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Catherine A. Gehring · Rebecca C. Mueller
Thomas G. Whitham

Environmental and genetic effects on the formation of ectomycorrhizal and arbuscular mycorrhizal associations in cottonwoods

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Abstract Although both environment and genetics have been shown to affect the mycorrhizal colonization of host plants, the impacts of these factors on hosts that can be dually colonized by both ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) fungi are less understood. We examined the influence of environment and host crosstype on the EM and AM colonization of cottonwoods (*Populus angustifolia* and natural hybrids) by comparing levels of colonization of trees growing in common gardens that differed in elevation and soil type. We also conducted a supplemental watering experiment to determine the influence of soil moisture on AM and EM colonization. Three patterns emerged. First, garden location had a significant impact on mycorrhizal colonization, such that EM colonization was 30% higher and AM colonization was 85% lower in the higher elevation garden than the lower elevation garden. Second, crosstype affected total (EM + AM) colonization, but did not affect EM or AM colonization. Similarly, a significant garden × crosstype interaction was found for total colonization, but not for EM or AM colonization. Third, experimental watering resulted in 33% higher EM colonization and 45% lower AM colonization, demonstrating that soil moisture was a major driver of the mycorrhizal differences observed between the gardens. We conclude that environment, particularly soil moisture, has a larger influence on colonization by AM versus EM fungi than host genetics, and suggest that environmental stress may be a major determinant of mycorrhizal colonization in dually colonized host plants.

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C. A. Gehring (✉) · R. C. Mueller · T. G. Whitham
Department of Biological Sciences, Merriam-Powell
Center for Environmental Research,
Northern Arizona University, Flagstaff, AZ 86011-5640, USA
E-mail: catherine.gehring@nau.edu
Tel.: +1-928-5239158
Fax: +1-928-5237500

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Introduction

Although most plant species generally form only one of several possible types of mycorrhizal association, members of a few plant families, including the Fagaceae, Myrtaceae and Salicaceae, routinely form functional mycorrhizal associations with ectomycorrhizal (EM) fungi and arbuscular mycorrhizal (AM) fungi simultaneously (Molina et al. 1992). In singly colonized plants, the extent of colonization of plant root systems by mycorrhizal fungi is influenced by both environmental factors (Smith and Read 1997; van der Heijden and Sanders 2002) and host plant genetics (Barker et al. 2002; Linderman and Davis 2004). Similarly, in dually colonized host plants, colonization by AM versus EM fungi is influenced by the local soil environment (Smith and Read 1997) and water availability (Lodge 1985, 1989), and recent studies also suggest that host plant genetics may play a role in determining the dominant mycorrhizal type in dually colonized hosts (Walker and McNabb 1984; Tagu et al. 2001; van der Heijden and Kuyper 2001; Khasa et al. 2002; Tagu et al. 2005). However, few studies have simultaneously examined host plant genetics and environment to determine their relative influence on mycorrhizal colonization.

The purpose of this study was to examine the degree to which environmental parameters and host crosstype influenced the mycorrhizal relationships of narrowleaf cottonwood (*Populus angustifolia* James) and its naturally occurring hybrids with Fremont cottonwood (*P. fremontii* S. Wats). We compared colonization by EM and AM fungi on the root systems of 15 different cottonwood clones growing in two contrasting common gardens established in natural riparian sites. We also manipulated soil moisture levels in the field using paired watered and control seedlings to determine if variation in

soil moisture would result in shifts in EM and AM colonization. We addressed three specific questions. First, do levels of total (AM + EM) mycorrhizal colonization and the prevalence of AM versus EM associations vary with environment as determined by common garden location? Second, does the tendency of cottonwood ramets to form EM versus AM associations have a significant genetic component? Third, does increasing soil moisture lead to changes in overall rates of mycorrhizal colonization and/or levels of AM and EM colonization? Understanding the roles of environmental factors and host genetics in determining the relative mycorrhizal colonization of dually colonized plant species may provide valuable insights into the functioning and importance of these mutualisms not only for species capable of forming mycorrhizal association with both AM and EM fungi, but also for plants that form a single type of mycorrhizal association.

