Short communication

Association of ectomycorrhizal mats with Pacific yew and other understory trees in coniferous forests *

Robert P. Griffiths, Amy C. Chadwick, Merrilee Robatzek, Krista Schauer and Kimberly A. Schaffroth
Department of Forest Science, Forest Science Laboratory 020, Oregon State University, Corvallis, OR 97331-7501, USA

Abstract

This study was designed to determine whether ectomycorrhizal mats (ECM) are more likely to be present in soils at the base of common understory trees than in soils distant from trees and to determine whether occurrence of ECM is related to tree size. Three understory trees were studied: Pacific yew (*Taxus brevifolia* Nutt.), western hemlock (*Tsuga heterophylla* (Raf.)Sarg), and vine maple (*Acer circinatum* Pursh). The 12 sites studied represent a range of climatic conditions and management histories. More than 2,900 plots were surveyed over 18 months. The incidence of ECM was higher at the base of all three species than in control plots. Incidence of mats was also positively correlated with tree size. Saplings consistently had a lower incidence of ECM than did larger trees.

Introduction

Certain ectomycorrhizal fungi form dense fungal mats in the litter layer and A horizon and can compose up to 50% of the mass of forest mineral soils (Ingham et al., 1991). Because of the concentration of fungal material, ECM have proven to be excellent systems for measuring mycorrhizal function in forest soils (Griffiths et al., 1990). These fungi can increase nutrient availability to trees by weathering mineral soil and decomposing soil organic material (Aquilera and Griffiths, 1993; Griffiths et al., 1994) and also can enhance survival of Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco seedlings in low light (Griffiths et al., 1991).

The commercial importance of yew bark for production of the anticancer drug and an increased interest in vegetation associated with old-growth Douglas-fir have renewed interest in determining the factors influencing establishment and survival of Pacific yew (*Taxus brevifolia* Nutt.). We have informally observed

that Pacific yew in old-growth Douglas-fir forests are usually associated with ECM. This observation is somewhat curious, because *T. brevifolia* usually forms symbiotic relationships with vesicular arbuscular mycorrhizal (VAM) fungi, but not with ectomycorrhizal fungi (J M Trappe, pers. commun.). The same is generally true of other *Taxus* species in Canada and Europe (Bakshi and Thapar, 1960; Prat, 1934), although there is one report of ectomycorrhizal colonization of roots of Canadian yew, *Taxus canadensis* Marsh. (Boullard and Ferchau, 1962). Establishment of *Taxus* from seed is plagued by poor seed germination and root disease caused by *Cylindrocarpon radicicola* (Wollenweber) (Manka et al., 1968) and other fungal pathogens. Since ectomycorrhizal fungi protect trees from root pathogens (Marx, 1972), we hypothesized that the presence of ECM is related to establishment and survival of *T. brevifolia* seedlings in coniferous forests of the Pacific Northwest. Because of the implications of this relationship, we initiated a study to determine if ECM are always associated with *T. brevifolia* and to determine if they were more likely to be associated with seedlings or with larger trees.

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We compared the incidence of ECM at the base of understory trees with that in nearby, randomly selected plots without understory trees. The main objective was to confirm the informal observation that most yew trees have ECM associated with soils near their main stem. For comparison, we also wanted to determine if mats are at the base of hemlock and maple, two other common understory trees found in the same sites as yew. The study included 12 locations in Oregon that represented a wide range of climates and vegetation successional states. We also measured tree size (diameter at breast height, DBH) to determine if this would provide insight into the mechanism behind this relationship.

Materials and methods

Site selection and descriptions

All sites were selected for the relatively high abundance of yew, but also had various amounts of maple and hemlock. All sites at the HJA but one were in old-growth stands dominated by Douglas-fir in which there had been no harvesting; site 6 had been heavily thinned, but the remaining trees were all old-growth (Table 1). In other areas, site 10 was a stand of second-growth Douglas-fir that had been thinned to a 70% crown cover. Sites 11 and 12 were both old-growth stands that had had minor harvesting, leaving the sites with typical old-growth structure. Site 13 had been old growth, but was clear-cut and not burned 3 years before this study and replanted in Douglas-fir 2 years later. The yew at this site had typically resprouted from older trees. Sites 14 and 15 were paired plots in which mat distributions in old-growth and harvested stands in the much drier climate of southern Oregon were compared to those in the wetter sites. Site 15 had been harvested 5 years before this study but was left as a shelterwood to facilitate stand reestablishment; the concentration of remaining old-growth trees was 7 trees ha^{-1}.

Experimental design

Randomized circular plots 10–20 m in diameter were examined for the presence of understory trees including yew, maple, and hemlock. Subplots (tree plots) 25 cm from the base of each tree within the circular plot were examined for the presence of ECM. For each tree plot examined, there was a control area of equal size. The direction and distance of each control plot relative to its corresponding tree plot were determined by a throw of a die. All control plots were 1 to 6 m from the boundary of the corresponding tree plot. If a large rock or log occupied more than 50% of the control plot or the control plot contained a tree, another plot was chosen.

