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Endo- and ectomycorrhizas in *Quercus agrifolia* Nee. (Fagaceae): patterns of root colonization and effects on seedling growth

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Abstract We documented the patterns of root occupancy by Glomalean and ectomycorrhizal (EM) fungi in *Quercus agrifolia*, and host plant responses to inoculation with each mycorrhizal type alone or in combination. Glomalean hyphae, coils and vesicles, and EM root tips were recorded. Colonization patterns conformed to a succession from Glomalean and EM fungi in 1-year-old seedlings to predominantly EM in saplings (≥11 years old); both mycorrhizal types were rarely detected within the same root segment. Inoculation of *Q. agrifolia* seedlings with EM or Glomalean fungi (AM) alone or in combination (EM+AM) altered the cost:benefit relationship of mycorrhizas to the host plant. Seedling survival, plant biomass, foliar nitrogen (N), and phosphorus (P) status were greatest in EM- or AM-only inoculated seedlings. Seedlings inoculated with both mycorrhizal types (AM+EM) exhibited the lowest survival rates, biomass, foliar N, and P levels. Roots of these plants were highly colonized by both EM (38% root length colonized) and Glomalean fungi (34%). Because these levels of colonization were similar to those detected in 1-year-old field seedlings, the presence of both mycorrhizal types may be a carbon cost and, in turn, less beneficial to oaks during establishment in the field. However, the shift to EM colonization in older plants suggests that mycorrhizal effects may become positive with time.

Keywords Cost:benefit relationship · Immunofluorescence · Oak woodlands · Mycorrhizal succession

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Introduction

The majority of vascular plants establish either ecto- (EM) or arbuscular (AM) mycorrhizas with symbiotic fungi. Nevertheless, these different types of mycorrhiza periodically co-occur within the root as dual (co-dominant) or successional mycorrhizal associations (Molina et al. 1992).

In dual AM–EM associations of *Abies*, *Tsuga*, *Pseudotsuga*, *Pinus* (Cázares and Trappe 1993; Horton et al. 1998), *Alnus* (Molina 1981), *Populus* (Lodge and Wentworth 1990), *Adenostoma* (Allen et al. 1999) and certain legumes (Frioni et al. 1999), each mycorrhizal type occurs within the same root segment and forms physiologically active mycorrhizas (Lapeyrie and Chilvers 1985). In contrast, successional mycorrhizas are characterized by the temporal replacement of one mycorrhizal type by another. For example, the transition from AM–EM seedlings to EM plants occurs in *Helianthemum* (Read et al. 1977), *Salix* (Lodge 1989; Lodge and Wentworth 1990; Dhillion 1994; Van der Heijden and Kuyper 2001), *Uapaca* (Moyersoen and Fitter 1999) and *Eucalyptus* (Lapeyrie and Chilvers 1985; Chilvers et al. 1987; Chen et al. 2000). However, these two categories are not mutually exclusive. Host plants that demonstrate a temporal replacement of mycorrhizas may also possess dual mycorrhizas (*Eucalyptus*, Lapeyrie and Chilvers 1985; *Uapaca*, Moyersoen and Fitter 1999). In addition, residual colonization by AM fungi may persist long after the completion of temporal succession, either when a host tree is distant from sources of EM inoculum (Dominik 1957) or in response to certain environmental conditions, such as flooding (Lodge 1989).

Empirical studies have repeatedly demonstrated that AM or EM facilitate the uptake of soil resources, such as nitrogen, phosphorus and water, to the host plant in exchange for photosynthates (Smith and Read 1997 and references therein). However, the role of the dual or successional mycorrhizas on host plant survival, productivity and nutrient status has received little attention (Lodge and Wentworth 1990; Chen et al. 2000), even though

combinations of mycorrhizal types may alter the cost:benefit relationship between mycorrhiza and host plant (Fitter 1991; Read 1991). The cost:benefit relationship may be modified in two ways. Firstly, the presence of two mycorrhizal types may increase the uptake of nutrients because AM and EM may explore and exploit soil resources differentially (Lapeyrie and Chilvers 1985). Alternatively, the presence of such a large fungal sink may comprise a significant carbon cost from the host, especially if nutrient acquisition is limited (Smith and Smith 1996). In this study, we document the patterns of root colonization of Glomalean and ectomycorrhizas in *Quercus agrifolia* Nee. (coast live oak, Fagaceae) with season and host ontogeny, and the cost:benefit relationship of the two mycorrhizal types, alone or in combination, on host plant productivity and nutrient status.

