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Suppression of ectomycorrhizae on canopy tree seedlings in *Rhododendron maximum* L. (Ericaceae) thickets in the southern Appalachians

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Abstract Thickets of *Rhododendron maximum* (Ericaceae) (Rm) in the southern Appalachians severely limit regeneration of hardwood and coniferous seedlings. Experimental blocks were established in and out of Rm thickets in a mature, mixed hardwood/conifer forest in Macon County, N.C. Litter and organic layer substrates were removed, composited and redistributed among plots within the blocks (except for control plots). Seedlings of northern red oak (*Quercus rubra*) and eastern hemlock (*Tsuga canadensis*) were planted in the plots and harvested at the end of the first and second growing seasons. Litter manipulation had no effect on total mycorrhizal colonization, but the distribution of *Cenococcum geophilum* mycorrhizae was altered. After the first year, percent mycorrhizal colonization of hemlocks not in Rm thickets (62%) was at least three times higher than in Rm thickets (19%), and the ramification index (no. of mycorrhizae cm^{-1}) had increased by more than a factor of four (2.83 versus 0.61). In addition, colonization of 1-year-old hemlocks by *C. geophilum* was significantly higher within blocks with (10.4%) than without (4.6%) Rm. Differences in mycorrhizal colonization, ramification indices and colonization by *C. geophilum* were absent or less pronounced on 2-year-old hemlocks and 1- and 2-year-old oak seedlings. The biomasses of first year oak roots and shoots and second year shoots were 50% less in Rm thickets. Biomasses of first year hemlock roots and second year shoots were also reduced. Mycorrhizal parameters were correlated with some growth parameters only for hemlock seedlings, but did not explain most of the variation observed.

Key words Eastern Hemlock · Ectomycorrhiza · Mycorrhizal · colonization · Northern red oak · *Cenococcum geophilum*

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Introduction

Throughout the southern Appalachians, *Rhododendron maximum* L. (Ericaceae) (Rm) forms dense thickets in the understory of mesic north-facing slopes, stream banks, and coves. The Rm thickets, known as 'slicks', achieve heights of 4–5 m. The primary mycorrhizal associations of Rm are with ericoid mycoboints, which form dense intracellular coils in the cortical cells of Rm fine roots. Few extramatrical hyphae are associated with ericoid mycorrhizae, however. Dighton and Coleman (1992) reported ectomycorrhizal colonization of Rm, including *Cenococcum geophilum*, but were unable to quantify their occurrence. Smith et al. (1995) found that *Rhododendron macrophyllum* D. Don *ex* G. Don was rarely colonized by ectomycorrhizal fungi when grown in a greenhouse in soils from young Douglas-fir forests in the Pacific Northwest USA. Largent et al. (1980) also found evidence of ectomycorrhizal colonization of *Rhododendron* spp.

At the USDA Forest Service Southern Research Station Coweeta Hydrologic Laboratory (Coweeta) experimental forest, Rm occupies about 30% of the forest and has expanded more than 20% since 1975 (Dobbs 1995). Historically, areas where Rm occurs are also highly productive for quality hardwood lumber. The perception of strong canopy tree seedling inhibition in Rm thickets, beginning in the 1940s (Minkler 1941; Wahlenberg 1950), has engendered considerable concern among foresters and plant ecologists. Wahlenberg (1950) stated that "the hardwoods are hopelessly inhibited within the *R. maximum* slicks in comparison to

outside the slicks". More recently, Phillips and Murdy (1985) found that hardwood regeneration and rates of succession were reduced in Rm thickets. Significantly lower seedling density in gaps with heavy Rm cover was reported by Clinton et al. (1994). Numerous authors have considered Rm to be a problem weed for hardwood production (e.g. Martinez 1975), and control programs have been investigated (Wahlenberg and Doolitle 1950; Yawney 1962; Hooper 1969; Romancier 1971; Neary et al. 1984). Yet the biological basis of the interaction between Rm and tree seedlings remains poorly understood. Thus research into the mechanisms by which Rm thickets suppress the growth of canopy tree seedlings remains a high priority for forest biologists and foresters alike.

