that the vegetation in mat-colonized soil consisted of species typical of nutrient-poor soils. In a separate study of the distribution of *Hysterangium crassum* (*setchellii*) mats in 5 × 5 m plots in the coniferous forests of the Pacific Northwest, Cromack et al. (1979) found that up to 27.4% of the forest floor was colonized by *H. crassum* (mean 15%) and up to 17% of the top 10 cm of mineral soil (by volume) was colonized by this fungus (mean 9.6%).

At the finer scales, ectomycorrhizal mats occurred at the bases of the Pacific yew (*Taxus brevifolia*), western hemlock (*Tsuga heterophylla*), and, vine maple (*Acer circinatum*) with much greater incidence than in control plots (Griffiths et al., 1995), and trees taller than 1.5 m had a higher incidence of mats at their bases than smaller trees. In general, mat occurrence and tree diameter were positively correlated (Griffiths et al., 1995).

Our objective in this study was to quantify the first-order spatial distribution of ectomycorrhizal mats at the within- and between-stand scales. We expected, at these scales, to determine the extent to which rocks, coarse wood debris, stumps, understory and overstory trees, and stand age influenced the presence of mats. We used two experimental approaches: (1) we mapped mats and other forest floor features in gridded plots located in young, mature, and old-growth Douglas-fir forests; and (2) we took cores to determine the presence of mats relative to the closest overstory tree.

Materials and methods

Site descriptions

For the mapping study, three sites of each age class (young, mature, and old growth) were chosen in and near the H J Andrews Experimental Forest (HJA) in the central Cascade Mountains of Oregon. The young stands were all 35–40 years old and had had similar plot preparation, seedling planting regimes, and stand thinning schedules. The mature stands grew up after extensive natural fire events 90–125 years ago, and trees in the old-growth stands were more than 400

years old. All age classes were dominated by Douglas-fir and grew on similar soils.

For the coring study, two locations were chosen for transects; both sites were within 18 km of the HJA in forests dominated by Douglas-fir. Each site included a control and a "green tree retention" (GTR) treatment.

The Titan II site (44° 12' 30" N and 122° 15' 00" W) was flat to slightly sloping with a northwest aspect and an elevation of 670 m. The control was a 125-year-old stand of Douglas-fir that originally had a density of 200 trees per hectare. This site was thinned in 1976 to a density of 68 trees per hectare, approximately 35% of its original density. The GTR site had been harvested 2 years before this study. The site was not burned after harvest; however, woody debris was piled into windrows and burned. Mature green trees were left on the site at a concentration of 1 tree per hectare to provide refugia for animals and birds.

The second coring site, called the "Santiam Y" and located 20 km north of the Titan II site at 44° 25' 00" N and 122° 00' 00" W, had little to no slope and an elevation of 1060 m. The control for this site was a stand of old-growth Douglas-fir where some trees had been removed 11 years before the study; however, it retained the essential structural characteristics of an old-growth forest. On the contrasting GTR site, prepared 3 years before the study, the concentration of remaining mature trees was 4 per hectare.

Mapping and coring protocol

For the mat-mapping study, three 2 × 10 plots were chosen in each of the three sites per age class, for a total of 27 plots. Plots were located by the same procedure used in another study (Griffiths et al., 1995). A single die was thrown in order to determine the direction and distance of the lower left corner of the gridded plot from an arbitrary baseline at least 20 m from the edge of the stand. Plots were flagged at 0.5 m intervals and raked to a depth of 5 cm. To-scale drawings of the type, size, and location of all ectomycorrhizal mats, rocks, logs, stumps, and all trees and shrubs were recorded in the field on hand-drawn maps with the flagged grid used as a guide.

Field identification of these mats was based on previous studies in which we identified these mats to species using sporocarp analyses (Griffiths et al., 1991b). We found that in the geographical area used in this study, we could field identify *Gautieria* mats based on mat morphology essentially 100% of the time and *Hysterangium* >90% of the time. With this back-

ground, we were able to identify the two mat types found in the field (*Gautieria* and *Hysterangium*) by mat morphology. *Gautieria* mats were those that were restricted to the top portion of the mineral soil and typically very dry, almost powdery in consistency. These fungal mats caused the soils they colonized to have a lighter color than adjacent soils that had not been colonized, which was another field identification feature (Griffiths et al., 1991b). *Hysterangium* mats were typified by relatively coarse white to cream rhizomorphs normally found in the litter and/or top of the mineral soil (Griffiths et al., 1991b). In the discussion of our results, "*Hysterangium*" will be understood to include those other few fungi that form similar mats. Both types of mats are sufficiently dense and their edges sufficiently well defined that mapping them was not difficult. The same field crew was used throughout the mat mapping work, reducing interpretation errors. The locations of neighboring dominant overstory trees were also noted. Twenty-seven maps were made, one for each plot. These maps were used to generate digitized maps for the computer analysis described below.