Materials and methods

Host plant hybridization and common garden environment

This study was conducted along the Weber River in north-central Utah, USA. Within this watershed, *P. angustifolia* occupies higher elevation riparian habitats (1,400–2,300 m), while *P. fremontii* is found at lower elevations (1,300–1,500 m). These species naturally cross to produce F_1 hybrids which then backcross only with narrowleaf cottonwood, an example of unidirectional introgression (Keim et al. 1989; Martinsen et al. 2001). This results in a 13-km hybrid zone consisting of parental species, F_1 hybrids and a variety of complex backcross hybrids (Keim et al. 1989; Whitham 1989).

We compared levels of AM and EM colonization on cottonwoods planted as cuttings at the same time in two common gardens, one at lower elevation (lower garden) in the *P. angustifolia* × *P. fremontii* hybrid zone and one at higher elevation (upper garden) in the pure *P. angustifolia* zone. Cottonwood ramets within both gardens were generated from cuttings collected in the late winter from parental trees, rooted in a greenhouse, and transplanted into the common gardens as 1- to 1.5-m stecklings in the spring of 1985. The crosstype (i.e., *P. angustifolia*, F_1 and backcross hybrids) of all study trees had been previously determined by Martinsen et al. (2001) based on the proportion Fremont markers using 35 RFLP markers (1 cpDNA, 1 mtDNA, 33 nDNA) that were diagnostic of the parental species. In both gardens, trees were planted parallel to the Weber River in the lowest terrace of the natural riparian zone. During establishment, trees at both sites were watered weekly from May to October.

In addition to elevation, the common gardens also differed in soil type, soil moisture, total N and C (Schweitzer 2002), and tree growth (Table 1). Soil in the upper garden was classified as loamy-sand, and soil in the lower garden was sandy-loam. The percentage sand (particles 0.05–2.0 mm) and silt-clay (particles < 0.05 mm) was significantly greater in the upper garden than the lower garden, while the percentage gravel (particles > 2.0 mm) was significantly greater in the lower garden than the upper garden. Particle size was based on USDA soil classifications. In addition, gravimetric soil moisture averaged more than twofold higher at the upper elevation garden than at the lower elevation garden at the time of root sampling. The pH of the upper garden soil was slightly, but not significantly, higher than that of the lower garden soil. These soil differences were reflected in tree performance; tree height and trunk diameter were nearly threefold higher in the upper garden than the lower garden (T.G. Whitham and K.M. Floate, unpublished data) (Table 1).

Influence of environment and host genetics on mycorrhizal colonization

To determine if environment and/or host plant genetics influenced mycorrhizal relationships among *P. angustifolia*, and hybrids, we collected root samples from cottonwood ramets of the 15 clones growing in each of two common gardens. One to three stecklings of each clone were sampled, and mycorrhizal colonization was averaged when more than one replicate was sampled. The ramets from which roots were collected included pure *P. angustifolia*, F_1 hybrids, and complex backcross hybrids. The ramets in both gardens were 8 years old at the time of root collections in June 1992. Because trees sampled were the same age, differences in EM and AM colonization due to successional changes (e.g., Dhillion 1994; Chen and Brundrett 2000; dos Santos et al. 2002) were likely minimal. In addition, by collecting roots from ramets of the same genetic makeup in both gardens, we were able to examine the influence of environment while holding plant genetics constant.