Several studies have examined the relationship between mycorrhizal fungi and allelopathy. Reduced ectomycorrhizal colonization and growth of Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] seedlings in response to litter leachates in vitro was reported by Rose et al. (1983). Robinson (1972) found that "living" heather [*Calluna vulgaris* (L.) Hull; Ericaceae] produced a compound that reduced the growth of ectomycorrhizal fungi. Lyon and Sharpe (1996) found that hayscented fern [*Dennstaedtia punctilobula* (Michx.) Moore] reduced growth and mycorrhizal colonization of northern red oak (*Quercus rubra* L.) in mini-terracosms. Hansen and Dixon (1987) carried out a pot study with red oak and reported that inoculation with an ectomycorrhizal fungus [*Suillus luteus* (L.) Fr.] reduced the allelopathic effect of interrupted fern (*Osmunda claytoniana* L.) on seedling mortality.

Similar interactions between ericaceous shrubs and tree seedlings have been the focus of research in the Pacific Northwest (Messier 1993) and central Newfoundland (Yamasaki et al. 1998). In coastal British Columbia, salal (*Gaultheria shallon* Pursh), also a member of the Ericaceae inhibits the growth and survival of seedlings. Messier (1993) found no difference between levels of mycorrhizal colonization in sites with various densities of salal, and similar results for vegetation removal versus control treatments. Containerized seedlings also were not colonized differentially over a range of salal planting densities. Messier (1993) attributed the seedling inhibition to competition for limited soil resources between the seedlings and the salal, and ruled out light as a factor because the seedlings were taller than the salal. In central Newfoundland, Yamasaki et al. (1998) found that black spruce (*Picea mariana* Mill.) seedlings grown close to *Kalmia angustifolia* L. (Ericaceae) had significantly lower mycorrhizal colonization (66%) than seedlings grown further away (96%). The reduced mycorrhizal colonization was attributed to allelopathic compounds produced by the *K. angustifolia*, based on the results of in vitro studies by Titus et al. (1995).

The objective of this present study was to experimentally investigate the effects of Rm litter and organic substrates, and the presence of Rm thickets in the subcanopy separately on the development of total mycorrhizal colonization, the composition of the ectomycorrhizal community (as indicated by *C. geophilum* Fr.), and the growth of two species of tree seedlings. We hypothesized that components of the Rm thickets (litter substrates, organic substrates, and/or presence of Rm in the subcanopy) would be associated with reduced total mycorrhizal colonization levels, increased colonization by *C. geophilum*, and reduced growth of canopy tree seedlings.

Materials and methods

Site description

The study was conducted at the Coweeta Hydrologic Lab, located in the Blue Ridge Physiographic Province of western North Carolina (35° 02' 29" N, 83° 27' 16" W). General vegetation types at Coweeta have been described as northern hardwood, cove hardwood, oak, or oak–pine communities (Day et al. 1988). High moisture levels and mild temperatures typify the area, climatically classified as marine, humid. Precipitation is distributed equally throughout the year, averaging 1800 mm annually (Swank and Crossley 1988).

Field plots were established at an elevation of 1000 m on a single north-facing slope. The site was dominated by mature northern red oak (*Q. rubra*), and also included hickory (*Carya* spp.), red maple (*Acer rubrum* L.) yellow poplar (*Liriodendron tulipifera* L.), sweet birch (*Betula alleghaniensis* L.), eastern hemlock (*Tsuga canadensis* L.), witch hazel (*Hamamelis virginiana* L.), and flowering dogwood (*Cornus florida* L.). Tree species composition was similar in blocks inside and outside Rm thickets.

Plot layout and site preparation

Six 1/4-ha blocks were randomly positioned, three within dense Rm thickets (with Rm), and three in areas where no Rm was found (without Rm). Within each block, 15 2×2-m plots were systematically located and randomly assigned one of five treatments (i.e. 3 replicate treatments per block): 1) unmanipulated controls, 2) litter and organic substrates from Rm thickets (Rl and Ro, respectively), 3) litter and organic substrates from forest without Rm thickets (Fl and Fo, respectively), 4) Fl and Ro, 5) Rl and Fo.