The presence of fungi having characteristics of the mat-forming ectomycorrhizal fungi *Hysterangium* spp., *Gautieria* spp. and *Piloderma bicolor* (Peck) Jülih was determined visually. *Gautieria* and *Piloderma* were the easiest to identify because they can be confused with few other ECM in Douglas-fir forests. *Gautieria* mats are usually restricted to the top portion of the mineral soil; they are typically very dry, almost powdery, and associated with bleached soils (Griffiths et al., 1991). *Piloderma* mats are typically found in the litter layer and at the interface between litter and mineral soil; they have relatively coarse, bright yellow rhizomorphs. *Hysterangium* mats are normally found in the litter or top of the mineral soil, or both (Griffiths et al., 1991). They are typified by relatively coarse white to cream rhizomorphs and are the most difficult to identify by mat morphology in the field. If there was any doubt that a mat was mycorrhizal, the investigator determined visually whether roots running through the mat were mycorrhizal. Tree DBH, mat thickness and type, and presence of large quantities of wood were noted.

Results

ECM occurred more frequently in plots containing yew trees than in control plots (Table 2). The mean occurrence of all mats in all sites was 79.4% in the yew plots and 51.6% in the controls. The most common ECM type was *Hysterangium*. Even though the percentage of *Gautieria*-like mats was lower than that of *Hysterangium*-like mats under yew trees, the relative difference between yew and control plots was greater in the *Gautieria*-like mats (60% higher, as compared with 43% for *Hysterangium*).

We found the same trends for both hemlock and maple. The hemlock showed essentially the same results as the yew (Table 2). Again, the most common mat found was *Hysterangium*-like. *Gautieria*-like mats were also found, but not as frequently as in the yew plots. The maple plots also showed a trend toward enrichment for ECM relative to the control plots. The occurrence of ECM was lower than that found at the base of yew and hemlock, however, and the differ-

Table 1. Site descriptions

Location/Site	Management history	Vegetation	Aspect	Moisture	Elevation (m)
Central Cascades					
H J Andrews Exp. Forest (HJA)					
4	Old growth	PSME, THPL, RHMA, BENE	West-facing	Moderate	730
5	Old growth	PSME, THPL, BENE	West-facing	High	850
6	Heavily thinned old growth	PSME, THPL, RHMA	North-facing	Moderate	1040
7	Old growth	PSME, THPL, RHMA	West-facing	High	850
8	Old growth	PSME, THPL, RHMA	West-facing	High	900
9	Old growth	PSME, THPL, RHMA, ABAM	West-facing	High	1060
20 Km NW of HJA					
10	Thinned mature	PSME, THPL, RHMA, ABAM	Flat	High	610
11	Thinned old growth	PSME, THPL, RHMA, ABAM	Flat	High	620
12	Thinned old growth	PSME, THPL, RHMA, ABAM	Flat	Moderate	1070
13	Old growth	PSME, THPL, RHMA, ABAM	Northwest-facing	High	1070
Southern Cascades					
14	Old growth	PSME, ABCO, PIAL	Northwest-facing	Dry	1370
15	Shelterwood	PSME, ABCO, PIAL	Flat	Dry	1430

ABAM-*Abies amabilis* (Pacific silver fir), ABCO-*Abies concolor* (white fir), BENE-*Berberis nervosa* (Oregon grape), PIAL-*Pinus albicaulis* (white pine), PSME-*Pseudotsuga menziesii* (Douglas fir), RHMA-*Rhododendron macropyllum* (rhododendron), THPL-*Thuja plicata* (Western redcedar).

Table 2. The percentage of plots that contained mats under trees and in the control plots

Fungus	Yew		Hemlock		Maple		All	
	Tree	Control	Tree	Control	Tree	Control	Tree	Control
Hysterangium	70.0	40.4**	64.8	41.2*	57.4	40.9*	64.7	39.3***
Gautieria	43.3	17.2**	24.4	15.9	21.3	13.6	27.0	14.4**
All Mats	79.4	51.6**	77.1	52.0**	68.1	51.5	75.1	50.2***

Significant differences between tree and control plots, for each tree species.
* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
n: yew, 670; hemlock, 555; maple, 233; all, 1458.

ence between tree and control plots was not significant (Table 2). ECM were present in 75% of all 1,458 tree plots considered together, as compared to 50% of the controls.

