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Effects of microtopography on mycorrhizal infection in Atlantic white cedar (*Chamaecyparis thyoides* (L.) Mills.)

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Abstract The presence and intensity of mycorrhizal infection in wetland trees has received relatively little attention. We report here a study of mycorrhizal infection in Atlantic white cedar (*Chamaecyparis thyoides*), a member of the Cupressaceae, which forms monospecific stands in swamps throughout the Atlantic Coastal Plain of North America. The trees grow on the tops of elevated hummocks, but the fine roots extend along the sides of the hummocks to the flooded hollows. Roots from all microtopographic positions on the hummocks are colonized by vesicular-arbuscular mycorrhizae (VAM). In addition to arbuscules and vesicles, occasional hyphal coils are observed within the cortex cells. However, frequencies of occurrence of vesicles and arbuscles are significantly higher on the tops and sides than at the bottoms of the hummocks. These differences correspond to higher concentrations of acetylglucosamine in the roots at these positions. Frequencies of all mycorrhizal structures (arbuscles, vesicles and hyphae) in roots at the base of the hummocks are very low. These results suggest that mycorrhizal colonization in wetland trees is greater in aerobic microsites, a finding in accord with results from studies of both herbaceous wetland plants and other wetland trees.

Key words Vesicular arbuscular mycorrhizae · *Chamaecyparis thyoides* · Cupressaceae · Wetlands · Swamp · Microsites · Hummocks · Anoxia · Restoration

Introduction

The presence of mycorrhizal infection in wetland plants has received little attention, compared with the extensive studies of infection rates in many other kinds of habitat (Jurgensen et al. 1997). This may reflect the assumption that fungi are not usually abundant in anoxic environments (Mexal and Reid 1973; Lodge 1989; Khan 1993). Studies of some aquatic plants have demonstrated high levels of mycorrhizal infection (Sondergaard and Laegaard 1977; Clayton and Bagyaraj 1984; Ragupathy et al. 1990). However, plants characteristic of wetland habitats – as opposed to open water – have often been found to have low rates of infection. Such patterns have been demonstrated for the British flora (Peat and Fitter 1993), the Florida Everglades (Aziz et al. 1995), midwestern prairie potholes (Wetzel and Van der Valk 1996), and widespread species e.g., *Lythrum salicaria* (Stevens and Peterson 1996). Studies of wetland trees and shrubs also suggest that mycorrhizal colonization tends to decrease under flooded conditions (Shuja et al. 1971; Filer 1975; Stenström 1991); however, the relationship with flooding is often quite variable (Lodge 1989; Coutts and Nicoll 1989; Khan 1993; Jurgensen et al. 1997; Torti et al. 1997). Moreover, much less is known of mycorrhizae in wetland trees than in wetland herbs and graminoids (Jurgensen et al. 1997).

Many wetlands have aerobic or subaerobic microhabitats associated with microtopographic relief, in the form of hummocks and hollows (Karlin and Bliss 1984; Gignac 1994, Ehrenfeld 1995a, b). In many wetlands, these raised features are only a few tens of centimeters above the permanently saturated or flooded hollows (Titus 1990; Ehrenfeld 1995a, b), yet they provide habitat for a large number of wetland species that cannot tolerate permanently flooded, anoxic soils. Indeed, the observation that most woody species in wetlands are not tolerant of permanent flooding (Benforado and Clark 1981) suggests that much of the fine root biomass of woody plants in wetlands is in relatively dry or aerobic microsites. Under these conditions, mycorrhizae may be important to the ecology of the woody wetland plants. Conversely, if surface microtopography is important to the development of mycorrhizal symbioses,

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then plans for the restoration of forested wetlands should emphasize this feature.

