Occurrence of Rhizomorphs of *Armillaria* in Soils from Declining Red Spruce Stands in Three Forest Types

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ABSTRACT

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The occurrence of rhizomorphs in soil around dead trees was determined in stands of declining red spruce in hardwood, transition, and montane boreal forest types that differ in elevation. Rhizomorph incidence and population density were significantly lower in the higher elevation transition and montane boreal forest types. These data suggest that previously reported infrequent colonization of declining red spruce at high elevations is due to low levels of inoculum of *Armillaria* in forest soils. High lead concentration and low pH of the organic layer of soils in the higher elevation spruce-fir stands in the Northeast were correlated with low levels of inoculum, but these factors alone do not explain the variation in occurrence of the fungus.

Additional key words: heavy metals, root disease

Decline of red spruce (*Picea rubens* Sarg.) in both basal area and stand density has been reported for a large part of its native range in the northeastern United States (6,10,25). Decline is most severe in the higher elevation transition and montane boreal spruce-fir forests, but its cause(s) is unknown (10,24). A survey of red spruce for Armillaria root disease showed that the fungus occurred on dead and declining trees at all elevations but that the incidence and severity of tree colonization were lower at higher elevations (4).

The reasons for the scarcity of the pathogen in declining and dead trees in the higher elevation forests are unknown. Soil characteristics, host species, and fungal isolate are known to influence the rate of food base colonization and subsequent production of rhizomorphs (15,16,19,20,23). Low soil moisture, antagonistic organisms, and heavy-metal contamination also have been suggested to affect inoculum levels (4). Lead contamination of the forest soils is higher in upper elevation forests than in lower elevation forests in the Northeast (7,11,22), and lead is toxic to several fungi (14,27,28).

This study was conducted to determine the incidence and population density of rhizomorphs of *Armillaria mellea*, sensu lato (29), in the soil in three major forest types in which red spruce grows on mountainous slopes and to relate any differences in inoculum to pH and concentrations of trace metals in the soil.

MATERIALS AND METHODS

Soil was sampled at seven sites where red spruce was reported and observed to be declining; these included five northern sites, 1) Whiteface Mountain, Wilmington, NY; 2) Camel's Hump, Huntington, VT; 3) Mt. Washington and 4) Wildcat Mountain, Glen House, NH; and 5) Hubbard Brook Experimental Forest, West Thornton, NH; and two southern sites, 6) Gaudineer Knob, Bartow, WV, and 7) Mt. Mitchell, Ashville, NC. Four of these sites (1, 2, 3, and 5) had been included in our initial survey for Armillaria root disease (4).

Sample design. At each site, a contour transect was located in the hardwood, transition, and montane boreal forest types, which differ in elevation. Elevations for these forest types were 600–770, 760–1,000, and 1,000–1200 m in the northeastern sites (1–5); 1,600, 1,640, and 1,890 m at Mt. Mitchell; and 1,200, 1,300, and 1,350 m at Gaudineer Knob, respectively. There is no montane boreal spruce forest at Hubbard Brook. Six plots were located along and within ±10 m of the elevation contour near a standing dead spruce tree (dead >3 yr). Each plot was at least 50 m from the previous plot. Four plots, in the hardwood forest type where spruce occurred in patches, were located near dead trees other than spruce to keep the plot within the spruce patch. This accounted for fewer than 5% of the plots. Three soil samples were taken within 0.5 m of the dead tree (18,26). The unincorporated litter was brushed away and a 15-cm-square block of soil about 25 cm deep was cut with a keyhole saw. The surrounding material was removed from one side of the block, and the block was cut free and transferred to a plastic tarp. The mineral soil, if discernable, was separated from the organic soil (forest floor), and each was bagged separately. The thickness of each soil type was measured. The samples were returned to the laboratory and processed immediately for rhizomorph measurement or refrigerated until processed (not more than 1 wk).

Rhizomorph measurement. Blocks of soil were placed on a laboratory table and gently teased apart by hand. The woody roots were examined for rhizomorphs, which were removed. The remaining fine roots and soil were examined carefully for rhizomorphs, which were identified on the basis of morphology, color, and elasticity. Incidence of rhizomorph occurrence was based on their presence or absence in each plot. When rhizomorphs were found, the length of each rhizomorph and its branches was measured to the nearest 0.1 cm. The total length of rhizomorph per soil sample was calculated and divided by the soil volume to give centimeters of rhizomorph per cubic centimeter of soil (density).