Both the surface litter and organic horizon were removed from all but the control plots. Each substrate type (Fl, Fo, Rl, Ro) was pooled and homogenized prior to being redistributed to treatment plots within each block. After the first growing season, all Rm leaves which fell on Fl treatments in Rm blocks were removed and equally distributed among the Rl treatment plots in blocks with no Rm.

Following the substrate manipulation, seedlings of hemlock and acorns of northern red oak were planted in the plots. The acorns were collected in the vicinity of the plots after natural stratification and planted (16 per plot, equally spaced) in April. Nine hemlock seedlings were planted per plot, spaced equally. The hemlock seeds (Cherokee Seed Co, Murphy, N.C.) were stratified for 2 months at 4 °C in separate substrates from within and outside Rm thickets. The hemlock were then germinated in greenhouse flats and maintained for 1 month under shade cloth (10% full sunlight) prior to transplanting into the plots. Levels of ectomycorrhizal colonization of the seedlings were visually assessed prior to planting in the field. Colonization levels were less than 5% on the seedlings at that time, and colonization by *C. geophilum* was not observed.

Seedling harvest and sampling

One seedling of each species was randomly selected and harvested from each of the plots after the first and again after the second growing seasons, prior to the onset of senescence. Selection of the seedlings was randomized by having one individual count the seedlings in the plot until reaching a random number chosen sequentially by another individual from a table. Seedlings with insufficient leaf material for identification were excluded. Although all plots had several seedlings of each species in 1996, five Rm plots had no surviving oaks and three Rm plots had no surviving hemlocks in 1997. The entire seedling was removed with the surrounding soil and stored at 5 °C. The roots were carefully washed free of debris and stored frozen in deionized water until they were examined for ectomycorrhizal colonization. The roots and shoots of the seedlings were dried at 70 °C for 3 days and weighed, except for roots from the second harvest.

On average, approximately 10 cm total of secondary roots (<2 mm diameter), taken from throughout the length of the root system, was examined. These root segments were used for quantification of mycorrhizal colonization (% of living root tips which were ectomycorrhizal) and to calculate the ramification indices (number of mycorrhizae per cm root) (Meyer 1987). Due to the rocky soil conditions, some root tips were damaged during harvest and the ramification indices may be underestimated compared with other studies.

After a comparison of numerous root tips, which were confirmed as non-mycorrhizal at high magnification with a compound microscope, morphological criteria were established for macroscopic identification of non-mycorrhizal root tips. Non-mycorrhizal root tips were characterized by several-to-many root hairs, sloughing epidermal cells which were suberized and light brown, lack of a fungal mantle, and a non-swollen appearance. Roots were placed in water in large petri plates and examined under a dissecting microscope (×0.9–4 magnification). Ectomycorrhizal root tips with a black mantle and typical stiff black rhizomorphs characteristic of the mycobiont *C. geophilum* Fr. were recorded separately from all other morphotypes. The identity of *C. geophilum* mycorrhizae were further confirmed by checking frequently for the characteristic stellate mantle pattern (Hatch 1934; Trappe 1964) with a compound microscope.

In addition, we examined numerous samples of Rm root systems and found no evidence of ectomycorrhizal colonization. Although ectomycorrhizal morphotypes were found tangled amongst the Rm fine roots, careful examination showed that they did not originate from an Rm root.

Statistical analysis

Means for all parameters were analyzed using analysis of variance with a generalized linear model with two block types (Rm, no Rm), three replicates of each block type, and three treatment replicates in each block replicate with SAS statistical software (SAS Institute, Cary, N.C.). Percent mycorrhizal colonization and percent colonization by *C. geophilum* were arcsine-square root transformed. Differences for the means between Rm and no Rm blocks were compared using *F*-tests with the type three mean square error term for block replicates with 4, 1 degrees of freedom. Differences between means for the control plots between block types were analyzed using *T*-tests for equally or unequally varying samples with SAS statistical software. Correlation was performed with the Pearson Product Moment test using SigmaStat statistical software (Jandel Corp., San Rafael, Calif.) with Bonferonni correction. Values of *P* less than .05 were considered statistically significant for all tests. Variance is presented as ± the standard error of the mean (SEM).

