

Oak seedling growth and ectomycorrhizal colonization are less in eastern hemlock stands infested with hemlock woolly adelgid than in adjacent oak stands

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Summary Invasive, non-indigenous, phytophagous insects have caused widespread declines in several dominant tree species. The decline in dominant tree species may lead to cascading effects on other tree and microbial species and their interactions, affecting forest recovery following the decline. In the eastern USA, eastern hemlock (*Tsuga canadensis* (L.) Carr) is declining because of infestation by the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand). Northern red oak (*Quercus rubra* L.) is a common replacement species in declining hemlock stands, but reduced mycorrhizal inoculum potential in infested hemlock stands may cause oak to grow more slowly compared with oak in oak stands. We grew red oak seedlings for one growing season in declining hemlock-dominated stands infested with HWA and in adjacent oak-dominated stands. Ectomycorrhizal root tip density and morphotype richness in soil cores were 63 and 27% less, respectively, in declining hemlock stands than in oak stands. Similarly, ectomycorrhizal percent colonization and morphotype richness on oak seedlings were 33 and 30% less, respectively, in declining hemlock stands than in oak stands. In addition, oak seedlings in declining hemlock stands had 29% less dry mass than oak seedlings in oak stands. Analysis of covariance indicated that morphotype richness could account for differences in oak seedling dry mass between declining hemlock stands and oak stands. Additionally, oak seedling dry mass in declining hemlock stands significantly decreased with decreasing ectomycorrhizal percent colonization and morphotype richness. These results suggest that oak seedling growth in declining hemlock stands is affected by reduced ectomycorrhizal inoculum potential. Further, the rate of forest recovery following hemlock decline associated with HWA infestation may be slowed by indirect effects of HWA on the growth of replacement species, through effects on ectomycorrhizal colonization and morphotype richness.

Keywords: *Adelges tsugae*, foundation species, herbivory, invasive species, mycorrhizae, regeneration, *Quercus rubra*, seedling establishment, *Tsuga canadensis*.

Introduction

Invasive non-indigenous plants, insects and pathogens may dramatically alter tree abundance and forest composition (Ramkrishnan and Vitousek 1989, Mack et al. 2000, Schowalter 2000). Reductions in the abundance of foundation tree species may have particularly far-reaching effects because these species define and regulate the structure and processes of forests (Ellison et al. 2005). Relatively little is known about indirect effects resulting from the decline of foundation species even though indirect effects may play a critical role in forest responses to invasive organisms. For example, invasive plants indirectly inhibit recruitment of native trees by altering mycorrhizal fungal communities (Stinson et al. 2006). Because mycorrhizal fungal communities may also be altered by defoliation of host trees (Last et al. 1979, Gehring and Whitham 1991, Del Vecchio et al. 1993, Rossow et al. 1997, Saikkonen et al. 1999), defoliation of foundation species by invasive insects may be expected to indirectly affect native forests through effects on mycorrhizal fungal communities.

Herbivory affects mycorrhizal fungi by disrupting the carbohydrate supply to mycorrhizae (Gehring and Whitham 1994). Ectomycorrhizal fungi use as much as 25% of host carbohydrate production (Lewis and Strain 1996, Hobbie 2006), and decreased carbohydrate supply to roots has been shown to reduce mycorrhizal root tip abundance (Marx et al. 1977, Lewis et al. 1994) and alter community composition (Dixon et al. 1981, Rygielwicz et al. 2000). Herbivory also creates canopy gaps that affect mycorrhizal fungi by altering microsite conditions (Kranabetter and Wylie 1998, Durall et al. 1999,

Kranabetter et al. 1999, Hagerman et al. 1999). Because the effects of herbivory on mycorrhizal fungal communities may increase with the extent of defoliation (Meyer et al. 1988, Gange et al. 2002), the relative impacts of native insects and invasive non-indigenous insects on these communities may differ substantially. Although native insects generally consume 10% or less of net primary production in temperate forests, invasive non-indigenous insects often exhibit dramatic population increases after introduction (Barbour et al. 1999), leading to extensive defoliation and increased mortality of one or a few tree species (Liebhold et al. 1995, Davidson et al. 1999, Anagnostakis 2001).