Soil chemistry. Organic and mineral layers of the same soil block were analyzed separately. After all root and rhizomorph material was removed, the remaining soil was mixed thoroughly and a subsample was removed for chemical analysis. Soil pH was measured with a pH meter after mixing 5 g of air-dried soil with 100 ml of distilled water and allowing the slurry to stand overnight. The remaining subsample was air-dried, ground in a Wiley mill, and oven-dried at

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80 C to constant weight. Two grams of the ground dry soil was ashed at 500 C overnight. Weight loss on ignition was used to estimate the organic matter content in each sample. The ash was digested by boiling in 10 ml of 6 N HNO_3 and 1 ml of distilled H_2O for 15 min, filtered, and diluted to 50 ml with distilled H_2O. The solution was analyzed for aluminum, copper, manganese, nickel, lead, and zinc with a Perkin-Elmer Model 403 Atomic Absorption Spectrophotometer. Bureau of Standards orchard leaves were used as reference standards for the analyses.

Data analysis. Chi-square analysis on a per-plot basis was used to determine if there were significant differences in rhizomorph incidence among forest types. Rhizomorph density was analyzed on a per-sample basis using regression and covariance analyses. Regression analyses were used to determine what form of the data met assumptions of normal distribution and to determine the model that best described the relationship among density of *Armillaria* rhizomorphs, the covariates of concentrations of metals and H^+ ion in the soil, and site and forest type factors. Covariance analysis was used to determine if there were significant differences in rhizomorph density among sites and forest types and among soil pHs and metal concentrations. A multivariate analysis was conducted to determine if there were significant differences in metal concentrations and pHs among sites and forest types.

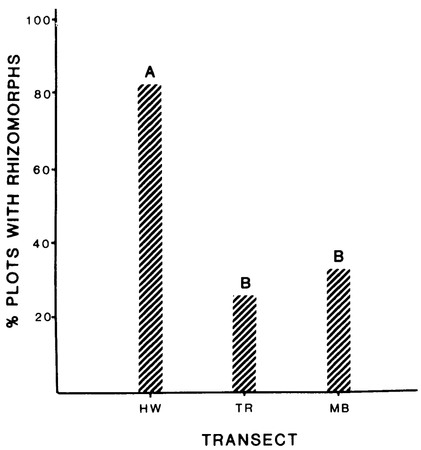

Fig. 1. Percentage of all plots with *Armillaria* rhizomorphs in declining red spruce stands in hardwood, transition, and montane boreal forest types in five northern mountainous forest sites (n = 30, 27, and 24 for the three forest types, respectively). Different letters above columns indicate significant differences at $P = 0.05$.

RESULTS

Rhizomorphs. Rhizomorphs were found in 27% (95) of 351 samples taken from 117 plots. Of the 95 soil samples with rhizomorphs, 48 (50%) of these had rhizomorphs only in the organic layer, 25 (26%) had them in both organic and mineral soils, and 22 (24%) had rhizomorphs only in the mineral layer. A total of 3,708 cm of rhizomorph were found in all samples; 3,471 cm (94%) came from the organic layer and 237 cm (6%) came from the mineral layer. Therefore, only data for the organic layer (forest floor) are presented.

For the five northern sites, the incidence of rhizomorphs of *Armillaria* in the organic layer in transition and montane boreal forests was significantly less than that in hardwood forests (Fig. 1, Table 1). Rhizomorph incidence in transition or montane boreal forest was less than half that in the hardwood forest type for all northern sites but Mt. Washington. Rhizomorphs occurred infrequently in all forest types at the two southern sites (Table 1).

Regression analysis of the rhizomorph density data indicated that a quadratic model of log 10 transformation of metals and pH gave the "best" fit for predicting rhizomorph density.