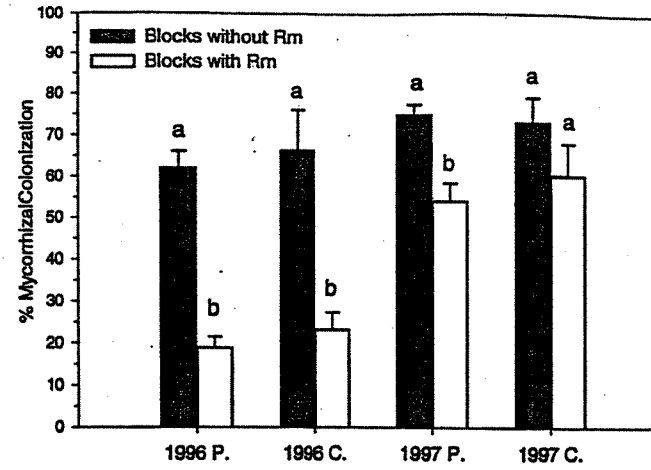

Fig. 1 Hemlock (*Tsuga canadensis*) total mycorrhizal colonization. Means for pairs of bars with different letters are significantly different ($P<.05$); *error bars* represent SEM (*Rm Rhododendron maximum*, *P* pooled mean from all samples including controls, significance analyzed using *F*-tests; *n* (blocks without Rm/blocks with Rm) for 1996=44/45, *n* for 1997=45/43, *C* control plots mean, significance analyzed using *T*-tests, $n=9$)

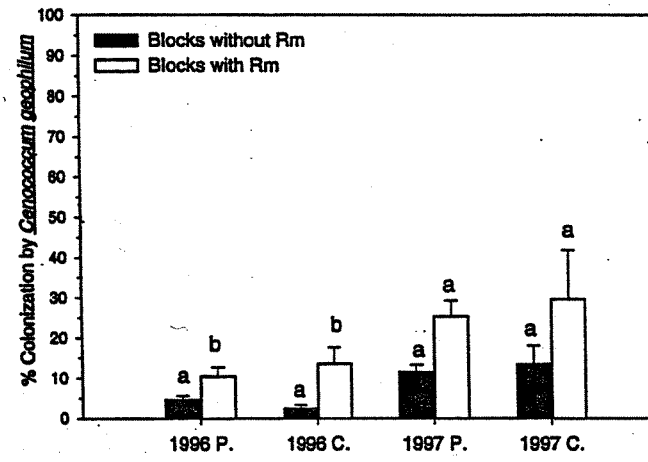

Fig. 2 Hemlock mycorrhizal colonization by *Cenococcum geophilum*. Abbreviations, statistics and sample sizes as for Fig. 1. Means for pairs of bars with different letters are significantly different ($P<.05$); *error bars* represent SEM

Results

1996 and 1997 hemlock mycorrhizae

The percent mycorrhizal colonization of 1-year-old hemlock seedlings was more than three times higher in blocks without than in blocks with Rm (Fig. 1). Percent colonization by *C. geophilum* was higher in blocks with Rm by a factor of 2.3 (Fig. 2). The ramification index was approximately 4.5-fold higher in blocks without than with Rm (Fig. 3). Seedlings from control plots showed similar responses, which were significant, for the above three parameters. Two-year-old hemlock seedlings in blocks with Rm had significantly lower to-