Table 1 The upper and lower gardens differed in soil properties and tree growth

Site and tree parameters	Garden		*P*
	Upper	Lower	
Elevation (m)	1,582	1,381	
Soil composition[a]			
% Gravel fraction	3.62 (1.79)	48.47 (7.43)	< 0.001
% Sand fraction	92.0 (2.05)	48.47 (7.43)	0.001
% Silt-clay fraction	4.38 (0.90)	1.45 (0.31)	0.015
Soil pH	8.46 (0.10)	8.04 (0.17)	0.075
% Soil moisture (g/g)[b]	26.17 (1.18)	12.97 (3.33)	< 0.001
Soil total C (%)[c]	3.9	2.6	
Soil total N (%)[c]	0.17	0.10	
Tree height (m)	8.5 (0.03)	2.9 (0.2)	< 0.001
Trunk diameter (cm)	14.4 (1.3)	5.0 (0.4)	< 0.001

Data presented are means or means±1SE

[a] Wilks' Lambda = 0.148, $F = 11.55$, $p = 0.007$. Mean gravel, sand and silt-clay fractions based on five samples per site

[b] Gravimetric soil moisture based on five samples per site

[c] From Schweitzer 2002

Root samples were collected using a trowel to dig to a constant maximum depth of 15 cm. Most of the fine roots of the trees were located in the upper 15 cm of the soil profile. Roots were traced to their origin to ensure that they were from the desired tree. Roots were heated for 1 h in 10% potassium hydroxide, bleached in dilute hydrogen peroxide, and stained in acid fuchsin (Kormanik and McGraw 1982). Percentage mycorrhizal colonization was assessed using a dissecting microscope at 40× and a gridline intersect method (Giovanetti and Mosse 1980). Root intersections containing arbuscules, vesicles, or internal hyphae connected to one of these two structures were scored as AM while root segments covered by a fungal mantle were scored as EM. A subset of the samples were examined using a compound microscope at 200× at a later date to verify that AM fungal structures were accurately identified. Hand sections were made and examined on microscopes slides with a compound microscope at 100× to verify the presence of a Hartig net in a subset of the EM samples. Because we never observed fungal structures of both symbionts in the same root intersection, we were able to calculate overall levels of mycorrhizal colonization and the percentage of that amount attributable to EM and AM fungi. Percent colonization by AM and EM were calculated as the number of cross-sections with AM or EM fungal structures present divided by the total number of cross-sections examined.

To determine the influence of environment as determined by common garden location and crosstype as determined by the proportion Fremont alleles (Martinsen et al. 2001) on mycorrhizal colonization, EM and AM colonization of the two gardens were analyzed using a multivariate analysis of variance with the location of the common garden and proportion Fremont alleles as the treatment factors and overall levels of mycorrhizal colonization, colonization by AM fungi, and colonization by EM fungi as response variables. All percentage data were arcsin-square root transformed prior to analysis (Zar 1984). Non-transformed data are presented in the figures.

Watering experiment

To determine if the differences we observed between gardens in the amount of AM versus EM colonization could be partially attributed to variation in soil moisture, we performed a watering experiment using naturally established backcross hybrid seedlings growing in a hybrid zone. The environmental conditions at this site were similar to those of the lower garden; soil was classified as sandy-loam, and total C and N in these soils were 2.9 and 0.15%, respectively (Schweitzer 2002). Although several environmental features varied between the common gardens that could have contributed to the differences we observed in mycorrhizal colonization, including elevation, tree size, soil moisture, and soil particle size distributions (Table 1), we selected soil moisture for further study for two reasons. First, mean soil moisture was more than twofold higher at the upper elevation site than at the lower elevation site (Table 1), and second, a study by Lodge (1989) of *P. deltoides* suggested that EM versus AM colonization of poplars may be linked to soil moisture.

Within a 50-m transect parallel to the Weber River on the lower floodplain, 22 cottonwood seedlings were selected and paired for size (height and number of branches) and location. Members of a pair were no more than 3 m apart. One randomly selected member of each pair received 7.5 L of supplemental water on a weekly basis for 6 weeks beginning in early July and extending through mid-August 1996. Seedlings were watered slowly and surrounded by a rubber dam placed 10 cm beyond the drip line and buried approximately 5 cm. This dam ensured that the root system of the target seedling was well watered and minimized runoff toward neighboring plants. Control seedlings received no supplemental water. During the 6 weeks of watering, the daytime high temperatures averaged 33.2°C and the sites received 24.1 mm of rain.