In the coring study, mats were identified in cores taken along transects. At each site, a 30-m transect line was mapped and flagged every 25 cm, starting from a living mature or old-growth tree. A stainless steel corer with a diameter of 4.8 cm and a length of 30 cm was used to take 4.8 × 10 cm cores. The cores were extruded into plastic bags and transported to the laboratory in an ice cooler. All cores were scored for the presence and type of mat as well as the presence or absence of decayed wood. If there was any doubt about the existence or type of mat present in a core, the ground adjacent to the core was examined for mat presence. Alternate cores were saved for assays of moisture content measured by methods reported by Griffiths et al. (1991a). The locations of all of the closest large (mature or old-growth) green trees were noted for calculating distances (± 25 cm) from each core to the closest tree.

Mat map construction and statistical analyses

Data on mat size, shape, and location were digitized with a GIS (Arc/Info, Environmental Systems Research Institute). Separate digital maps were constructed for each mat type (*Gautieria* and *Hysterangium*) and for all other forest floor attributes within the plot—rocks, coarse woody debris (CWD—stumps, surface logs, and buried logs), and plants (vine maple, Pacific yew, and rhododendron (*Rhododendron macro-*

phyllum)). All features were considered as potential contributors to mat patterns at the two scales. Spatial statistics and pattern indices were calculated for each mat map in order to quantify mat distribution by mat species, spatial correlations of mats with other forest floor features, and stand age. Estimates of total mat areas (MA), number of mats (NM), mean mat size (MMS), mat size standard deviation (MSSD), mean nearest neighbor (MNN), and mean shape index (MSI) were calculated with FRAGSTATS (K McGarigal and B Marks, FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure, PNW Technical Report, PNW-GTR-351). These indices were chosen to provide estimates of general mat quantity, size, size variability, configuration, and distribution relative to other mats.

An analysis of variance (ANOVA) was conducted on the variables MA, NM, MMS, MNN, MSSD, and MSI (PC Statgraphics; STSC Inc., Rockville, MD) in order to identify statistically significant differences among mats as a function of species and stand age. Variables not exhibiting a normal distribution (MMS, MSSD) were log transformed. Interactions between mat type and stand age were analyzed for all variables (only MA and MSSD showed second-level interactions). Least significant difference (LSD) values at the 95% confidence level were calculated accordingly. Where there were no second-level interactions, LSDs were estimated for each mat type by stand age. In the coring study, the nonparametric Spearman Rank correlation was used to demonstrate the significance of the correlation between distance from tree and the presence of mats.

A "C" program calculated the empirical autocorrelation function (or semivariogram) for both maps and core transects for each mat type; C was used interactively to calculate a spatial cross-correlation function for the gridded map data and provide measures of spatial correlation between substrate variables. Although both data sets were generally found to satisfy the condition of local stationarity (see Isaaks and Srivastava, 1989, for definitions of geostatistical terms), there were some cases where trend and anisotropy (i.e. values of semivariogram differing according to the direction of calculation) at larger lags were observed; in these instances, higher-lag information was disregarded. Otherwise, no preanalysis corrections (e.g. detrending) were performed. The semivariogram program used a maximum lag distance of 33% (33% of rows and columns in an image).

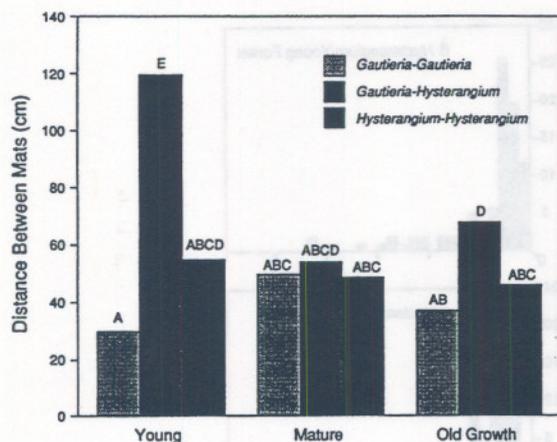


Figure 1. Intra- and interspecies comparisons of mean distances between mats for different age stands. There were second-level interactions between stand age and both mat types as determined by multifactor ANOVA. Groups sharing the same letter are not significantly different.