A covariance analysis with log 10 and $(\log 10)^2$ values for pH and all metal concentrations as covariates showed that there were no significant differences in rhizomorph densities among sites, but there were signficant ($P = 0.05$) differences among forest types. Rhizomorph density (centimeters of rhizomorph per cubic centimeter of soil) for all sites was significantly (10 times) greater in hardwood forests than in transition or montane boreal forests (Fig. 2). This relationship was similar at each site (Table 1). When rhizomorph density was compared among forest types only for those forest floor samples that had rhizomorphs, density in the hardwood forest floor (26.9×10^{-3} cm/cm^3 of forest floor) was still four to five times higher than in transition (6.5×10^{-3} cm) and montane boreal (5.2×10^{-3} cm) forest types.

Soil chemistry. There were significant differences in pH and concentrations of metals among sites and forest types, but differences or trends among forest types were not consistent for all sites (Table 2). Concentrations of lead were higher in the transition and montane boreal forest types than in the hardwood forest type at all sites except Mt. Mitchell (Table 2) and increased with increasing elevation. Soil pH decreased with elevation and was significantly higher in the hardwood forest in three of the sites (Table 2).

Concentrations of manganese decreased with increasing elevation and except for Whiteface and Wildcat mountains were highest in the hardwood type and lowest in montane boreal type. Manganese differences among forest types were significant ($P = 0.05$) only at Mt. Washington. Concentrations of nickel

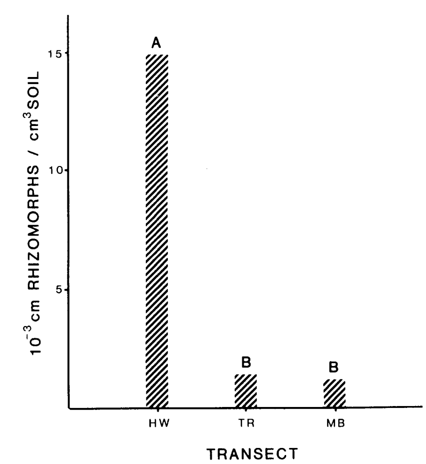

Fig. 2. Average length of rhizomorphs per volume of soil (density) in forest floor samples in declining red spruce stands in hardwood, transition, and montane boreal forest types in five northern and two southern mountainous sites (n = 126, 117, and 108 for the three forest types, respectively). Different letters above columns indicate significant differences at $P = 0.05$.

Table 1. Frequency and density of *Armillaria* rhizomorphs in samples of forest floor from red spruce stands in hardwood, transition, and montane boreal forest types in five northern and two southern sites

Rhizomorph measurement	Forest type	Northern sites[a] WF	CH	HB	MW	WC	%	Southern sites[a] CK	MM	%
Frequency[b]	Hardwood	6/6	5/6	5/6	5/6	5/6	87	1/6	1/6	17
	Transition	2/5	1/6	3/6	3/6	1/4	37	0/6	1/6	8
	Montane boreal	2/6	1/6	···	5/6	2/6	42	0/6	0/6	0
							Av.			Av.
Density[c]	Hardwood	6.8	29.4	17.5	12.4	23.3	17.9	9.7	2.7	6.2
	Transition	2.0	0.8	0.6	5.7	0.0	1.8	0.0	0.5	0.25
	Montane boreal	0.0	1.9	···	2.9	2.1	1.7	0.0	0.0	0.0

[a] Northern sites from west to east: WF = Whiteface Mountain, New York; CH = Camel's Hump, Vermont; HB = Hubbard Brook, New Hampshire; MW = Mt. Washington, New Hampshire; and WC = Wildcat Mountain, New Hampshire. Southern sites: GK = Gaudineer Knob, West Virginia, and MM = Mt. Mitchell, North Carolina.

[b] Number of plots out of six in which rhizomorphs occurred (three samples per plot).

[c] Density is centimeters of rhizomorphs $\times 10^{-3}$/cm^3 of forest floor. $n = 3 \times$ Number of plots per forest type.

were similar in the hardwood and montane boreal forests, and at four sites, nickel was significantly lower in the transitional forest. Concentrations of aluminum, copper, and zinc showed no trends among the forest types, but there were large site differences for aluminum.