Two to three days after the last watering treatment, root samples were collected from the watered and control seedlings as described above for the common garden trees. Levels of mycorrhizal colonization were determined as described above. Data were arcsine-square root transformed and analyzed using a multivariate analysis with watered and control trees as treatment groups and overall levels of mycorrhizal colonization, colonization by AM fungi, and colonization by EM fungi as response variables. Data are presented as means±1SE.

Results

Environment, crosstype and mycorrhizal colonization

Common garden environment had a significant effect on the overall levels of mycorrhizal colonization in cottonwood ramets (Fig. 1). The results of the MANOVA showed that the two sites differed significantly in their patterns of mycorrhizal association (Wilks' lambda = 0.088, $F_{3,12} = 41.691$, $P < 0.0001$), and a univariate F test demonstrated that total mycorrhizal colonization contributed significantly to this difference ($F_{1,28} = 73.458$, $P < 0.001$). Ramets growing in the upper garden had significantly higher levels of mycorrhizal colonization than those in the lower garden. Total mycorrhizal colonization of the upper garden was 97.9±0.69%, compared with 91.1±2.26% in the lower garden. In addition, univariate F-tests showed that patterns for both EM and AM colonization contributed significantly to the overall MANOVA (EM: $F_{1,28} = 33.281$, $P < 0.0001$; AM: $F_{1,28} = 15.610$, $P = 0.001$). Ramets growing in the lower elevation garden had 30% lower levels of EM colonization and 85% higher levels of AM colonization than ramets growing in the higher elevation garden (Fig. 1a). Ectomycorrhizal colonization in the upper and lower gardens was 94.1±1.99 and 65.6±4.62%, and AM

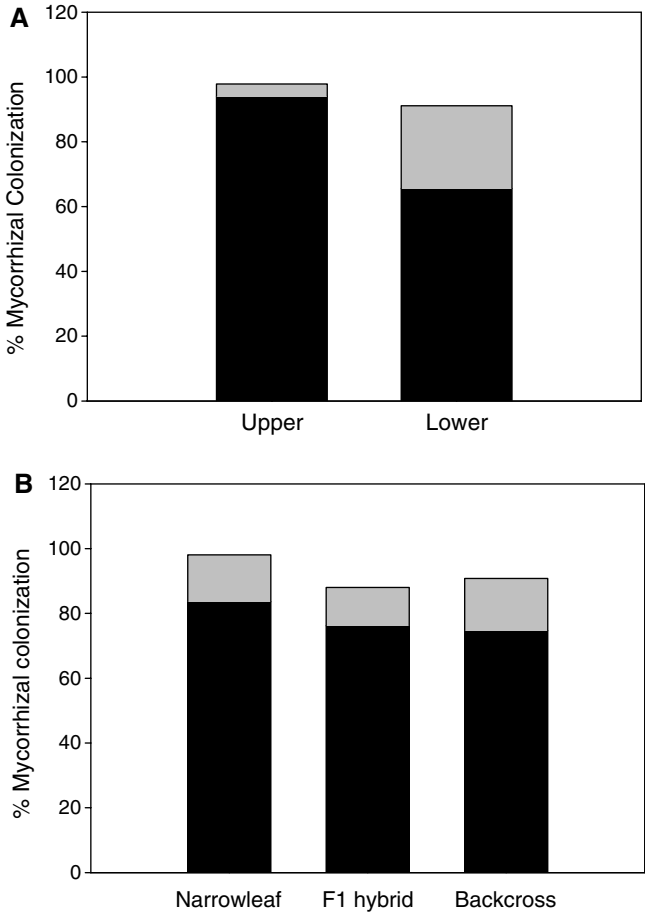

Fig. 1 Percent EM (*black portion of bar*) and AM (*gray portion of bar*) colonization of cottonwoods (*Populus angustifolia* and natural hybrids). The height of the bar represents the mean total % mycorrhizal colonization attributed to both types of symbionts. **a** Percent EM colonization was significantly higher in the upper garden, while percent AM colonization was significantly higher in the lower garden. Total mycorrhizal colonization was significantly greater in the upper garden than the lower garden. **b** Percent EM and AM colonization of different crosstypes growing in both gardens was not significantly different, but total colonization varied by crosstype

colonization of these sites was 3.8±1.66 and 25.5±4.09%, respectively.