Forest responses to the introduction of invasive insects may also be affected by differences in host specificity among mycorrhizal fungal species. Invasive insects often target only one or a few tree species, and forest responses to infestations often involve increased growth and recruitment of uninfested tree species (Liebhold et al. 1995, Orwig 2002). However, mycorrhizal fungi associated with infested tree species may not colonize the replacement tree species. For example, conifers generally host ectomycorrhizal fungi, whereas many hardwoods, such as maple (*Acer*), generally host arbuscular mycorrhizal fungi (Molina et al. 1992). Further, many ectomycorrhizal fungal species form guilds that associate with specific taxonomic groups of hosts, such as conifers or hardwoods (Perry et al. 1989, Massicotte et al. 1999). This host specificity may negatively affect growth and recruitment of replacement tree species if there are differences in the mycorrhizal fungal communities hosted by infested and replacement tree species.

Invasive insects have had a particularly acute impact on the forests of the eastern USA, leading to reductions in the abundances of many tree species (Liebhold et al. 1995, Orwig 2002). In this paper, we focus on the decline of eastern hemlock (*Tsuga canadensis* (L.) Carr) as a result of infestation by the hemlock woolly adelgid (HWA; *Adelges tsugae* Annand). Eastern hemlock, a foundation species, is a widespread dominant species in the eastern USA and is associated with a unique suite of habitat characteristics, including dense shade, acidic soils, deep litter layer and cool moist conditions (Ellison et al. 2005). Hemlock woolly adelgid is an aphid-like insect native to Asia that was introduced into the eastern USA in the 1950s (Souto et al. 1996). Eastern hemlock has no apparent resistance to HWA, and HWA introduction generally leads to mortality of infested trees within 5–15 years (McClure 1991, Orwig and Foster 1998). Infested trees have reduced vigor owing to extensive defoliation (Orwig and Foster 1998). Within the current geographic range of hemlock decline, replacement tree species are generally hardwoods such as birch (*Betula*), maple and oak (*Quercus*) species (Orwig and Foster 1998, Orwig et al. 2002).

Forest recovery following eastern hemlock decline may be affected if the growth of these replacement species is affected by mycorrhizal inoculum potential in infested hemlock stands. Recent research has shown that ectomycorrhizal root tip abundance and morphotype richness is lower on oak seedlings grown in soil from infested eastern hemlock stands than on oak

seedlings grown in soil from oak-dominated stands (Turner 2003). Our specific objectives were to determine if ectomycorrhizal inocula differ between healthy oak stands and declining hemlock stands infested with HWA and, if so, whether these differences result in differences in mycorrhizal characteristics and dry mass accumulation of oak seedlings in oak stands versus oak seedlings in declining hemlock stands. We hypothesized that: (1) ectomycorrhizal root tip density and morphotype richness differ between oak-dominated stands and stands dominated by dead and declining hemlock trees; and (2) oak seedling growth reflects differences in ectomycorrhizal percent colonization and morphotype richness. To test these hypotheses, we grew red oak (*Quercus rubra* L.) seedlings from acorns for one growing season in oak-dominated and in declining hemlock stands. Intact seedlings were harvested at the end of the growing season and assessed for biomass accumulation, and ectomycorrhizal percent colonization and morphotype richness. Differences in ectomycorrhizal inoculum potential between oak and declining hemlock stands were assessed in soil cores collected from beneath overstory red oak (oak-dominated stands) and eastern hemlock trees (declining hemlock stands).

Materials and methods

Study site

The study was conducted in the Black Rock Brook, Canterbury Brook and Mineral Springs watersheds in Black Rock Forest, Orange County, NY, USA (41° N, 74° W). Black Rock Forest is a 1500-ha natural area operated as a research station within the New York-New Jersey Highlands Physiographic Province, which overlies Precambrian gneiss, schists and limestones (Schubert 1968). Red oak, chestnut oak (*Q. prinus* L.) and eastern hemlock dominate tree composition in these watersheds (Mates-Muchin 2006). The study plots were selected from plots originally established in 1985 in oak- and hemlock-dominated stands, which were delineated based on aerial photos (Friday and Friday, Black Rock Forest, Cornwall, NY, unpublished report). For our study, one plot location was randomly selected from each of three discrete oak- and hemlock-dominated stands in each watershed, for a total of 18 plots. All of the hemlock plots exhibited extensive defoliation and mortality associated with HWA (see below). In all plots, all trees > 1 cm diameter at breast height (DBH) were identified following Brockman (1986) and DBH measured. Basal area and frequency of each tree species were calculated from these data. Based on relative basal area and frequency, hemlock-dominated plots contained about 70% eastern hemlock on average, whereas oak-dominated plots contained about 50% oak on average, whereas hemlock-dominated plots contained about 20% oak on average.