Results

In the mapping study, at the within-stand scale, the spatial cross-correlation function indicated that very little physical overlap occurred between *Gautieria* and *Hysterangium*. Statistically significant second-level interactions by stand age and mat type were found in the mean distances between mats (Fig. 1). The largest distances were observed between *Gautieria* and *Hysterangium* mats in young stands, and the next largest between these mats in old growth. Distances between mats of the same species did not differ significantly with stand age (Fig. 1).

Frequency histograms of different classes of distances suggest that in the young stands, *Gautieria* mats start out as clusters with a relatively narrow range of distances between mats (Fig. 2a); the most common range is from 10 to 20 cm. In the mature stands, the distance between mats becomes greater as new mat loci become established, resulting in a wider range of distances between mats (Fig. 2b). In the old-growth forest, more mats become established and the spacing again resembles that found in the young stand (Fig. 2c). The pattern for *Hysterangium* mats suggests that as the stands mature, there are fewer occasions when spacing between mats is wide; i.e. the spacing is more homogeneous with increasing stand age (Figs. 2d–2f).

There was no correlation between rocks and the presence of *Gautieria* mats, and no correlation between buried logs and *Hysterangium* mats. In fact, nearest neighbor and cross-correlation results showed no sig-

nificant correlations between presence of *Gautieria* or *Hysterangium* mats and any of the features in the plots, including understory trees.

In the coring study, our objective was to determine whether there was a correlation between the presence of mats and distance from the closest potential host (generally speaking, mature or old-growth Douglas-fir). We found an inverse relationship between the percentage of cores having mats and the distance to the closest potential host tree ($r = -0.212$, $p < 0.0001$ for the Titan II site; $r = -0.334$, $p < 0.0001$ for the Santiam Y). This relationship is shown in Figure 3, where in the control sites (Fig. 3a), the percentage of cores with mats decreased with distance from the closest tree (combined data set from both sites). Within each of the first three 100-cm increments, 48% of cores contained mats; beyond that, the frequency generally decreased, with the lowest frequency in the range of 600 to 700 cm from the closest tree.

The pattern in GTR plots (Fig. 3b) for all cores within the first 600 cm was essentially the same as that in the control plots. However, the highest percentage of mats in the cores nearest the trees was only about 28%. Beyond 600 cm, mat frequency once again increased, with the original decreasing pattern repeated between 700 and 1000 cm. There was then another increase in frequency between 1000 and 1100 cm. With the exception of the interval between 1400 and 1500 cm, this pattern of increasing and decreasing mat frequency occurred within two more intervals of approximately the same width (at 1000 to 1600 cm and 1700 to 2200 cm). Data (not shown) of GTR transects from both sites show the same trend in all transects to varying degrees.

As shown above, there were large differences in the percentages of cores with mats among stands with different ages or treatments. These differences were most extreme at the Santiam Y site; in the control site (an old-growth stand), 53.4% of the cores had mats, but in the GTR site only 14.2% had mats. Similarly, distribution patterns in the mapping study showed that in young stands, the total area covered by *Gautieria* mats was relatively small compared with that occupied by *Hysterangium*; these latter mats varied greatly in size and appeared to have an irregular distribution (Fig. 4a). In the old-growth stand, *Gautieria* mats covered a greater total area than *Hysterangium* mats, and both seemed to have a more regular distribution (Fig. 4b). When all data for total mat areas per plot were considered, *Gautieria* showed significantly less total area than *Hysterangium* in young stands (Fig. 5a). In