In addition to the impact of environment on mycorrhizal colonization, we found a significant overall effect of crosstype (Wilks' lambda = 0.059, $F = 3.292$, $P = 0.001$). However, although we did find a significant effect of crosstype on the total mycorrhizal colonization of cottonwoods ($F = 14.236$, $P < 0.001$), we found no crosstype effect on either EM colonization ($F = 1.217$, $P = 0.354$) or AM colonization ($F = 0.943$, $P = 0.495$) of host plants (Fig. 1b).

We also found a significant overall effect of garden × crosstype on mycorrhizal colonization (Wilks' lambda = 0.035, $F = 4.316$, $P < 0.001$), but univariate tests showed that only the total mycorrhizal colonization was significantly affected ($F = 10.258$, $P < 0.001$). No significant interaction effect was detected for either EM colonization ($F = 1.112$, $P = 0.404$) or AM colonization ($F = 0.663$, $P = 0.681$).

Watering experiment

Watering resulted in major quantitative and qualitative changes in mycorrhizal colonization, a statistically significant overall effect (Wilks' lambda = 0.365, $F_{3,18} = 10.433$, $P < 0.001$) (Fig. 2). However, we found no differences in overall mycorrhizal colonization between watered and control trees ($F_{1,20} = 1.241$, $P = 0.278$). In contrast to the overall levels of mycorrhizal colonization, AM and EM colonization showed significant responses to experimental watering. Ectomycorrhizal colonization increased by 33% in response to the experimental increase in soil moisture ($F_{1,20} = 26.121$, $P < 0.001$). Ectomycorrhizal colonization of cottonwood seedlings receiving supplemental water was 62.6±2.88%, while EM colonization of control seedlings was 41.5±2.95%. In addition, although colonization by EM fungi increased in response to increased soil moisture, watering resulted in a 45% decline in AM colonization ($F_{1,20} = 22.049$, $P < 0.001$). Colonization by AM of watered seedlings was 19.5±1.99%, compared to 36.0±2.88% for control seedlings.

Discussion

Soil moisture effects on EM versus AM colonization

The results of the watering experiment showed that increasing soil moisture caused rapid, but opposite shifts

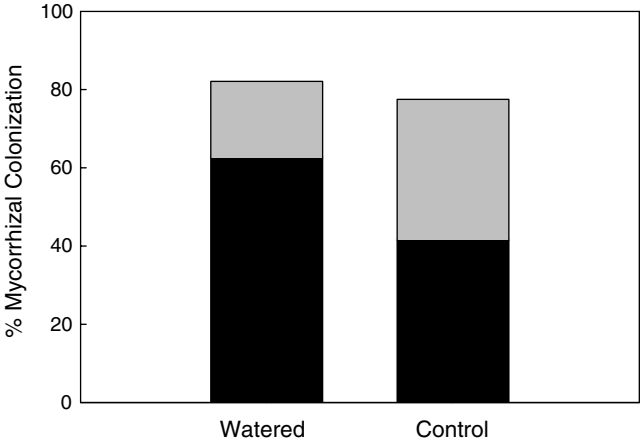

Fig. 2 Percent ectomycorrhizal (*black portion of bar*) and arbuscular mycorrhizal (*gray portion of bar*) colonization of cottonwood seedlings that either received supplemental water or served as non-watered controls. The height of the bar represents the mean total percent mycorrhizal colonization attributed to both types of symbionts. Percent ectomycorrhizal colonization of watered trees was significantly higher than control trees, while percent AM colonization of watered trees was significantly lower than control trees. Total mycorrhizal colonization of watered and control trees were not significantly different

in the relative colonization of cottonwood seedlings by AM and EM fungi.