The extent of hemlock decline associated with HWA was measured by assessing crown-level defoliation and plot-level mortality. Crown-level defoliation of each hemlock tree in each plot was assessed based on an index of crown defoliation

(Orwig and Foster 1998), where defoliation was visually scored in one of five categories: 0–5, 5–25, 25–50, 50–75 and 75–100% defoliated. Trees that were completely defoliated were considered dead. Crown-level defoliation of each hemlock was averaged across each plot to estimate canopy-level defoliation. Based on these measurements, mean crown defoliation within each hemlock plot was > 50% and plot-level hemlock mortality was > 50% during the study period (Mates-Muchin 2006).

Stand variation in ectomycorrhizal root tip density and morphotype richness

To examine variation between stand types in ectomycorrhizal root tip density and morphotype richness, within each plot in June 2004, one 5-cm-diameter soil core was collected within 1 m of the bole of each of three randomly selected overstory trees representative of that stand type (i.e., eastern hemlock in declining hemlock plots, red oak in oak-dominated plots). A total of 27 trees were sampled for each species (three trees × three plots × three watersheds). Soil cores were collected down to the mineral horizon, which typically was less than 10 cm below the soil surface. Soil samples were taken to the laboratory and stored at 4 °C until processed. Soil cores were wet sieved on a 1-mm-mesh soil sieve. Roots were transferred to square, gridded petri dishes. With the aid of a Leica MZ12.5 stereomicroscope (Leica Microsystems, Wetzlar, Germany), ectomycorrhizal tips were divided by morphological type according to characteristics including branching pattern, mantle texture, presence or absence of cords or emanating hyphae, mantle color and mantle structure as described by Goodman et al. (1996–2000), Agerer (1987–2002) and Ingleby et al. (1990).

Oak seedling growth and mycorrhizal community properties

Red oak (*Q. rubra*) was used to examine whether oak seedling growth differed between oak and declining hemlock stands and, if so, whether these differences were related to differences in ectomycorrhizal percent colonization and morphotype richness. Acorns (Sheffield Seed, Locke, NY) were surface sterilized by immersion in a 9:1 (v/v) mixture of deionized water and bleach for 15 min followed by rinsing for 3 min in sterile, deionized water. Three acorns were randomly assigned to each of three trees in each plot. At each tree, acorns were planted 1 m from the bole in three cardinal directions (E, S and W). Acorns were watered weekly with sterile deionized water for the first 3 weeks after planting. To minimize herbivory, each acorn location was enclosed in a 30-cm-tall by 20 cm diameter cylinder constructed from 1-cm hardware cloth. Nonetheless, there was extensive seedling mortality such that only 17 seedlings survived in oak-dominated plots and 10 seedlings survived in hemlock-dominated plots, all in the Black Rock Brook watershed. Surviving seedlings were harvested 12 weeks after planting. Plants were separated into roots, stems and leaves. Stems and leaves were dried at 60 °C to constant mass. Roots were transferred to square, gridded petri dishes and ectomycorrhizal types were identified as de-

scribed above. Roots were dried at 60 °C to constant mass and all plant tissues were weighed to determine dry mass accumulation.

Statistical analysis

Effects of stand type and watershed on ectomycorrhizal fungal community properties on mature trees were assessed by two-way analysis of variance (ANOVA). Because there were no significant differences between watersheds and there were no significant interactions between watersheds and stand types ($P > 0.10$ in all cases), only stand type effects are presented. Because oak seedlings survived in only one watershed, one-way ANOVA was used to assess the effects of stand type on ectomycorrhizal fungal community properties and dry mass accumulation of oak seedlings. Assumptions of normality of data and homogeneity of variances were supported based on normal scores plots and plots of predicted versus residual values. Effects were considered significant if $P = 0.10$.