The full quadratic model with pH and metals included as covariates and site and forest type as independent variables accounted for 32% of the variation in rhizomorph density for all sites (Table 3). When pH and metals were excluded from the model, there was a significant decrease in the amount of variation of rhizomorph density explained by the reduced model (Table 3). When pH and metals were removed individually from the model, only removal of pH caused a significant increase in the residual sum of squares (Table 3). A significant increase in residual sum of squares also occurred when forest type was removed from the model. Forest type, pH, and metal concentrations were correlated, and removal of one from the model caused a significant increase in the sum of squares for the remaining variables. When lead was removed from the model, the sum of squares for forest type doubled, indicating a strong correlation between lead and forest type. When rhizomorph density was analyzed within a forest type, lead was significantly correlated (−0.7935) with rhizomorph density in the montane boreal forest. Soil pH was significantly correlated (+0.7143) with density in the transition forest. No variable was significantly correlated with rhizomorph density in the hardwood forest type.

A discriminant model was developed to distinguish between those plots that did or did not have rhizomorphs and to estimate the amount of variability in rhizomorph incidence that was explained by soil trace metal concentrations, pH, and forest type. Elevation measurements were substituted for forest type because elevation differences among sites approximated forest type differences and elevation was a continuous variable. Forest type, lead, pH, and manganese yielded a discriminatory model accounting for 29% of the variation in rhizomorph occurrence at all sites. The same variables accounted for 26% of the variation at the northern sites (sites 1–5). No variables were useful discriminators of *Armillaria* frequency at the southern sites. When plots were classified into categories with or without rhizomorphs using the discriminant function, 84% of those with rhizomorphs and 76% of those without rhizomorphs were classified correctly.

DISCUSSION

Rhizomorphs of *Armillaria* occurred in soils in all three forest communities, but there were large differences in the incidence and density of rhizomorphs between the hardwood and transition and montane boreal communities. Associ-

Table 3. Comparison of full and reduced models of *Armillaria* rhizomorph density with pH and metals as covariates where included in the model

Model	R^2	RSS	df	F	Significance[a]
Full[b]	32	2.954	309	···	···
Reduced A[c]	24	3.300	323	2.59	<0.010
Reduced B[d]	28	3.119	311	8.63	0.001
Reduced C[e]	28	3.135	311	9.47	0.001

[a] Significance pertains to increase in residual sums of squares above that in the full model.
[b] Full model included log 10 and $(\log 10)^2$ of pH and six metals and site, forest type, and site by type interactions.
[c] Reduced model without pH and metal covariates.
[d] Reduced model without site variable.
[e] Reduced model with pH covariate.

Table 2. Mean concentrations of trace and other metals and H^+ ion in samples of forest floor from declining red spruce stands in hardwood (Hw), transition (Tr) and montane boreal (Mb) forest types in five northern and two southern sites

		Trace metal concentrations ($\mu g\ g^{-1}$ dry weight)							
	Forest	Northern sites[x]					Southern sites[x]		
Metals	type[w]	WF	CH	HB	MW	WC	GK	MM	Tukey's W[y]
Al	Hw	3,869 a[z]	9,026 b	6,316 b	6,936 a	2,596 a	2,515 a	9,305 a	2,629-S
	Tr	4,088 a	2,865 a	2,650 a	6,277 a	5,260 a	2,620 a	9,266 a	3,718-F
	Mb	6,184 a	5,253 a	···	4,591 a	5,131 a	2,659 a	9,044 a	
Pb	Hw	87 a	72 a	79 a	81 a	57 a	61 a	64 a	37-S
	Tr	121 a	215 b	90 a	100 a	88 a	114 b	66 a	52-F
	Mb	153 b	248 b	···	102 a	84 a	129 b	57 a	
Mn	Hw	160 a	275 a	311 a	328 b	156 a	159 a	152 a	145-S
	Tr	50 a	138 a	150 a	323 b	180 a	114 a	67 a	205-F
	Mb	70 a	123 a	···	115 a	137 a	102 a	35 a	
Zn	Hw	76 a	74 a	70 a	72 a	63 a	53 a	46 a	28-S
	Tr	88 a	92 a	51 a	57 a	67 a	73 a	57 a	40-F
	Mb	51 a	76 a	···	65 a	58 a	65 a	25 a	
Cu	Hw	7 a	17 a	11 a	17 a	12 a	11 a	19 a	4-S
	Tr	12 a	16 a	12 a	18 a	13 a	11 a	18 a	6-F
	Mb	8 a	16 a	···	14 a	17 a	16 a	14 a	
Ni	Hw	12 b	18 c	10 a	13 b	11 b	6 a	10 a	2-S
	Tr	7 a	7 a	8 a	8 a	8 a	5 a	8 a	3-F
	Mb	10 b	12 b	···	13 b	12 b	7 a	8 a	
pH	Hw	4.11 b	3.82 b	4.08 b	3.98 a	3.99 a	3.54 a	3.66 a	0.20-S
	Tr	3.57 a	3.52 a	3.67 a	3.87 a	3.88 a	3.40 a	3.61 a	0.28-F
	Mb	3.84 b	3.54 a	···	3.78 a	3.83 a	3.39 a	3.51 a	