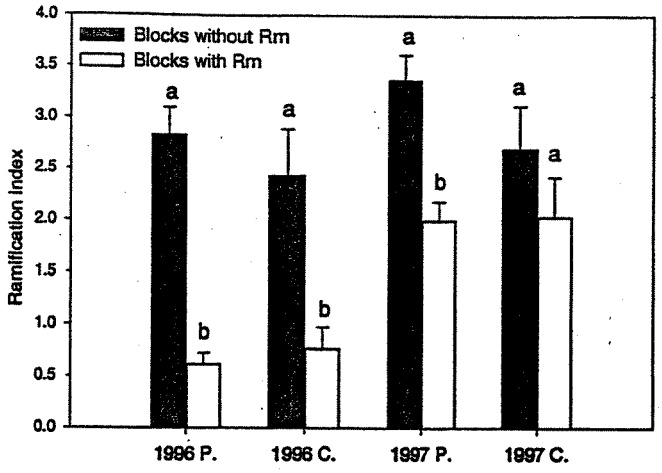

Fig. 3 Hemlock ramification indices (no. of mycorrhizal roots/cm secondary root). Abbreviations, statistics and sample sizes as for Fig. 1. Means for pairs of bars with different letters are significantly different ($P<.05$); *error bars* represent SEM

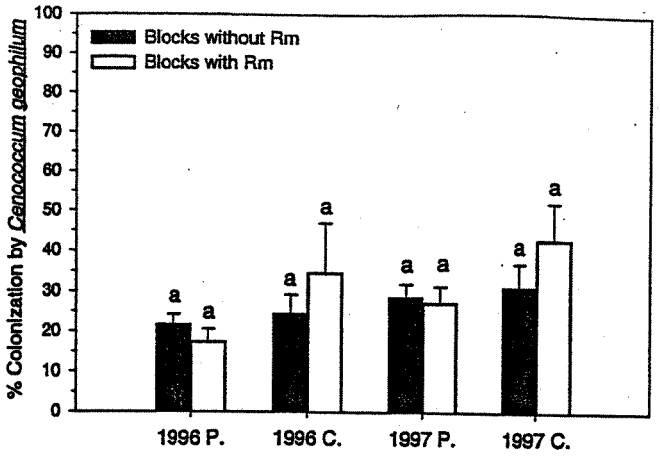

Fig. 5 Red oak mycorrhizal colonization by *C. geophilum*. Abbreviations and statistics as for Fig. 1, sample sizes as for Fig. 4. Means for pairs of bars with different letters are significantly different ($P<.05$); *error bars* represent SEM

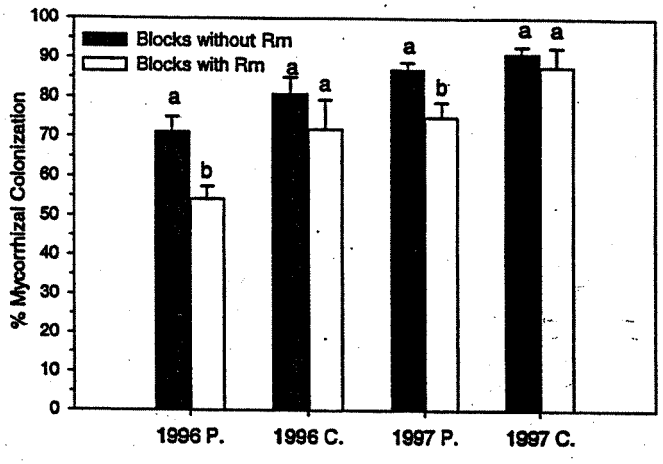

Fig. 4 Red oak (*Quercus rubra*) total mycorrhizal colonization. Abbreviations and statistics as for Fig. 1. *n* (blocks without Rm/blocks with Rm) for 1996 P.=44/40, *n* for 1997 P.=41/36, *n* for 1996 C.=9/8,*n* for 1997 C.=9/7. Means for pairs of bars with different letters are significantly different ($P<.05$); *error bars* represent SEM

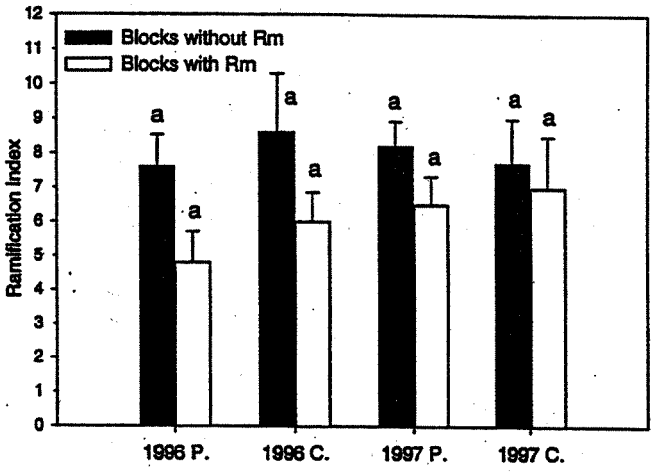

Fig. 6 Red oak ramification indices (no of mycorrhizal roots/cm secondary root). Abbreviations and statistics as for Fig. 1, sample sizes as for Fig. 4. Means for pairs of bars with different letters are significantly different ($P<.05$); *error bars* represent SEM