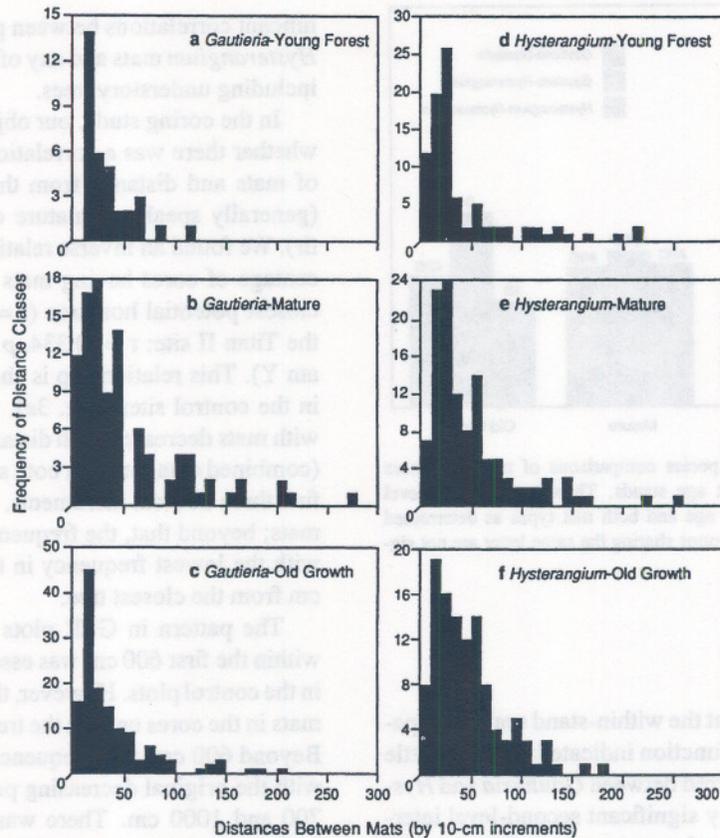


Figure 2. Frequency histograms of distances between mats. Distances between *Gautieria* mats in a young, b mature, and c old-growth stands, and between *Hysterangium* mats in d young, e mature, and f old-growth stands.

mature stands, the two species exhibited very similar total areas. In old-growth stands, the total area for *Gautieria* mats was significantly greater than in young and mature stands. No significant trends were observed for *Hysterangium* mats by stand age. The area covered by both mat types in these plots ranged from 10% of the total area in the young stand to 20% in the old growth.

To determine whether the increase in total *Gautieria* mat area with stand age (Fig. 5a) was caused by an increase in the number of mats per plot or an increase in mat size, we measured both of these factors (Figs. 5b and c). Like total mat area (Fig. 5a), the number of *Gautieria* mats per plot increased significantly with stand age, but there was no comparable increase in *Hysterangium* mat numbers (Fig. 5b). Mean *Gautieria* mat size showed essentially the same pattern; i.e. *Gautieria* mat size increased significantly with stand age, but there was no comparable increase in *Hysterangium* mat size (Fig. 5c).

We were also interested in assessing mat size variability by stand age for both types of mats (Fig. 6a).

Gautieria mats showed a significant increase in mat size standard deviation (MSSD) with stand age, but *Hysterangium* mats did not. Analyzing the mean shape index (MSI) allows quantification of mat shape regularity for different stand ages (Fig. 6b). MSI measures the average complexity of patch shape compared with a circle; MSI equals 1.0 for a circle and increases without limit as the patch shapes become more irregular. The only significant successional trend in MSI was an increase with stand age in *Gautieria* mats (Fig. 6b), where mats in old growth were significantly more complex than those in young stands.

Discussion

The study focused on four factors that could influence mat distribution at different scales: (1) intraspecies and interspecies interactions (i.e. between-mat influences); (2) non-vegetative forest floor features; (3) neighboring vegetation; and (4) stand age. Spatial variability

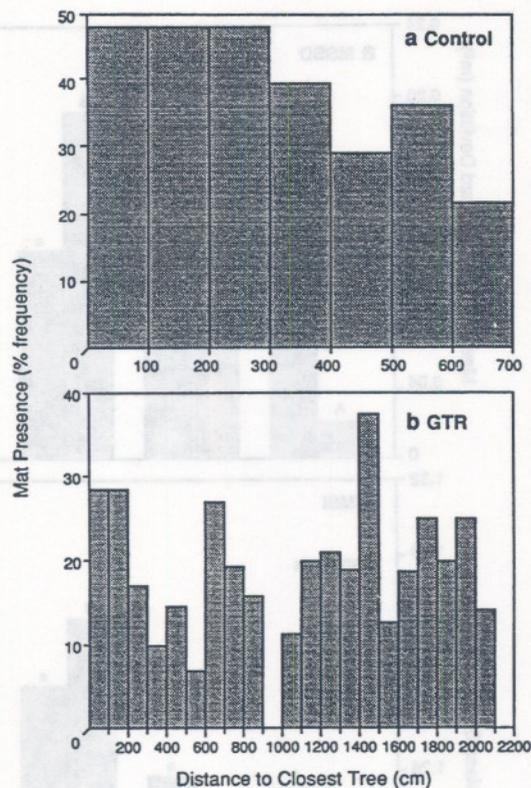


Figure 3. The percentage of cores containing mats as a function of distance to the closest tree on a control sites and b "Green tree retention" (GTR) sites in the coring study.

was examined at two scales: at the intra- (or within-) and inter- (or between-) stand levels. The study was undertaken with the assumption that processes functioning at higher spatial orders (i.e. greater than the plot size) did not contribute to measured patterns.