Atlantic white cedar (*Chamaecyparis thyoides* (L.) Mills.) is typical of many wetland trees in that, although it is considered an obligate wetland species (Reed 1988), it is sensitive to both excessive flooding and to drought (Little 1950). It grows on hummocks within seasonally flooded, groundwater-fed swamps (Ehrenfeld and Schneider 1991; Ehrenfeld 1995a). The hummocks are composed of poorly to highly decomposed organic matter (Ehrenfeld 1995b), and are very acidic (pH ≈ 3.5; Vedagiri and Ehrenfeld 1992). The fine roots extend from the tree base at the top of the hummock down the sides of the hummocks, and may extend at lower densities into the surface sediments of the hollows (Floyd and Ehrenfeld 1986). Conditions of moisture and redox potential can vary dramatically from the hummock tops to the hollows, especially when the hummocks lack a cover of *Sphagnum* moss (Ehrenfeld 1995b).

We have examined *Chamaecyparis* roots from the top, middle and bottom of hummocks in two undisturbed, mature cedar swamps in the New Jersey Pinelands, in order to determine (1) whether this species supports mycorrhizal fungi, (2) if so, whether the infection is endo- or ecto-mycorrhizal, and (3) whether the microtopographic position of the roots affects the intensity of infection.

Materials and methods

The two undisturbed swamps [along the South Branch Mt. Misery (SBMM), and the Middle Branch Mt. Misery (MBMM)] are located within Lebanon State Forest in the New Jersey Pinelands. These stands were previously described by Ehrenfeld (1995a). Both swamps have a canopy of mature Atlantic white cedar (>100 years old) and small numbers of red maple (*Acer rubrum* L.), black gum (*Nyssa sylvatica* L.), and sweetbay magnolia (*Magnolia virginiana* L.), together with a sparse understory of shrubs (mostly in the Ericaceae). Sites were sampled in early October 1995 following an unusually prolonged drought in August and September.

In each swamp, five hummocks were randomly selected along a transect established parallel to the direction of water flow, equidistant from the stream (approximately 30 m distant) and the upland boundary (approximately 50 m distant) of the wetland. Soil cores (7 cm diameter × 10 cm deep) were taken on the top, middle and bottom of each hummock, (the bottom recognized as the point at which the steeply sloping side met the flat hollow floor). Cores were gently teased apart in the field to ensure that sufficient fine root material had been collected; if necessary, additional peat was sampled from the sides of the core hole. The peat was placed in sealed bags and returned to the laboratory on ice. The roots were washed free of soil, blotted on paper towels, and frozen in moist toweling until analyzed.

Thawed samples were analyzed by taking subsamples of 100 cm of fine root (≤1 mm diameter) cut into 5-cm lengths for processing. The method of Koske and Gemma (1989) was modified to permit removal of the deep pigmentation of the roots. Root samples were prepared by incubating in 5% KOH at 70 °C for 12–16 h, rinsing with deionized distilled water, incubating in alkaline 3% H_2O_2 at room temperature for 3 h, and acidifying in 1% HCl overnight. The cleared roots were then stained with 0.05% trypan blue in 1% HCl and 50% glycerol. Infection was measured on 20 1-cm lengths of root (3–5 per slide), following the protocol of McGonigle et al. (1990). One hundred fields of view per sample were tallied.

Chitin concentrations (as acetylglucosamine) in each root sample were also determined as an independent indicator of infection level, following the method of Vignon et al. (1986).

Frequencies of each form of infection (e.g., vesicles, arbuscles, etc.) were analyzed by two-way analyses of variance (site versus hummock position), using arcsin-transformed data and SuperANOVA 1.11 and Statview 4.5 software (Abacus Concepts, Inc., Berkeley, Calif.). Chitin concentrations were similarly analyzed using data after inspection for normality and heteroscedasticity. The Bonferroni-Dunn test was used for *post-hoc* comparisons of means.