tal colonization and ramification indices than in blocks without Rm (Figs. 1,3). Although similar patterns were observed for the control seedlings, the results were not significant (Figs. 1–3). On second-year hemlock seedlings, treatments with Ro substrates produced significantly lower percent mycorrhizal colonization by *C. geophilum* (12.2% ±3.7) than treatments with Fo substrates (23.1% ±5.2).

1996 and 1997 red oak mycorrhizae

In blocks with Rm, 1-year-old red oak seedlings had significantly lower mycorrhizal colonization than in blocks without Rm (24%) (Fig. 4). There was no difference in the ramification indices in blocks with or without Rm (Fig. 6). Percentage colonization by *C. geophilum* was nearly equal in blocks with or without Rm (Fig. 5). There were no significant differences in total mycorrhizal colonization, ramification index or percent colonization by *C. geophilum* for control seedlings (Figs. 4–6).

After the second growing season, red oak seedlings had lower total mycorrhizal colonization (13%) in Rm blocks than in blocks without Rm (Fig. 4). Again, percentage colonization by *C. geophilum* was nearly equal in blocks with or without Rm (Fig. 5). The ramification indices were not significantly different between blocks with or without Rm (Fig. 6). Control seedlings again showed no significant differences in total mycorrhizal colonization, ramification index, or colonization by *C. geophilum* (Figs. 4–6). There was significantly higher

percent colonization by *C. geophilum* in treatments with Ro substrates (30.20% ± 6.0) than in treatments with Fo substrates (21.83% ± 6.2). The ramification indices were significantly lower in treatments with Rl substrates (0.611 ± 0.097) than in treatments with Fl substrates (0.850 ± 0.142).

Seedling growth parameters

One-year-old hemlock seedlings had significantly lower root weights (−1.75 mg, controls) and root/shoot ratios (−0.12, Poded samples) in blocks with versus without Rm. Shoot weights were similar in blocks with and without Rm. After the second year, shoot weight was significantly reduced in blocks with versus without Rm (–12 mg) (Table 1). After the second year, no significant differences were detected in shoot weight between controls with or without Rm.

First year red oak seedlings from control plots had significantly lower root weights (–220 mg) and shoot weights (–352 mg) in blocks with Rm than blocks without Rm. The root/shoot ratios were not different in blocks with or without Rm. After two growing seasons, the red oak seedlings had a significant reduction in shoot weight (–457 mg) in blocks with Rm.

Correlation of mycorrhizae and seedling growth parameters

First year hemlock seedlings showed a positive correlation between total percent mycorrhizal colonization and both root weight and root/shoot ratio (Table 2). Shoot weight was positively correlated with both total percent mycorrhizal colonization and ramification index for 2-year-old hemlock seedlings (Table 2). Red oak seedlings showed no correlation between growth parameters and mycorrhizal parameters (Table 2). Mycorrhizal parameters explained from 9–13% of the variation in seedling growth parameters for significant correlations.