The mat mapping study was our first attempt at documenting factors influencing ectomycorrhizal mat distribution patterns. The results of this study demonstrated the need to conduct studies at different scales and with different designs if we were to obtain a clearer understanding of the factors affecting distributions. A later study that specifically looked at the associations between mats and understory vegetation demonstrated a high incidence of mats at the base of understory trees (Griffiths et al., 1995); this trend had not been observed in the original mapping study where there were too few understory trees to show a consistent trend. The coring study reported in this paper was our attempt to better understand larger-scale patterns of mat distributions. This study showed that the size of the original

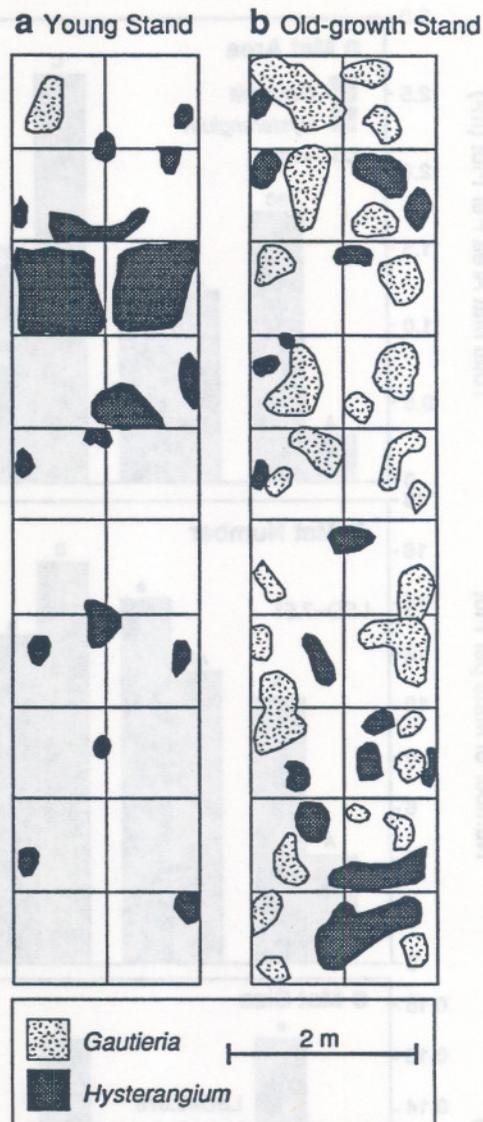


Figure 4. A graphic representation of the size, shape, and distribution of *Gautieria* and *Hysterangium* mats in typical 2×10 m plots in a: a young Douglas-fir stand and b: an old-growth stand.

grid was too small to show the influence of individual overstory trees on mat distributions.

Influence of intraspecies and interspecies interactions

Earlier studies have indicated that mats tend to be clustered (R P Griffiths, unpubl. data). These observations suggest that a component of intra-stand variability in mat distribution may be attributed to the presence (or absence) of other mats. Using the spa-