Effects of ectomycorrhizal percent colonization and morphotype richness on seedling dry mass accumulation were assessed by regression analyses. When regression analysis indicated a significant relationship between dry mass accumulation and percent colonization or morphotype richness, analysis of covariance (ANCOVA) was conducted using percent colonization or morphotype richness as a covariate to determine if stand type effects on seedling dry mass were significant after adjusting for the specified continuous variable. All tested ANCOVA models met the assumption of homogeneity of slopes.

Results

Ectomycorrhizal root tip density ($P = 0.002$) and morphotype richness ($P = 0.029$) were 63 and 27% less, respectively, in soil cores from beneath mature declining hemlock trees than in cores from beneath mature oak trees (Figure 1). However, ectomycorrhizal morphotype diversity measured by the Shannon-Weiner index did not differ significantly between oak and declining hemlock trees. A total of nine morphotypes were identified across the two stand types and the three watersheds. Seven of these morphotypes were found in both stand types, whereas two were unique to oak plots. When sorted by watershed, seven, six and five morphotypes were found in the hemlock plots, whereas eight, six and seven morphotypes were found in the oak plots in the corresponding watersheds.

Percent colonization of root tips ($P = 0.005$) and morphotype richness ($P = 0.038$) were 33 and 30% less, respectively, on oak seedlings grown in declining hemlock plots compared with oak seedlings grown in oak plots (Figure 2). The lower percent colonization of oak seedlings grown in declining hemlock plots compared with oak plots appeared to be associated with both greater numbers of uncolonized tips and lower numbers of colonized tips (Table 1). However, the variation within each stand type was large enough that there were no significant differences between stand types in the numbers of colonized and uncolonized root tips, or in the total number

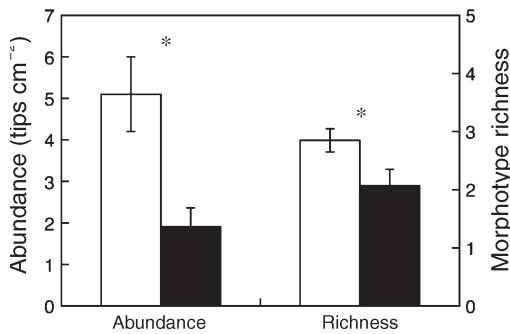


Figure 1. Mycorrhizal root tip abundance and morphotype richness on mature oak trees (open bars) in oak-dominated plots and on mature HWA-infested hemlock trees (filled bars) in hemlock-dominated plots. Values are means \pm SE of 27 trees. An asterisk (*) indicates means that are significantly different at $P = 0.10$ based on two-way ANOVA with stand type and watershed as main effects.

of root tips on oak seedlings. As with mature trees, ectomycorrhizal morphotype diversity measured by the Shannon-Weiner index did not differ significantly between oak seedlings grown in oak versus declining hemlock plots.

Oak seedlings grown in oak plots had 41% more total dry mass than oak seedlings grown in declining hemlock plots (Table 1). Differences in total seedling dry mass between stand types reflected differences in aboveground dry mass. Seedlings grown in oak plots had 39 and 48% more stem and shoot dry mass, on average, than oak seedlings grown in declining hemlock plots. However, leaf ($P = 0.133$), tap root ($P = 0.271$), fine root ($P = 0.579$), and total root dry mass ($P = 0.245$) of oak seedlings did not significantly differ between stand types.

Across stand types, total seedling dry mass increased with increasing morphotype richness (Figure 3), but did not vary significantly with percent colonization of root tips. Analysis of covariance indicated that the significant effect of stand type on total seedling dry mass was not significant ($P = 0.206$) after taking into account differences in morphotype richness. Both

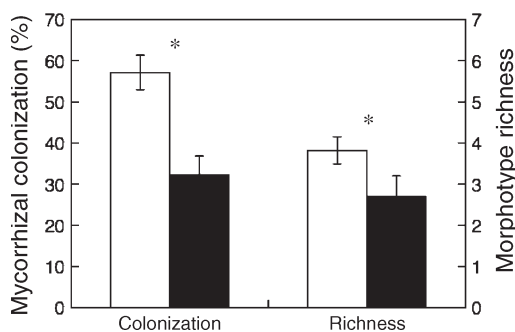


Figure 2. Mycorrhizal fungal colonization and morphotype richness on oak seedlings grown in oak- (open bars) and hemlock-dominated (filled bars) plots. Values are means \pm SE of 17 seedlings in oak-dominated stands and 10 seedlings in hemlock-dominated stands. An asterisk (*) indicates means that are significantly different at $P = 0.10$ based on one-way ANOVA.