Previous studies have implicated other factors, including fungal inoculum potential (Baon et al. 1992; van der Heijden and Votsaka 1999; Trowbridge and Jumpponen 2004), litter accumulation and quality (Chilvers and Pryor 1965; Reddell and Malajczuk 1984; Read 1991; Conn and Dighton 2000), and host vigor (Power and Ashmore 1996; Swaty et al. 2004), in influencing both AM and EM colonization of host plants. However, although all of these factors could have contributed to the differences observed in mycorrhizal colonization between the upper and lower gardens, these variables were held constant for the watering experiment, where seedlings were of uniform size and age and were growing under similar environmental conditions. The rapid shift in mycorrhizal colonization in response to water addition, in agreement with the findings of Lodge (1989), demonstrates that soil moisture has a strong influence on patterns of mycorrhizal colonization of cottonwoods. Under conditions of high water availability, EM colonization increases, while AM colonization declines. Similar patterns of EM versus AM colonization of *P. deltoides* were observed by Lodge (1989) and Lodge and Wentworth (1990).

Genetic influences on AM versus EM colonization

Mycorrhizal responses to host plant genetics have been demonstrated in numerous ecosystems and with diverse host plants. Plant genotypes have been shown to differ in both their ability to form mycorrhizae, and in the relative benefit received from mycorrhizal colonization (Smith and Read 1997; Barker et al. 2002). Studies of *Populus* have also shown that EM formation is under genetic control (Tagu et al. 2001, 2005). In addition, a study by Khasa et al. (2002) in a single common garden found that the relative susceptibility to colonization by AM versus EM fungi varied among different species and hybrids of *Populus*, suggesting that mycorrhizal status of dually colonized host plants can also be influenced by host plant genetics. In the present study, we detected a significant influence of crosstype on total mycorrhizal colonization, but allocation to EM versus AM was unaffected by crosstype. Lack of consistent results between the present study and the findings of Khasa et al. (2002) could be due to differences in the scale of examination; we examined only a single species of *Populus* and various hybrids, while the study by Khasa et al. (2002) included 28 clones of various *Populus* species and hybrids, and did not include *P. angustifolia* or *P. fremontii*.

Similarly, the interaction between garden × crosstype significantly affected total mycorrhizal colonization, but did not influence allocation to EM versus AM fungi. This lack of significant interaction shows that even in vastly different environments, the influence of crosstype on colonization by EM versus AM fungi was limited. In other words, regardless of environmental conditions, crosstype did not have a significant impact on the patterns of colonization by the two types of mycorrhizal fungi.

Although we detected no influence of crosstype on colonization by EM versus AM fungi, differences in ramet crosstype may have a greater impact on the community composition of either ectomycorrhizal or AM fungal species than on whether EM or AM associations dominated at a given site. For example, Wimp et al. (2005) found that cottonwood crosstype did not influence the richness or abundance of arthropods, but it did significantly affect arthropod community composition. Similarly, genetic diversity of cottonwood host plants accounted for nearly 60% of the variation in arthropod diversity (Wimp et al. 2004). The effects of host plant genetics on mycorrhizal community composition is not well understood, but differences in host specificity of both AM and EM fungi (Molina et al. 1992) suggest that the composition of mycorrhizal fungi is likely to be responsive to differences in host plant genetics.

Stress, competition and mycorrhizal colonization

The shifts in mycorrhizal colonization in response to supplemental water we observed were consistent with the findings of Lodge (1989), who found that EM fungi colonized roots in moist but well drained soils, while AM fungi had higher levels of colonization in flooded and very dry soils (Lodge 1989). We did not have the opportunity to sample flooded soils, but both very dry and flooded soil can represent stressful conditions for host plants (Entry et al. 2002). The shifts observed by Lodge (1989) and the findings of this study suggest that AM respond positively to stressful conditions, while EM are negatively affected by stress.