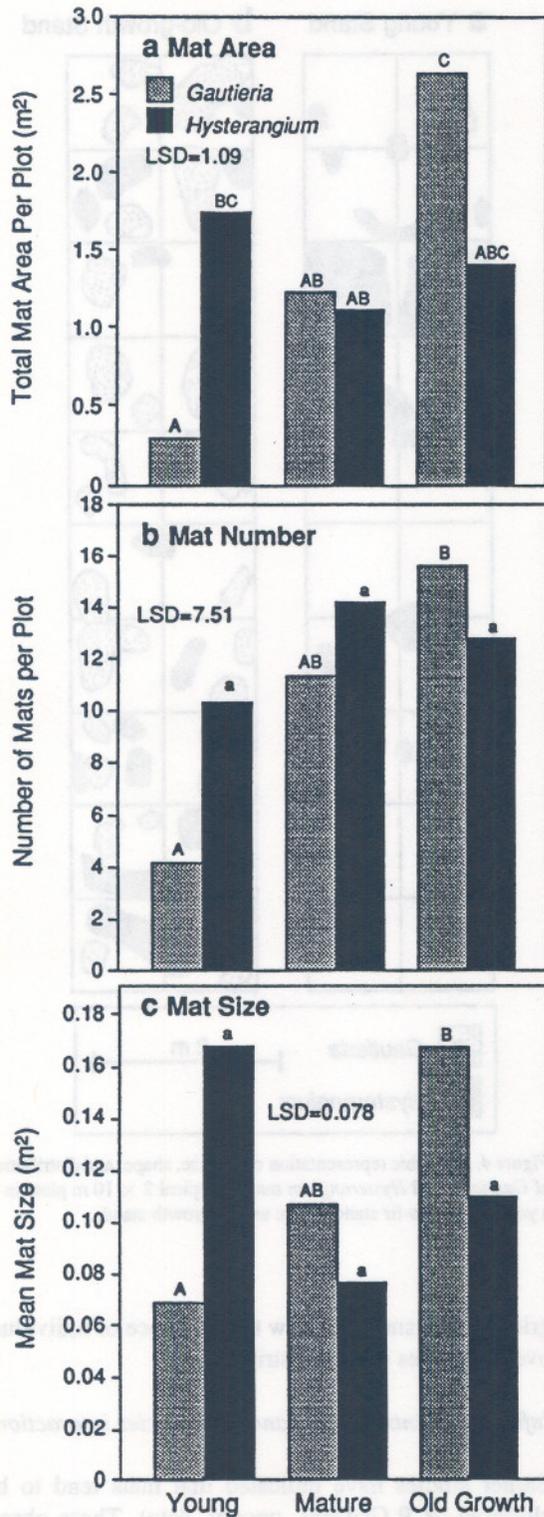


Figure 5 a: The total mat area, b: number of mats and c mean mat size per 2 × 10 m plot for both mat types at each successional stage; means of 9 plots per stage. In a, groups sharing the same letter are not significantly different. In b and c, there were no second-level interactions by stand age or type; upper case letters show *Gautieria* mat comparisons by stand age, and lower case letters indicate that there were no significant differences by stand age for *Hysterangium* mats.

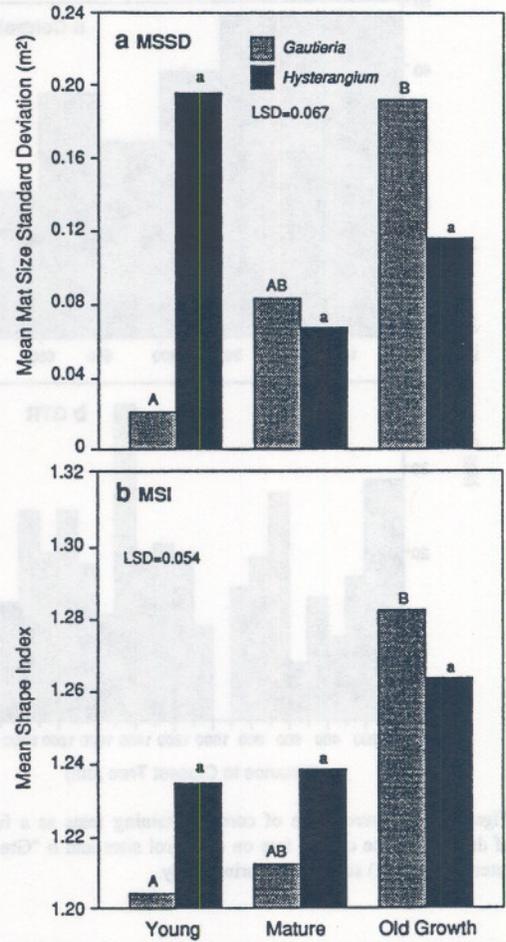


Figure 6 a: The mean mat size standard deviation MSSD and b: mean shape index (MSI) for each 2 × 10 m plot for both types of mats at each successional stage; means of 9 plots per stage. Significant differences are shown as in Figure 5b and c.

tial cross-correlation function calculated from the digitized mapped mats and nearest neighbor estimations (FRAGSTATS), we calculated the influence of one mat on the presence of another. The lack of overlap found between species supports a phenomenon frequently observed in the field; i.e. *Gautieria* and *Hysterangium* mats are mutually exclusive, but they can be found adjacent to each other.

Influence of non-vegetative forest floor features

A central objective of our mapping rocks and decaying wood was to determine whether these features influenced mat distribution within the 2 × 10 m plots. In previous studies, *Gautieria* mats were often found in high concentrations in rocky soils (R P Griffiths, unpubl.

observ.); this distribution might be expected from *Gautieria* biogeochemistry (Griffiths and Caldwell, 1992). When the chemistry of *Gautieria* mat soil solutions and that of adjacent soils with no obvious mats are compared, the *Gautieria* soils show very high concentrations of organic acids and higher concentrations of a range of ions than the non-mat soils (Griffiths et al., 1994). From these observations, Griffiths et al. (1994) concluded that these mats are responsible for accelerating mineral soil weathering. We hypothesized that within the grids, rocks would increase the frequency of *Gautieria* mats. However, our GIS analysis of forest floor features showed no apparent relationship between the presence of rocks and the distribution patterns of *Gautieria* mats.