Discussion

Total mycorrhizal colonization and ramification

Overall colonization levels were lower for hemlock than oaks, an observation which could be related to the slower growth of the more shade-tolerant hemlocks, to the fact that the hemlocks were not germinated at the site, or to the larger seed reserves in the oak acorns. In addition, adult hemlock existed as individuals or small clusters on the study site and may suffer greater isolation from compatible mycobionts than the ubiquitous

Table 1 Seedling growth in blocks with and without *Rhododendron maximum* (Rm). Means followed by different letters are significantly different ($P<0.05$). *Pooled samples* is pooled means for all samples including controls, significance analyzed using *F*-tests. *Controls* is means for control plots only, significance analyzed using *T*-tests (*U* Unequal variance *T*-test, *E* equal variance *T*-test, *n* blocks with Rm/blocks without Rm)

Pooled samples	No Rm		Rm		*n*	*P*
	Mean	SEM	Mean	SEM		
Hemlock 1996						
Root weight (mg)	5.7	0.49	3.7	0.31	40/43	0.12
Shoot weight (mg)	12.6	0.84	13.3	0.59	45/44	0.77
Root/Shoot	0.41[a]	0.02	0.29[b]	0.02	40/43	0.03
Hemlock 1997						
Shoot weight (mg)	34.7[a]	2.20	22.8[b]	1.50	45/42	0.04
Oak 1996						
Root weight (mg)	493.0[a]	43.20	206.0[b]	16.3	43/41	0.00
Shoot weight (mg)	727.0[a]	38.60	409.0[b]	31.5	45/45	0.00
Root/Shoot	0.69	0.05	0.64	0.11	43/42	0.40
Oak 1997						
Shoot weight (mg)	907.0[a]	67	450.0[b]	33.4	44/40	0.01
Controls						
Hemlock 1996						
Root weight (mg)	5.0[a]	0.45	3.2[b]	0.4	9/9	(E) 0.014
Shoot weight (mg)	13.5	2.40	12.2	1.3	9/8	(E) 0.66
Root/Shoot	0.39	0.06	0.27	0.04	8/8	(E) 0.12
Hemlock 1997						
Shoot weight (mg)	25.5	4.80	22.9	3.00	9/9	(E) 0.65
Oak 1996						
Root weight (mg)	429.0[a]	75.00	209.0[b]	34.1	9/8	(U) 0.022
Shoot weight (mg)	703.0[a]	86.40	351.0[b]	46.2	9/9	(E) 0.002
Root/Shoot	0.6	0.05	0.7	0.15	9/8	(U) 0.51
Oak 1997						
Shoot weight (mg)	808.0[a]	148	393.0[b]	67.3	9/9	(U) 0.026

Table 2 correlation of mycorrhizal colonization and seedling growth parameters (* significant with Bonferroni correction, *r* Pearson correlation coefficient)

	Total % colonization			Cenococcum % colonization			Ramification index		
	r	*P*	*n*	*r*	*P*	*n*	*r*	*P*	*n*
Hemlock 1996									
Root weight (mg)	0.354*	0.001	82	−0.069	0.540	82	0.232	0.036	82
Shoot weight (mg)	0.119	0.271	88	0.093	0.390	87	0.096	0.372	88
Root/Shoot	0.334*	0.002	82	−0.203	0.067	82	0.241	0.029	82
Hemlock 1997									
Shoot weight (mg)	0.341*	0.001	87	−0.095	0.384	87	0.301*	0.005	87
Oak 1996									
Root weight (mg)	0.183	0.101	81	0.100	0.380	79	0.109	0.331	81
Shoot weight (mg)	0.228	0.037	84	−0.073	0.514	83	0.261	0.016	84
Root/Shoot	−0.003	0.979	81	0.195	0.086	79	−0.074	0.511	81
Oak 1997									
Shoot weight (mg)	0.173	0.134	76	0.058	0.619	76	0.159	0.171	76

oaks. Also, due to a high mortality rate of the red oak seedlings in Rm blocks during the second year of the study, poorly colonized seedlings may have died more frequently than other seedlings. Therefore, the total percent colonization of oaks may be overestimated in the Rm blocks.

Comparisons of mycorrhizal colonization levels between studies are difficult due to differences in site preparation, host tree composition, edaphic conditions, and measurement techniques. In this study, colonization of first-year northern red oak seedlings was 71% in blocks without Rm (Fig. 4). Dahlberg et al. (1997) found that 95% of all short roots were ectomycorrhizal in an old growth Norway spruce (*Picea abies* Karst.) forest. Messier (1993) found 92–98% colonization on western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) seedlings, and 99% colonization on Sitka spruce (*Picea sitchensis* Bong. Carr.) seedlings. Zhou et al. (1997) reported 37.6% mycorrhizal colonization on 2-year-old northern red oak seedlings in uncut oak and pine stands.