Results

Chamaecyparis roots showed structures typical of VAM infection. Well-developed arbuscles and vesicles were frequently seen (Fig. 1a), in addition to fungal hyphae within the root cortex and on the root surface. Branched mycelia at the point of entry of the hyphae into the roots were also occasionally noted. Root hairs were not found on any of the inspected roots. In addition to these structures, hyphal coils were also occa-

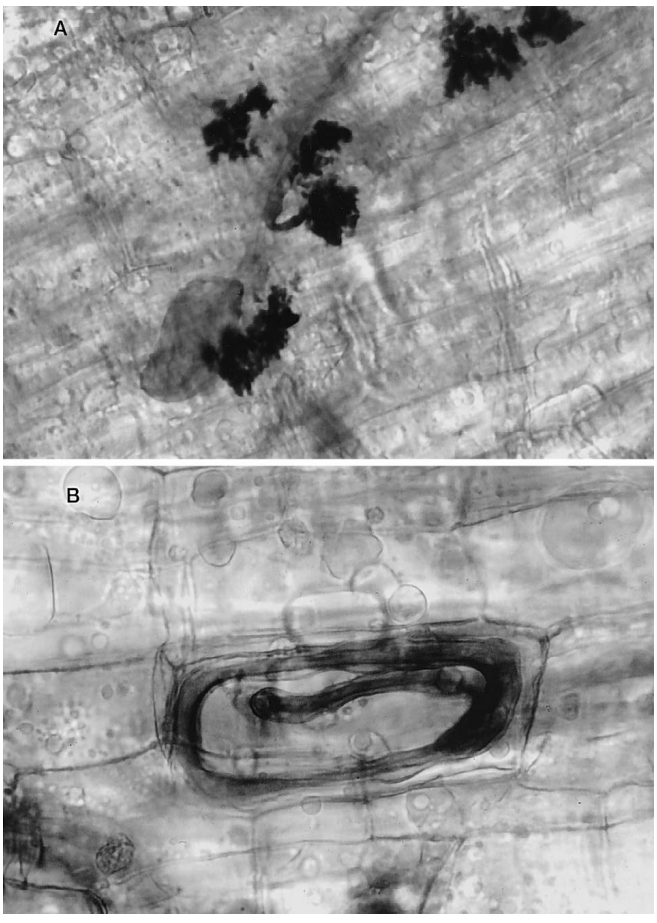

Fig. 1 Endomycorrhizal structures in *Chamaecyparis thyoides*, **a** arbuscles, vesicles and hyphae in a fine root from the middle of a hummock, **b** hyphal coil in a root from the top position

sionally observed (Fig. 1b). None of the roots showed external or internal evidence of ectomycorrhizal infection.

The frequencies of mycorrhizal structures varied considerably across the hummock-hollow gradient (Fig. 2). Arbuscles were equally abundant on the tops and middles of the hummocks, but were almost absent in roots from the hummock bottoms (*anova* $F_{2,24}=60.194$, $P<0.0001$; Fig. 2A). In contrast, vesicles were significantly more abundant on the hummock tops than in the other positions ($F_{2,24}=11.268$, $P=0.0004$; Fig. 2B). However, overall rates of occurrence of both arbuscles and vesicles were low, as is indicated in Fig. 2. Intercellular hyphae were the most abundant fungal structure, and there were significant differences in the frequency of hyphae among the three hummock positions ($F_{2,24}=61.869$, $P<0.0001$). The hyphae were distinguished from saprophytic and parasitic hyphae by the characteristic diameters and morphology of mycorrhizal hyphae (Smith and Read 1997). The tops of hummocks had the greatest amounts of intraradical hyphae, while the roots from the bottom positions had very little (Fig. 2C). Only one sample was found to completely lack mycorrhizal structures; it was taken from a bottom position. The much higher frequency of hyphae than vesicles and arbuscles dominated the patterns of overall infection (position differences $F_{2,24}=65.615$, $P<0.0001$). No significant differences were found between the two sites, and there were no significant interactions between hummock position and site, suggesting that the pattern of differential mycorrhizal occurrence across the hummock-hollow gradient is a general phenomenon.

Although the frequencies of arbuscles in top and middle positions were not significantly different, there was a conspicuous difference in the size and structure of these features in the two microtopographic positions. Roots from the hummock tops were typically colonized by poorly developed arbuscles, with few branches; many appeared to be intermediate between hyphal coils and branched structures. The arbuscles from roots in the middle positions, in contrast, were invariably highly branched.