We also expected to find a relationship between the presence of CWD in advanced decay states and the distribution of *Hysterangium* mats. In the field, we have often observed that *Hysterangium* mats are associated with highly decayed buried CWD and litter. Similarly, Harvey et al. (1979) discovered a strong positive correlation between the occurrence of ectomycorrhizal fungi and advanced decay state wood during a study of ectomycorrhizal fungal distributions in Montana forests. Laboratory studies of exoenzyme activity associated with *Hysterangium*-colonized soils showed that enzyme activities were much higher than in non-mat soils and were also generally higher than in *Gautieria* mat-soils (Griffiths and Caldwell, 1992). Although these observations suggest that *Hysterangium* mats may be well adapted to decomposing organic matter, we did not see a correlation between buried logs and the presence of *Hysterangium* mats.

In fact, nearest neighbor and cross-correlation results showed no significant correlations between presence of *Gautieria* or *Hysterangium* mats and any of the features in the plots. It is still possible, however, that correlations do exist but that the number of plots or the type of analysis did not show these correlations. It is also possible that mat distribution is controlled at scales larger than a few meters, swamping out any localized relationships.

Influence of neighboring trees

To determine how both understory and overstory (potential host) trees influenced mat distribution, we have taken two different approaches. The first approach was to specifically look for mats in plots at the bases of understory trees and compare the incidence of mats in those plots with mats in control plots (without trees)

of the same size (Griffiths et al., 1995). The second approach was the coring experiment conducted after the mat mapping phase of the present study.

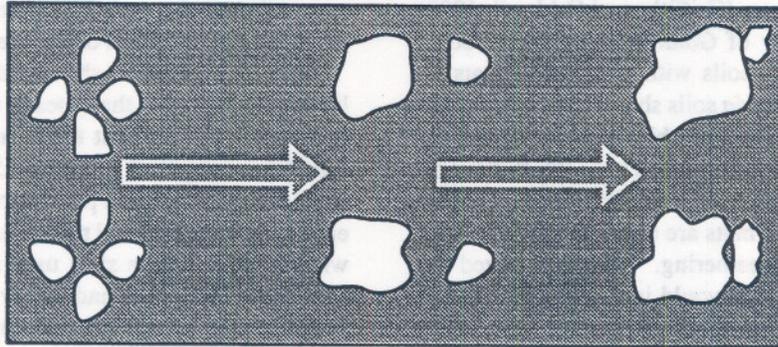
The first approach showed that mats were more likely to be found at the bases of understory trees than in control plots without trees. In that tree-plot study (Griffiths et al., 1995), almost 1,500 tree plots and an equal number of control plots were studied for the presence of ectomycorrhizal mats. Ten of the 12 sites were within 12 km of the sites used in the current study. More than 75% of the understory tree plots containing Pacific yew, vine maple, or western hemlock had ectomycorrhizal mats associated with them, as opposed to only 50% in control plots (Griffiths et al., 1995). Although this result demonstrates that mats are more commonly found at the bases of understory trees, no such correlation was observed in the mapping portion of the current study.

In the coring study, the inverse relationship between the percentage of cores having mats and the distance to the closest potential host tree showed that mat distribution patterns in our mapped 2 × 10 m plots (on the scale of a few meters) may be driven, in part, by a larger pattern caused by the presence of host trees. One explanation for the "periodicity" found in the GTR plots may be related to an increased number of active roots near the drip line of the canopy for the remaining mature trees. However, this explanation does not adequately account for the repeating pattern seen between 1100 and 1600 cm and between 1700 and 2200 cm (Fig. 3). We have generally assumed that once the original trees have been harvested, energy from the host tree would be cut off and the mats would soon disappear. Because the GTR sites had been harvested at 2 (Titan II site) and 3 (Santiam Y) years, we did not expect the mat pattern to approximate the spacing in the original stand. However, it is possible that these mats are maintaining themselves saprophytically or are supported by alternate hosts (Read, 1993).

Influence of stand age

Prior to this study, we hypothesized that as a Douglas-fir stand evolved, *Gautieria* and *Hysterangium* mats would develop at about the same rate, with *Gautieria* mats providing the trees with P by weathering the mineral soil and *Hysterangium* mats providing N and P by decomposing litter and soil organic matter. In essence, our predictions matched the response of the *Gautieria* mats to stand age, but not the response of *Hysterangium* (Fig. 5a). Although P can be a limiting

a Coalescence of smaller mats.



b Deformity due to rocks, etc.