Table 1. Dry mass accumulation by oak seedlings grown in oak- and hemlock-dominated plots. Values are means (\pm 1 SE) of 17 and 10 seedlings in oak-dominated and hemlock-dominated stands, respectively. For each trait, significant differences between stand types are indicated by different lowercase letters ($P = 0.10$).

Seedling trait	Oak-dominated stands	Hemlock-dominated stands
<i>Root tips</i>		
Colonized tips (no. plant ⁻¹)	96.5 \pm 15.8	58.0 \pm 14.1
Uncolonized tips (no. plant ⁻¹)	82.0 \pm 18.6	108.4 \pm 21.5
Total tips (no. plant ⁻¹)	178.5 \pm 31.4	166.4 \pm 33.7
<i>Aboveground dry mass</i>		
Leaf (g)	0.34 \pm 0.05	0.23 \pm 0.03
Stem (g)	0.25 \pm 0.03 a	0.18 \pm 0.03 b
Shoot (g)	0.59 \pm 0.07 a	0.40 \pm 0.05 b
<i>Belowground dry mass</i>		
Tap root (g)	0.22 \pm 0.03	0.17 \pm 0.03
Fine roots (g)	0.06 \pm 0.02	0.04 \pm 0.01
Total roots (g)	0.27 \pm 0.03	0.21 \pm 0.04
<i>Total dry mass (g)</i>	0.86 \pm 0.09 a	0.61 \pm 0.07 b

ectomycorrhizal percent colonization and morphotype richness on oak seedlings had a significant positive effect on seedling dry mass in declining hemlock plots (Figure 4).

Discussion

The decline in foundation tree species in response to the introduction of invasive non-indigenous insects is expected to have cascading effects on forest ecosystems (Ellison et al. 2005). Mycorrhizal fungi may be expected to play a key role in forest recovery following such declines because of the importance of mycorrhizal fungi to tree growth. In this study, mycorrhizal root tip density and morphotype richness were less in declining eastern hemlock plots infested with HWA than in oak plots in the same watersheds. Further, red oak seedlings in declining

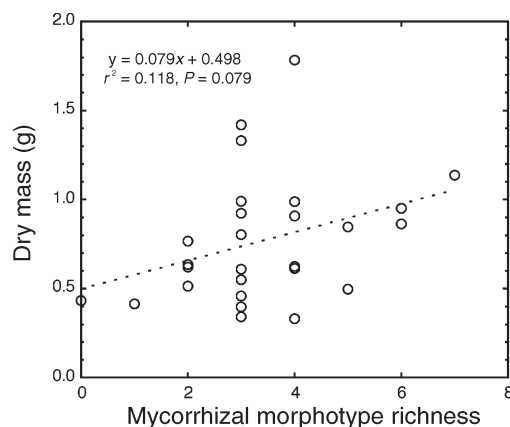


Figure 3. Relationship between total oak seedling dry mass and mycorrhizal morphotype richness across stand types.

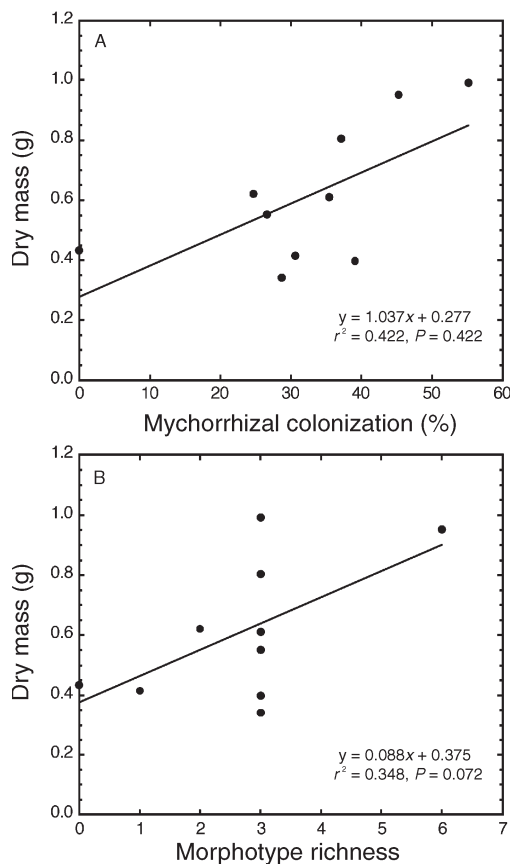


Figure 4. Relationships between total oak seedling dry mass and (A) mycorrhizal percent colonization and (B) morphotype richness in hemlock-dominated plots.