Acetylglucosamine concentrations (Fig. 3) were higher in the mid-hummock positions than in either the top or bottom positions (*anova* $F_{2,18}=5.401$, $P=0.0145$). Unlike the morphological estimates of infection, there were significant differences between the two sites ($F_{1,18}=10.745$, $P=0.0042$). However, the patterns with respect to microtopography were the same at the two sites (no significant interaction between site and microtopographic position). The higher concentrations of acetylglucosamine in the mid-hummock positions corresponded with more extensively developed arbuscles evident in the stained preparations.

Discussion

The data presented here clearly establish that *Chamaecyparis thyoides* supports VAM colonization, consistent with other reports on the Cupressaceae (Trofymow and van den Driessche 1990; Smith and Smith 1996; Smith

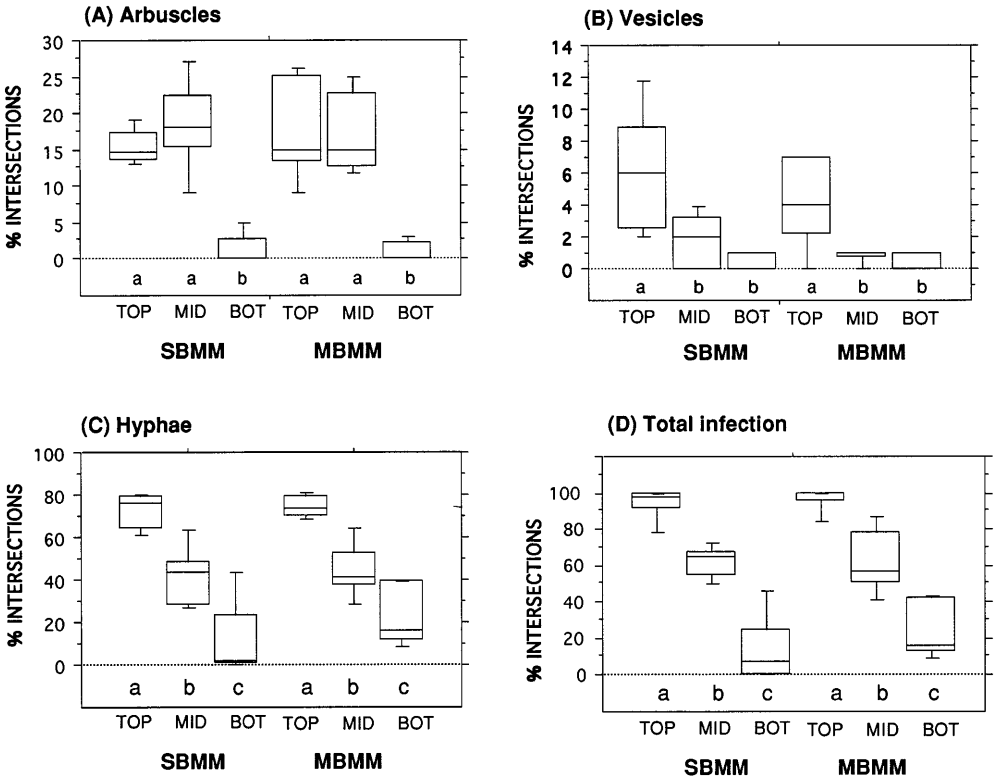

Fig. 2 Frequency of occurrence of mycorrhizal structures in 100 fields-of-view per hummock position and per site (*SBMM* South Branch Mt. Misery, *MBMM* Middle Branch. Mt. Misery). Figures show median, 25th and 75th percentiles, and 90th percentiles (*ends of bars*). *Letters beneath figures* indicate the results of Bonferonni-Dunn post-hoc tests following the anova