The patterns of EM versus AM colonization we observed could result from either preferential allocation to one type of mycorrhizal fungi, or competition between fungal symbionts in response to environmental conditions. For example, Saikkonen et al. (1999) hypothesized that under environmental conditions that result in host plant carbon limitation, allocation to EM may switch from fungal species with high carbon requirements to species with low carbon requirements. In support of this hypothesis, Markkola et al. (2004) found that colonization of thick-mantled EM fungal species declined in response to simulated herbivory. Similarly, AM colonization of oaks was positively correlated with wasp herbivory, while EM colonization was negatively associated with herbivory (Mueller et al. 2005). Because recent studies suggest that EM and AM may confer different benefits to their host plants (van der Heijden 2001; Gehring and Whitham 2002), carbon limitation in host plants that support both AM and EM may result in preferential allocation to AM, which still function in nutrient uptake but may have lower carbon requirements than EM (Janos 1983; Connell and Lowman 1989; Jakobsen et al. 2002).

Conversely, in favorable environments, hosts plants may preferentially allocate to EM, which have higher carbon requirements, but which may be more effective at nutrient uptake than AM (Jones et al. 1998; van der Heijden and Kuyper 2001). In support of this hypothesis,

Lodge (1985) found that EM were most abundant on members of the genera *Populus* and *Salix* in the eastern US where conditions for plant growth are optimal. In our system in the arid west, measures of growth showed that the ramets in the lower garden had lower growth rates than those found in the upper garden (Table 1). Because trees in the upper and lower garden were the same age, the differences suggest that the opposite patterns of EM versus AM colonization in these gardens could have been influenced by differential carbon allocation by host plants to the two types of mycorrhizae.

Alternatively, shifts in EM versus AM colonization could result from competition between these two types of mycorrhizal fungi. Several mechanisms of competition between established mycorrhizal fungi have been proposed, including differences in sink strength for host plant carbohydrates (Wilson and Tommerup 1992; Deacon and Fleming 1992), variable levels of aggressiveness for colonization sites (Wilson and Tommerup 1992), and competitive and antagonistic exclusion (Deacon and Flemming 1992; Bruns 1995). Competition between AM and EM on a single host plant could also occur through interactions between hyphae in the soil, or result from limitations of habitat space within roots (Chen et al. 2000). Observations of fungal interactions in the soil and at the root interface are necessary to evaluate these potential mechanisms.

Conclusions

We found that, compared to environmental factors, host crosstype played a minor role in determining levels of EM versus AM colonization in the field. Although a small percentage of plants are capable of forming dual mutualisms with both EM and AM (Trappe et al. 1987), many of these plants are dominant species, such as members of *Eucalyptus* and *Quercus*, and as a result, these findings are applicable to numerous ecosystems. In addition, studies of plant species such as cottonwoods that are capable of forming both AM and EM associations may provide valuable insights into the functioning and importance of these mutualisms, not only to dually colonized hosts, but also to plants that form only one or the other association. Our research and that of Lodge (1985, 1989) indicates that soil moisture may be an important environmental attribute determining the prevalence of AM versus EM. Although other factors may have had some influence on levels of mycorrhizal colonization, the results of our watering experiment showed that soil moisture was a major determinant of the levels of EM versus AM colonization. We suggest that this relationship be further explored with the view to incorporating it into the theories regarding the occurrence and importance of the various types of mycorrhizal mutualism in ecosystems (Allen et al. 1995) and how these patterns compare with those of other trophic levels and taxa. Furthermore, although the majority of studies have not examined both environmental and genetic effects on mycorrhizal colonization concurrently, our findings suggest that both factors are important determinants of mycorrhizal colonization of host plants.

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