The incidence of ECM under both yew and hemlock seedlings less than 1.5 m in height was lower than that under trees over 1.5 m (Table 3). Tree diameter at breast height for all trees was also positively correlated with the incidence of ECM at the base of those trees

($R = 0.27$; $p < 0.00001$). In other words, the larger, and presumably older, the tree, the higher was the probability that a mat was located at its base. The differential between ECM occurrence at the base of these understory trees and in the control plots was larger at the relatively dry sites (14 and 15) than in the wetter sites (Table 4).

Table 3. Comparison of the percentage of mat-containing plots under larger trees and seedlings

n/ Fungus	Yew Tree	Yew Seedling	Hemlock Tree	Hemlock Seedling	Maple Tree	Maple Seedling
n	475	186	286	260	70	30
Hysterangium	76.6	53.2	75.5	53.1	57.6	56.7
Gautieria	48.2	30.6	31.1	16.9	21.0	23.3
Piloderma	25.0	18.7	42.2	19.1	24.1	4.0
All mats	85.7	63.4	86.0	67.3	68.3	66.7

Table 4. The percentage of plots that contained mats under yew trees and in the control plots, by site

Site #	n	All mats Tree	All mats Control	Hysterangium Tree	Hysterangium Control	Gautieria Tree	Gautieria Control	Piloderma Tree	Piloderma Control
4	53	100.0	64.2	94.3	54.7	64.2	17.0	ND	ND
5	25	96.0	72.0	76.0	44.0	48.0	36.0	ND	ND
6	24	45.8	41.7	41.7	33.3	8.3	8.3	ND	ND
7	20	75.0	55.0	60.0	35.0	40.0	20.0	ND	ND
8	28	96.6	79.3	89.7	62.1	41.4	20.7	10.7	21.4
9	47	94.6	70.3	86.5	40.5	29.7	10.8	24.3	32.4
10	5	83.3	50.0	83.3	50.0	0.0	16.7	0	0
11	86	94.2	79.1	88.4	67.4	60.5	29.1	59.3	34.9
12	94	86.2	70.2	86.2	60.6	44.7	26.6	43.6	19.1
13	82	34.1	17.1	23.2	8.5	4.9	3.7	9.8	6.1
14	102	88.2	37.3	74.5	27.5	60.8	21.6	4.9	0
15	104	72.1	29.8	54.8	25.0	46.2	4.8	6.7	1.0

ND: no data.

Discussion

It is not clear why there is an enrichment of ECM at the base of understory trees in coniferous forests of the Pacific Northwest. It is possible that ECM are required for the establishment of these trees by suppressing root pathogens (Marx, 1972) or linking seedlings to the energy sources of overstory host trees (Griffiths et al., 1991; Read, 1993). The seedlings could provide a microclimate that is more conducive to ECM survival by providing a drier zone in the soil at the base of understory trees. If this last hypothesis is correct, the differential between mat occurrence at the base of these understory trees and in the control plots should be lower in the relatively dry sites (sites 14 and 15) in southern Oregon. The opposite was true.

Alternatively, the concentration of nutrients might be higher near the base of understory trees as the result of greater litter availability or of nutrients carried by water filtering through the canopy or flowing down the main stem. Several lines of evidence suggest these possibilities. Ectomycorrhizae form dense hyphal mats where the concentration of organic nutrients in the form of litter is elevated. Carleton and Read (1991), in a study of larch seedlings infected with an ectomycorrhizal fungus, found dense mycelial growth where litter was present in the soil. Harvey et al. (1979) found higher incidence of ectomycorrhizal fungi in soils with high organic content and in highly decayed wood within forest soils. Epiphytes, such as lichen, that can colonize yew and other understory trees fix nitrogen that reaches the soil through litter fall or in moisture filtering through the canopy or along the surface of the bark (Edmonds et al., 1991). Edmonds et al. (1991) found that nitrogen leached from leaves and bark can also enrich Douglas-fir stem flow; the pH of stem-flow was significantly lower than that of either precipitation or throughfall, which may account, in part, for

the lower soil pH at the base of Douglas-fir and other conifers (Zinke, 1962). They attributed this acidity to an increase in organic acids, which could increase the weathering of mineral soil and release plant nutrients that could be trapped by the mats and transferred to the host tree (Griffiths et al., 1994). Edmonds et al. (1991) concluded that stemflow could be a major source of nutrients to be taken up by fine roots and their associated mycorrhizae. Analyses of soil solutions suggest that this nitrogen is readily trapped by the roots and organisms in the upper soil layers (Edmonds et al., 1991).

Obviously more remains to be learned about the factors influencing ectomycorrhizal mat distribution in coniferous and other forest ecosystems. Because previous studies have shown that these fungi may be important in optimizing forest productivity, there is considerable interest in determining the factors influencing their distribution. This study has shown that the presence of understory trees may influence distribution patterns. At present, the best explanation for the association is that the mats are collecting nutrients in litter and through-fall associated with these trees.

Acknowledgements

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Section editor: J H Graham