[w] Average elevations for Hw, Tr, and Mb were 680, 900, and 1,070 m, respectively, for northern sites and 1,400, 1,470 and 1,620 m, respectively, for southern sites.
[x] Northern sites from west to east: WF = Whiteface Mountain, New York; CH = Camel's Hump, Vermont; HB = Hubbard Brook, New Hampshire; MW = Mount Washington, New Hampshire; and WC = Wildcat Mountain, New Hampshire. Southern sites: GK = Gaudineer Knob, West Virginia, and MM = Mt. Mitchell, North Carolina.
[y] Minimum difference between means for significance at $P = 0.05$, determined by Tukey's W procedure; upper value for sites (S), lower value for forest types (F).
[z] Means not followed by similar letters show significant differences at $P = 0.05$ among forest types within sites.

ated with the change from hardwood to transition forest type that occurred with increasing elevation were differences in tree species composition, lead concentration, and pH of the forest floor. Other soil characteristics and fungal genotype may also be involved in the distribution of rhizomorphs of the fungus.

Differences in incidence and severity of Armillaria root disease associated with elevation have been reported for Norway spruce (*Picea abies* Karst.) in the Thuringian Forest (8) and Carpathian and Beskid mountains (13) in Europe. In the Thuringian Forest (8), lower pathogenicity in the higher elevation stands was associated with the indigenous stands of Norway spruce on nutrient-poor podzolic soils. Stumps of felled trees in these stands, however, were readily colonized. In the Carpathian and Beskid mountains, disease caused by *Armillaria* in the early mid-1900s was confined essentially to spruce stands below 1,000 m in elevation (13). Studies on these stands revealed that disease incidence was related to site disturbance, soil type, and climate. Disease occurred primarily on former fir-beech sites with acid brown or leached brown soils, whereas healthy stands were also indigenous spruce stands growing in podsol soils (2).

Site disturbance seems to have had no role in site differences in rhizomorph populations observed in this study. Although the montane boreal forests in the northeastern United States have essentially been free of anthropogenic disturbance, the transition forest has not. These midelevation areas along with the lower hardwoods were logged during the height of land clearance for agriculture and timber harvest during the 19th and early 20th centuries. Most of the original forests below 1,000 m in elevation on the slopes of the White, Green, and Adirondack mountains were removed during this period (3,5,9,21).

There was a major change in overstory species composition from beech (*Fagus grandifolia* Ehrh.); birch (yellow, *Betula lutea* Michx., and white, *B. papyrifera* Marsh.); maple (sugar, *Acer saccharum* Marsh., and red, *A. rubrum* L.); red spruce; and balsam fir (*Abies balsamea* (L.) Mill.) in the hardwood forest type to predominantly spruce, balsam fir, and birch in the transition forest (6). This represents a substantial decrease in the amount of hardwood substrate for rhizomorph production. Although we sampled mostly around dead spruce trees, we did not trace rhizomorphs to the tree. The significantly greater frequency and amount of rhizomorphs in the forest floor in the hardwood forest type may be a function of the abundance of hardwood substrate in the soil and species of *Armillaria*.