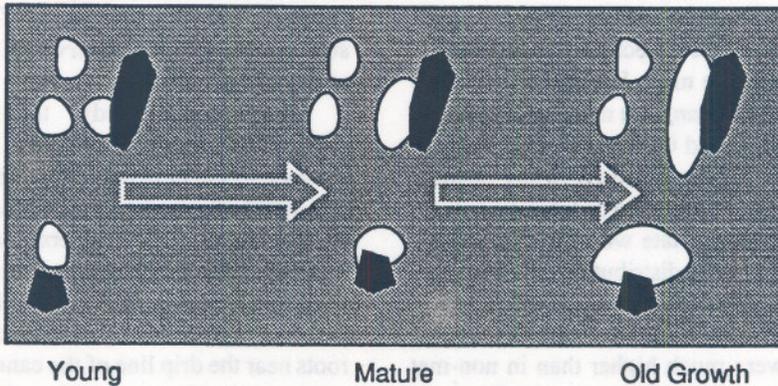


Figure 7. Possible mechanisms by which *Gautieria* mats may form colonies with stand age. a: Individual smaller colonies coalesce into larger colonies. b: As mats get larger they grow against rocks, stumps, buried logs, and other forest floor features and become disfigured.

factor for tree growth in these forests, N is the primary limiting nutrient in most forest ecosystems (Cole and Rapp, 1981). Early colonization by *Hysterangium* in the young stands suggests that N may be extracted from litter early in stand succession. The slower *Gautieria* mat development may reflect an abundance of P, if we assume that mat formation is regulated in some way by P availability.

On the basis of total mat area alone, we cannot determine whether the increase in total *Gautieria* mat area with increasing stand age is attributable to an increase in mat number or in mean mat size; further clues to factors influencing mat distribution may come from the GIS analyses. At least some of the increase, however, is due to an increased number of mats (Fig. 5b), although there was also a significant increase in mean mat size (Fig. 5c). Although the stand age differences observed in *Hysterangium* mats were not statistically significant, the trends are clear. The reduction

in *Hysterangium* mat area occurring in the transition from young to mature stands (Fig. 5a) was caused by a decrease in the mean mat size (Fig. 5c), even though there was an increase in the number of mats (Fig. 5b). These results indicate that the relationships between mat size or number and stand age are very different for these two types of ectomycorrhizal fungi.

Patterns of *Hysterangium* mat distribution also may be explained in terms of the distribution of active roots and the fact that the two mat types do not occur in the same location. The patchiness of the *Hysterangium* mats in the young stands (Fig. 4a), which had been thinned to approximately a third of their original density, may be due to the patchiness of active roots or of litter distribution. The development of smaller and more evenly sized *Hysterangium* mats in old-growth soils (Fig. 4b) may be due to an increase in competition from *Gautieria* for the same sites.

When analyzed in the context of mean mat size (Fig. 5c), the MSSD data (Fig. 6a) suggest that *Gautieria* mats may start out in young stands as small distinct entities of similar size, but as stand age increases, they join to form larger mats, resulting in a greater range of sizes (K Cromack, pers. commun.; Fig. 7a). There was a significantly greater amount of mat size variability in young stand *Hysterangium* mats than in *Gautieria* mats (Fig. 6a; see also sample mat distributions in Fig. 4).

The trend observed in MSI (Fig. 6b) reflects the pattern expected from the coalescence of two or more *Gautieria* mats to form larger mats with a more irregular shape (Fig. 7a); a similar result could occur if larger mats came into contact with rocks or other forest floor elements that could distort their shapes (Fig. 7b).

Conclusions

This study suggests that forest management practices may significantly influence colonization patterns of ectomycorrhizal mats in coniferous forests. For example, the total area of all mats was greater in old-growth forests than in clear-cut units containing few old-growth trees. Once a forest has been harvested, the reestablishment of mats at different stages of forest succession may vary significantly for different mat-forming fungi. The negative correlation between distance from nearest potential host tree and the presence of mycorrhizal fungi clearly shows that the presence of host trees is important to mat distribution patterns. The concentration and pattern of trees remaining at the stand or watershed scale, along with microclimatic factors, may be the strongest predictors of mat distribution at these scales.

If mat distribution patterns across the landscape are to be understood, future studies must focus on examination of microclimate and vegetation characteristics at larger (i.e. coarser) scales. For instance, the ability of these mats to act as propagules for colonization of the next generation of trees is not understood at this time. Another important focus for future work should be to determine whether colonization of trees in a regenerating stand by mat-forming fungi depends more on mats in adjacent stands or on remnant mats from the original stand. Thus, an understanding of the effects of spatial configuration on regeneration across scales will be integral for conserving forest productivity.

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