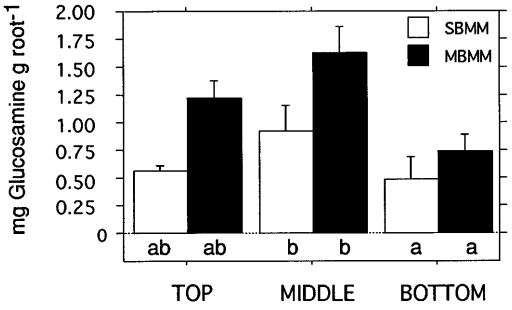

Fig. 3 Glucosamine concentrations in roots from three microtopographic positions in the two sites. *Letters* indicate significantly different groups. Abbreviations as for Fig. 2

and Read 1997). The presence of both intercellular hyphae and intracellular hyphal coils, as well as arbuscles, suggests that *Chamaecyparis* shows features of both *Arum*- and *Paris*-type mycorrhizae; however, the much higher frequency of arbuscules relative to coils argues for an *Arum* type (Smith and Read 1997). Other members of the Cupressaceae have been reported to have *Paris*-type symbionts, but Smith and Smith (1996) point out that mixtures of structures of the two types are not uncommon. Our findings are also consistent with literature suggesting that VAM are more common on woody plants in wetlands than are ectomycorrhizae (Truszkowska 1953; Lodge 1989; Khan 1993; Jurgensen et al. 1997; Cooke and Lefor 1998).

Our finding also supports the growing body of literature demonstrating that mycorrhizal colonization is present in wetland trees as well as forbs and graminoids. In a recent survey, Cooke and Lefor (1998) reported that mycorrhizal colonization was found in all 18 taxa of woody plants examined. Three were trees [*Acer rubrum*, *Populus deltoides*, and *Salix nigra*] and the rest shrubs; however, their small sample sizes (mostly $n=1$–3) make the results tentative. Jurgensen et al. (1997) reviewed the literature on mycorrhizae in bottomland hardwood trees; they found reports for 14 species. All of the species examined were mycorrhizal, most with VAM and some with both VAM and ectomycorrhizae (including *Populus* and *Salix*); only two species (both species of *Quercus*) were found to exclusively support ectomycorrhizal colonization. The authors suggest that VAM are better able to tolerate wet conditions than are ectomycorrhizae. However, they also reported considerable variability in the literature on the degree of tolerance to flooding and response to oxygen concentrations of both kinds of mycorrhizae. Previous studies of *Populus*, *Salix* and several Polish taxa have similarly shown that trees supporting both kinds of mycorrhizae have primarily VAM in wet soils (Truszkowska 1953; Lodge 1989; Khan 1993).

Our data suggest that mycorrhizal infection in *Chamaecyparis* varies strongly with the hydrology of the sediments, and that this variation is expressed over the microtopographic gradients created by the hummock-hollow structures. Hummocks in these swamps are on average 35 cm above the hollow floors, but may be as much as 1 m tall (Ehrenfeld 1995a). Gradients of moisture and redox potential occur across this micro-elevation gradient; in measurements at the same sites, but on different dates, Eh varied from >550 mv on the tops to <300 on the bottoms, and moisture varied from 100–500% on the tops to >1000% on the bottoms (Ehrenfeld 1995b). The frequencies of vesicles and hyphae increased rapidly from the permanently wet hollows to the drier tops of the hummocks, and arbuscles were also conspicuously more abundant in the drier microhabitats. These data support the inference that VAM colonization in *Chamaecyparis* varies with moisture status and the associated oxygenation of the sediments.

The higher concentrations of acetylglucosamine measured in the mid-hummock positions (Fig. 3) corresponded closely with the qualitative observation that arbuscles were more densely branched in this microhabitat. During summer months, the tops of the hummocks can become very dry, while the hummock sides remain moist. If mycorrhizal development is limited by dry soil, as demonstrated by Lodge (1989) for *Populus* roots, then it might be expected that the zone of maximal arbuscular production would vary in response to water table fluctuations. Our data were restricted to an autumn sample, at a time when the hummock tops were dry; sampling earlier in the season may have shown that arbuscle development (and the related concentration of acetylglucosamine) was higher in the hummock tops when these microsites were moist but aerobic. The higher density of vesicles in the top position, relative to the mid position, may in fact have arisen through the degeneration of abundant arbuscles earlier in the season. While the single sample used for this study is suggestive of seasonal movement of arbuscular development down the hummock with progressive drying, more extensive sampling is clearly needed to substantiate this hypothesis.