Members of the Fagaceae typically form EM with diverse fungi (Henry 1933; Trappe 1962). Available data also indicate that extra- and intraradical hyphae and vesicles typical of Glomalean fungi occur within the roots of *Fagus* and *Quercus* seedlings (Henry 1933; Grand 1969; Filer 1975; Williams and Aldon 1976; Rothwell et al. 1983). Sporocarp surveys in *Q. agrifolia* groves document the presence of more than 90 species of macrofungi that typically form EM, including *Pisolithus tinctorius* Pers. (Coker & Couch), *Boletus amygdalinus* (Thiers) Thiers, *Laccaria amethysteo-occidentalis* Muller and *Amanita ocreata* Peck. Colonization of *Q. agrifolia* roots by Glomalean fungi has not been recorded previously and the symbiotic efficacy of Glomalean fungi alone or in concert with EM in oaks is unknown. Nevertheless, the role of both mycorrhizal types in the establishment and survival of *Q. agrifolia* seedlings may become increasingly important. Exotic forbs and Mediterranean annual grasses have progressively invaded many coast live oak woodlands (Minnich and Dezzani 1998). Oak seedlings now establish in a matrix of plants that are largely AM or non-mycorrhizal and these weedy plant species may inhibit the formation of EM (Sylvia and Jarstfer 1997). In this study, our goals were to (1) investigate the patterns of root colonization, (2) investigate the relative importance of each mycorrhizal type during seedling establishment, and (3) use these data to determine the role of mycorrhizas in seedling establishment in oak–grasslands transitions.

Materials and methods

Root occupancy by Glomalean and ectomycorrhizas

During 1998 and 1999, we sampled *Q. agrifolia* plants at an oak savanna in the Shipley Reserve in southern-western Riverside County, California (33° 3′ N 117° 02′ E, 380 m asl). The region is typified by a warm Mediterranean-type climate (35°/14°C summer; 18°/3°C winter) and receives an average of 275 mm precipitation per annum with all rainfall occurring during the winter months. Vegetation associations within the reserve include an oak savanna of *Q. agrifolia* interspersed with *Q. engelmanii* Greene (Engelman oak), expanses of coastal sage shrub and chaparral, riparian zones and tracts of exotic Mediterranean grasses from previous site disturbances. The soils are decomposed granite (Lithic Haploxeroll), slightly acidic (mean pH 5.8), and contain significant pools of P (HCO_3-extractable P, 30 µg g^{-1}) and K (200 µg g^{-1}, Padgett et al. 1999).

Patterns of root occupancy by Glomalean and ectomycorrhizas were evaluated seasonally in a monospecific stand of 2-year-old *Q. agrifolia* plants located under the canopy of mature *Q. agrifolia* trees; exotic grasses were encountered within 10 m of the sampling area. On each occasion, soil cores were collected to depth 10 cm within the rhizosphere of each of 10 different plants. Root colonization along an ontogenetic sequence (1- to 30-year-old plants) was evaluated in samples collected in winter when both Glomalean and EM colonization levels were at their maximum. For the latter study, 10 individuals from each of four age categories (1, 6, 11 or ~30 years old) were sampled; plant age was determined by dendrochronology. Each sample was taken within the rhizosphere, and a composite formed by combining two immediately adjacent soil cores each 2.5 cm diameter and 10 cm deep.

Root samples were sieved from the soil cores, washed free of adhering soil particles and fine roots (≤1 mm) hand-picked from each sample. A subsample of roots was stained using Trypan blue (Koske and Gemma 1989) and evaluated for the presence and abundance of Glomalean, ecto- and dual mycorrhizas (Glomalean and EM within the same root segment) using the magnified root intersect method (McConigle et al. 1990). Short roots were considered ectomycorrhizal when covered by a mantle and Hartig net. Roots were examined under transmitted light and differential interference contrast optics on a Zeiss Axioskop2 microscope and images recorded digitally using a Zeiss Axiocam (v2.0.5).

A second subsample of roots was assayed for the presence of extraradical Glomalean hyphae using direct immunofluorescence; production of the immune serum is detailed in Egerton-Warburton and Allen (2000). Root segments were incubated in antisera raised against whole spore fractions of *Glomus deserticola* Trappe, Bloss & Menge, *Acaulospora laevis* Gerdemann & Trappe, *Gigaspora margarita* Becker & Hall, and *Scutellospora calospora* (Nicol. & Gerd.) Walker & Sanders, and scored for the abundance of fluorescent hyphae of each genus using the magnified root intersect method. Immunolabeled samples were examined and imaged using a Bio-Rad MRC600 confocal laser scanning microscope with a Kr-Ar mixed gas laser and single channel filter block for FITC (excitor filter 488 DF10, dichroic reflector 510 LP, emission filter OG515LP) fitted to a Nikon Optiphot-2 epifluorescence microscope. A series of optical *xy*-slices at 0.5-µm steps were collected from ectomycorrhizal root tips that demonstrated the presence of immunoreactive hyphae. Individual images were collected using Kalman averaging (8–10 scans) and subsequently merged using the Bio-Rad CoMOS program. Root segments incubated in deionized water were used as controls and also to check for autofluorescence associated with potential incompatibility reactions between Glomalean fungi and host roots (Allen et al. 1992).