Mycorrhiza inhibition by Rm could be attributed to many factors. However, it is important to note that the relationship of Rm thickets and tree seedling mycorrhization may be indirect if Rm areas represent a habitat less suitable for mycorrhizal development than areas without Rm. If Rm affects mycorrhizal colonization of tree seedlings directly, the following factors may be involved: 1) reduced light availability to tree seedlings resulting in lower carbohydrate availability for ectomycorrhizal fungi and reduced root development, 2) accumulation in the soil of biotoxic compounds produced by Rm or Rm ericoid fungi which reduce inoculum potential, seedling root growth, or mycorrhizal synthesis, or 3) competition for resources between the Rm ericoid root system and the tree seedling ectomycorrhizal root system.

Accumulation of biotoxic compounds from Rm in the soil is not strongly supported by this study. The effects of litter and organic substrate manipulation were limited and species specific. For example, *C. geophilum* colonization was species specific (higher on oak, lower on hemlock) in treatments with Rm organic layer substrates after the second year. Substrate removal has been shown to affect seedling mycorrhization in several studies reviewed in Baar (1997) where Rm was not a factor.

Colonization by *Cenococcum geophilum*

Mycorrhizal colonization of tree seedlings by *C. geophilum* increased in the presence of Rm thickets in a species-specific pattern. *C. geophilum* accounted for 50% of the ectomycorrhizae on hemlock seedlings in blocks with Rm thickets. On oak seedlings, however, *C. geophilum* was nearly equally abundant in blocks in and out of Rm thickets in all treatments except for the controls. Apparently, the presence of Rm had a greater affect on the mycorrhizal community or the process of mycorrhization associated with hemlock seedlings than that associated with red oak. Levels of colonization by *C. geophilum* were generally lower on hemlock than on red oak. This is not surprising, as Malloch and Malloch (1981) also reported species-specific colonization levels of *C. geophilum*, ranging from no colonization on *Pinus banksiana* Lamb. to 19 of 25 root segments colonized on *Abies balsamea* (L.) Mill.

Cenococcum geophilum is an ectomycorrhizal ascomycete with broad host compatibility (Trappe, 1964) which tends to favor periodic drought. Worley and Hacskaylo 1959; Pigott 1982). The ability of ectomycorrhizal fungi to promote seedling growth varies even among populations of *Suillus granulatus* Fr. (Kuntze) (Jacobson and Miller 1992) and, according to Marx et al. (1978), *C. geophilum* is less effective than several other ectomycorrhizal fungi in vivo. The findings of several studies indirectly support the idea that in-

creased levels of colonization by *C. geophilum* in Rm thickets are indicative of poor site conditions for mycorrhizal fungi under Rm. Dahlberg et al. (1997) found that the *C. geophilum* colonization level was 18% of the total mycorrhizal colonization in an "oligotrophic", old-growth, Norway spruce forest. A study by Antibus (1980) indicated that *C. geophilum* occurs four times more frequently on seedlings in oil seeps than in other areas near Barrow, Alaska. Although growth of other ectomycorrhizal fungi was reduced by litter leachates, Rose et al. (1983) found that *C. geophilum* growth had no response to any of the tested leachate preparations.

In conclusion, Rm thickets were associated with strong mycorrhizal inhibition of hemlock seedlings on a site in the southern Appalachians. Seedling biomass was also reduced in these Rm thickets. However, the mycorrhizal inhibition of the seedlings is probably only partially responsible for the reduced seedling growth both above and below ground. The ability of ectomycorrhizal fungi to access nutrients and promote seedling growth is known to vary intraspecifically (Antibus et al. 1981; Jacobson and Miller 1992) and interspecifically (Marx et al. 1978; Antibus et al. 1981). Shifts in dominance of mycorrhizal morphotypes, as seen on hemlock seedlings in this study, could be a factor in the seedling suppression observed under Rm. Other factors, such as the availability of light and the relationship between light quantity and mycorrhizal colonization, should be the focus of further investigations.

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