It is not clear from the existing literature whether mycorrhizal colonization in wetland plants is responding to hydrology, to oxygen concentration, to redox potential, to nutrient status, or to some combination of these factors. While these factors are all interrelated (Mitsch and Gosselink 1993), saturation does not necessarily imply anoxia, the intensity of reducing conditions can vary greatly, and moving water may remove toxic products of chemical reduction that would accumulate in stagnant water. In wetland herbs, several studies have reported higher rates of colonization in drier sites (e.g., Cooke and Lefor 1990; Wetzel and van der Valk 1995; Stevens and Peterson 1996), but the relative importance of water, oxygen and redox status was not investigated. Similarly, Lorio et al. (1972) showed that ectomycorrhizae have lower surface area on loblolly pine roots on wet flats than in better-drained mounds, and that mycorrhizae increase during dry periods, but they did not differentiate flooding from anoxia or redox conditions. In wetland trees, higher rates of mycorrhizal colonization have been de-

monstrated in the main root axes of flooded blackgum seedlings, compared with distal roots (Keeley 1980); this was attributed to higher oxygen concentrations in the aerenchyma of the root axes (Read and Armstrong 1972). Khan (1993) found that VAM in three species of wetland tree was lower in soils with low redox potentials (Eh < 300 mv) than in oxidized upland soils. While our previous studies (Ehrenfeld 1995b) showed that redox potentials are indeed low in the hummock bottom sites, we cannot determine whether limitation of mycorrhizal colonization is due to lack of oxygen or to presence of reduced chemical species (e.g., Fe^{+2}, Mn^{+2}, S^{-2}, or CH_4). Low redox potentials are also associated with increases in phosphorus (P) availability, (Ponnamperuma 1984), and high availability of P has been associated with decreases in mycorrhizal colonization in upland plants (Smith and Read 1997). Indeed, Wetzel and van der Valk (1995) found higher colonization rates of wetland herbs in praire potholes with low P concentrations than in sites with higher P availability, and Wigand and Stevenson (1994) showed that VAM infection in a submersed macrophyte was important for P acquisition. Experimental manipulations will be needed to ascertain the relative importance of water movement, oxygen availability, redox chemistry, and phosphorus availability in explaining the observed patterns of mycorrhizal infection in wetland plants. The variability of colonization in wetland trees noted by Jurgensen et al. (1997) and Torti et al. (1997) in response to flooding may reflect the variety of factors that could affect the fungi, the trees, and the interactions between them.

The differences in the distribution of mycorrhizal structures in different microsites may be important in current attempts to restore *Chamaecyparis* swamps. Although methods of propagating cuttings have been developed (Kuser and Zimmerman 1995), planting designs have received less attention. Our results suggest that microtopographic structures 30–40 cm high should be created, if they are not present, and the trees planted on their tops. By doing this, restorationists would ensure conditions under which the trees would become mycorrhizal and the zone of arbuscular development would migrate up and down the hummock in response to changing conditions of saturation and dryness. This recommendation parallels similar findings for the restoration of a variety of other peatland types (Wheeler et al. 1995).

In summary, VAM infection appears to be as important to wetland trees as it is to upland species, at least within oxygenated microsites. Such microsites are commonly found in swamps, and most woody wetland plants rely on these sites because they are intolerant of continuous flooding. Thus, it can be expected that mycorrhizal infection in wetland trees will prove an important aspect of their ecology and of the restoration of forested wetlands. Further research is needed, however, to determine the cause or causes of variation in infection found among wetland microsites.

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