Spruce and fir are suitable substrates for colonization and rhizomorph production by *Armillaria*. Singh (26) found numerous rhizomorphs in soils in pure conifer stands in Newfoundland. Rhizomorph production by *Armillaria* from roots of broad-leaved trees is better, however, and was greater both in quantity and longevity than that for pines (23). In a comparison of red maple and red spruce as substrates for *Armillaria*, significantly more rhizomorphs were produced from red maple segments (20). Morrison (15) also reported that rhizomorph production from hardwood substrates was greater than from conifers.

Morrison also observed that there were great differences in rhizomorph production among isolates of *Armillaria* (16). More recent work on the genetics of *Armillaria* (1,12,17) indicates that these differences in rhizomorph growth were related to different species of *Armillaria*. Classification of field isolates into species of *Armillaria* (23) has shown that certain species predominate on conifers while others predominate on hardwoods. Thus, differences in rhizomorph production observed in our study could also be related to the existence of different species of *Armillaria* in the different forest types. Gramss (8), in his studies on Norway spruce, observed distinct differences in rhizomorph production and pathogenicity between isolates of *Armillaria* from different elevations. His "lowland" isolates produced numerous brown rhizomorphs and were more pathogenic than his "highland" isolates, which did not produce brown rhizomorphs in the soil.

Our preliminary studies (*unpublished*) on the genetics of upper elevation versus lower elevation isolates of *Armillaria*, using growth responses of haploid tester strains of *Armillaria* paired with field isolates on agar plates (12), indicate that there are different biological species in hardwood and spruce-fir forest types. Studies are under way to determine if there is an elevational gradient of species of *Armillaria*.

Lead could be a factor responsible for low rhizomorph populations at higher elevations. Although correlations were not very high, the relationship of density of rhizomorphs and lead among all northern sites was highly significant, and within the montane boreal forest type, accounted for 62% (R^2) of the variation in rhizomorph density among all sites. Lead was also an important variable in the discriminant function model of rhizomorph frequency. Our preliminary studies indicate that concentrations of insoluble lead as low as 10 ppm, especially at pHs below 4.0, can significantly reduce growth and inhibit rhizomorph formation by *Armillaria* in culture (*unpublished*).

Although no single or combinations of the other trace metals were correlated highly with rhizomorph density, when included as covariates in the model for rhizomorph density, they did account for a significant portion of the variation of rhizomorph density. Spatial patterns and concentrations of trace metals in the forest floor observed in this study are comparable to those reported by Friedland et al (7) for northeastern forest sites and most likely accurately reflect the metal environment of the rhizomorphs.

Soil pH also is a potential inhibitor of rhizomorph initiation and development (19). No specific pH values were reported by Redfern (19), but he observed that more rhizomorphs were initiated and grew larger in alkaline sand, loam, and clay than in acid soils. These general categories suggest that pH differences, however, were large. Morrison (16) reported that rhizomorph production by some isolates of *A. mellea* were actually stimulated in acidic soils. However, the lowest pH reported was 4.4, which is 0.6–1.0 pH units higher than the pH of the transition and montane boreal soils that we measured in this study. Data on rhizomorph quantities in soils with pHs similar to those we measured exist for stands of Sitka spruce (*P. sitchensis* (Borg.) Carr., in Newfoundland (26). Rhizomorphs were abundant in humus layers with pHs as low as 3.5. Although differences in pH between hardwood and transition and montane boreal forest floor in our study were significant, when compared with the data on Sitka spruce, these differences are most likely not large enough to account for the reduction in rhizomorph frequency or density.

The lower incidence and density of rhizomorphs of *Armillaria* in forest soils in declining red spruce stands in transition and montane boreal forest communities correspond to the decrease in incidence and severity of colonization by *Armillaria* of root systems of dying and dead red spruce in similar stands throughout the Northeast (4). These data indicate that the limited colonization of spruce by the fungus in these upper elevation stands in the Northeast is a function of the limited occurrence of the fungus and amount of inoculum in forest soils. Limited amount of hardwood substrate, high concentrations of lead and other trace metals, and low soil pH were correlated with low levels of inoculum in these upper elevation forests, but they explain only a small portion of the variation in inoculum levels. Other variables are obviously involved.

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