hemlock plots had less shoot and total plant dry mass than red oak seedlings in oak plots. Analysis of covariance indicated that morphotype richness on seedlings could account for differences in seedling dry mass accumulation between declining hemlock and oak plots, though the association between seedling mass and morphotype richness was weak ($r^2 = 0.118$). In addition, seedling mass in hemlock plots decreased with decreases in mycorrhizal percent colonization and morphotype richness, suggesting that, as fungal species are lost from a community, there are functional consequences for productivity. However, although our results suggest that the ectomycorrhizal fungal community affects forest responses following hemlock infestation by HWA, invasive organisms may induce changes in a suite of factors, such as soil chemistry, that affect plant growth (Reinhart and Callaway 2006).

For example, HWA infestation generally increases soil N mineralization (Jenkins et al. 1999, Kizlinski et al. 2002, Yorks et al. 2003), reflecting changes in litter quality and litter fall (Stadler et al. 2005, Stadler et al. 2006), and litter decomposition (Cobb et al. 2006). In our study, it is unlikely that differences in oak seedling dry mass between oak and declining hemlock plots reflected differences in soil N pools or fluxes. Annual measurements between 2000 and 2006 indicated that

total soil N and KCl-extractable ammonium and nitrate concentrations were greater in declining hemlock plots than in oak plots (Sirulnik, Lewis, Tuininga and Johnson, unpublished data) or did not significantly differ between stand types (Mates-Muchin 2006, Turner et al., unpublished data). Increased soil N concentrations and mineralization should lead to increased rather than reduced seedling growth. However, the effects of HWA infestation on soil N cycling may be highly variable at local scales and within growing seasons, reflecting variation in the timing and extent of defoliation of individual hemlock trees (Jenkins et al. 1999, Mates-Muchin 2006). In addition, HWA may have affected unmeasured variables.

A related limitation of our study is that eastern hemlock forests normally differ from hardwood forests in a suite of environmental factors, including soil characteristics, understory light availability and microclimate (Ellison et al. 2005), which may alter seedling growth independently of effects of the ectomycorrhizal fungal community. Hemlock defoliation associated with HWA may cause hemlock stand characteristics to shift toward those of hardwood stands in the region because of the increased importance of hardwoods in hemlock stands (Jenkins et al. 1999). Consistent with such a shift, we found no significant differences between oak and declining hemlock plots in soil pH, soil water content, or soil Ca, K, Mg and Na concentrations (Turner et al., unpublished data). Further, the extensive defoliation (> 50%) in our hemlock stands represents a form of canopy gap with comparatively high light availabilities (Jenkins et al. 1999). Nonetheless, differences in seedling dry mass between hemlock and oak plots may reflect differences between stand types in a variety of unmeasured factors, such as temperature, or spatial and temporal variation in factors that were measured.

Despite these limitations, our study supports the hypothesis that the ectomycorrhizal fungal community affects oak seedling growth. After taking into account differences in morphotype richness, there was no significant difference in oak seedling dry mass between oak and declining hemlock plots. Further, variation in ectomycorrhizal relative abundance and morphotype richness could account for 42 and 35%, respectively, of the variation in seedling dry mass in declining hemlock plots (Figure 4). The mycorrhizal fungal community has been shown to affect plant community responses to invasive organisms in a growing number of studies (Richardson et al. 2000, Reinhart and Callaway 2006). For example, garlic mustard (*Alliaria petiolata* (Bieb.) Cavara & Grande), an invasive plant, reduces native seedling regeneration through effects on the arbuscular mycorrhizal fungal community (Roberts and Anderson 2001, Stinson et al. 2006). Similarly, forest recovery following the near-extirpation of American chestnut (*Castanea dentata* (Marsh.) Borkh.) by chestnut blight (*Cryphonectria parasitica* (Murrill) Barr), an invasive pathogen, may have been affected by displacement of ectomycorrhizal fungi by *Rhododendron maximum* L. (Walker et al. 1999, Walker et al. 2005). A common pattern in these studies is that the recovery of native forests following invasion by non-indigenous species is slowed or altered by reductions in mycorrhizal inoculum potential.

The reduced mycorrhizal inoculum potential we observed in declining hemlock plots may reflect the effects of hemlock defoliation as well as underlying differences between oak and hemlock stands. Crown defoliation averaged over 50% in the study hemlock plots, and ectomycorrhizal root tip density and morphotype richness were significantly less in these plots than in uninfested hemlock plots in the same watersheds (Sirulnik, Lewis, Tuinga and Johnson, unpublished data). Defoliation has been shown to alter ectomycorrhizal fungal communities in a variety of systems (Gehring and Whitham 2002), and can affect these communities both on defoliated trees and adjacent undefoliated trees of a different species (Cullings et al. 2001). It is likely that the potential impacts of hemlock defoliation are highly variable both in space and across time. The effect of defoliation on mycorrhizal fungi can vary with the extent of defoliation (Meyer et al. 1988, Gange et al. 2002), and defoliation by HWA typically occurs gradually over several years and can be highly heterogeneous spatially within and between stands (Jenkins et al. 1999, Stadler et al. 2005, Cobb et al. 2006). As a result, although invasive insects such as HWA may have larger impacts on ectomycorrhizal fungal communities than native insects, which typically consume a comparatively small fraction of leaves, the extent of the difference is likely to reflect the extent of host defoliation.

The potential impact of defoliation may be mediated by other factors as well. Compositional changes in ectomycorrhizal fungal communities may minimize the effects of defoliation on ectomycorrhizal fungal abundance or richness (Cullings et al. 2001). Relatedly, ectomycorrhizal fungal species may differ in their response to changes in carbohydrate availability associated with defoliation (Saikkonen et al. 1999). Seasonal changes in fungal activity may also affect the response to defoliation; ectomycorrhizal fungal species tolerant of low carbohydrate availability may be active during different times of the year than species that require high carbohydrate availability (Koide et al. 2007). The effect of defoliation on ectomycorrhizal fungi may also be mediated by soil nutrient availability (Gehring and Whitham 1994, Gehring and Whitham 1995, Markola 1996), and by interactions between plants and soil biota (Reinhart and Callaway 2006).

The lower dry mass accumulation by oak seedlings in declining hemlock plots compared with oak plots may reflect feedbacks between oak seedlings and mycorrhizal fungi in hemlock stands. Feedbacks between plant and mycorrhizal fungal communities can be a critical factor structuring interactions between plant species (Bever 2002, Dickie et al. 2006). For example, host specificity of mycorrhizal fungi has been shown to affect successional responses to disturbances by inhibiting the displacement of earlier-successional species by later-successional species (Richardson et al. 1994). Conifer-specific fungal species have been observed (Gardes and Bruns 1995, Massicotte et al. 1999, Dahlberg 2001), and oak seedlings may benefit less from these species than from generalist or hardwood-specific fungi. Accordingly, the reduced ectomycorrhizal morphotype richness on oak seedlings in hemlock plots compared with oak plots may reflect effects of host specificity of fungi growing in association with eastern hemlock.

Ironically, host specificity may slow plant invasions into new regions (Richardson et al. 1994, Reinhart and Callaway 2006), as well as slow forest recovery following invasion by non-indigenous insects and plants.

In conclusion, red oak seedlings accumulated significantly less dry mass in hemlock plots extensively defoliated by HWA compared with red oak seedlings growing in oak-dominated plots. Analysis of covariance indicated that morphotype richness on seedlings could account for differences in seedling dry mass accumulation between declining hemlock and oak plots. Seedling dry mass in hemlock plots also varied with ectomycorrhizal relative abundance. These results suggest that oak growth and establishment is slower in declining hemlock stands than in adjacent oak stands because of differences in ectomycorrhizal inoculum potential. These differences in inoculum potential may shift the competitive balance of tree species that replace eastern hemlock. Tree species, such as oak, that predominantly host ectomycorrhizal fungi may be more negatively affected than species, such as maple, that commonly host arbuscular mycorrhizal fungi. More research is required to understand how changes in the mycorrhizal fungal community affect forest recovery following hemlock decline by altering the competitive balance between tree species that replace hemlock, and how these changes are regulated by changes in environmental factors and other changes in the soil microbial community.

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