Root colonization data were analyzed with one-way analysis of variance (ANOVA, general linear model) (Zar 1988). Prior to analysis, assumptions of normality were checked, and data were $\log^{10}$ or arcsine square root transformed as required. The association between observed and predicted incidence of dual colonization in *Q. agrifolia* roots and differences in the numbers of roots with immunofluorescent hyphae of each AM genus per sample date were both analyzed by χ^2. Changes in mycorrhizal colonization (Glomalean versus EM fungi) along the ontogenetic sequence were analyzed by two-way ANOVA (season, mycorrhizal type), and Pearson's product moment correlation between plant age and the extent of root colonization by each mycorrhizal type.

Comparison of Glomalean and ectomycorrhiza inocula on plant productivity and nutrient status

Acorns collected from a single maternal tree (half-sib progeny) were used to reduce the influence of host plant genotype on mycorrhiza responses. *Quercus agrifolia* acorns were cool moist stratified (4°C) for 2 weeks and germinated in the dark in sterile

perlite (10°C). Germinants were planted into prepared pots (capacity 800 g) containing an autoclaved soil mixture composed of 1:1:1 Shipley Reserve soil (sieved to 2 mm):coarse sand:fine sand (final pH 6.8, HCO_3-extractable P 9 µg g^{-1}) that had been amended with three inoculation treatments as follows:

1. *Pisolithus tinctorius* spores from sporocarps collected on the Reserve (EM inoculum), 5 g of sporogenous mass per pot.
2. Soil from under heavily grassed areas (*Avena*) within the Shipley Reserve areas (AM inoculum), 25 g soil per pot. This inoculum contained an average of 117 Glomalean spores per gram soil and comprised 16 species of AM fungi representing the four major genera (*Glomus*, *Scutellospora*, *Gigaspora*, *Acaulospora*).
3. Combined EM and AM inocula using the same ratios as per treatments 1 and 2.

Ten replicate pots of each treatment and control (autoclaved inoculum) were initiated. Following the expansion of the first true leaves, the vestigial acorns were excised from each seedling to encourage the formation of mycorrhizas. Seedlings were maintained under greenhouse conditions (18°/27°C, night/day) for 5 months and watered to field capacity as required. Fertilizers were not applied at any time during the trial.

Plants were destructively harvested by washing under a stream of gently running water. Each plant was then divided into root and shoot components. A portion of the newly harvested roots from each plant was stained in Trypan blue and scored for colonization by Glomalean and ectomycorrhizas as described previously. An additional subsample of roots was evaluated for extraradical Glomalean fungi using immunofluorescence as described previously. The remaining root sample and all shoot material was oven-dried to constant weight (80°C, 24 h), after which the biomass of leaf, stem and root of each plant was determined. Replicate root and shoot samples from each inoculation treatment were analyzed for N and P content. Mycorrhizal dependency (%) was calculated as: [(dry wt. MYC – dry wt. NON)/dry wt. NON] × 100, where MYC is the total dry weight (leaf + stem + root) of an individual plant inoculated with mycorrhizas, and NON refers to total dry weight of a non-inoculated (control) plant.

Variation in seedling survival among treatments was analyzed using χ^2, while differences in seedling height, root, shoot and stem biomass, and N and P content were analyzed using one-way ANOVA (general linear model, type III sums of squares). Differences in root colonization and immunofluorescent assays of extraradical hyphae among inoculation treatments were tested as described previously.

Results

Root occupancy by Glomalean and ectomycorrhizas

Mycorrhizas in *Q. agrifolia* demonstrated structural elements characteristic of both Glomalean and ectomycorrhizas (Fig 1). Monopodial pinnate or irregular branched EM short roots exhibited a compact hyphal mantle with emanating extraradical hyphae, a cortical Hartig net and elongated cortical cells within the host root (Fig. 1A, B). Glomalean mycorrhizas were evidenced as extraradical hyphae loosely associated with EM root tips (Fig. 1A) or discrete points of vesicular and intraradical hyphal colonization (Fig. 1C, D, E) including a hyphal coil (Fig. 1C). Arbuscules were not detected in any root segments. In addition, incompatibility reactions between Glomalean fungi and *Q. agrifolia* roots were not observed.

On a seasonal cycle, mycorrhizal colonization peaked in winter (76.7%) and declined in summer (23.06%; F=57.59; P=0.001, Fig. 2A). Such patterns were in agreement with annual trends in colonization in Baja California (Sigüenza et al. 1996) and other Mediterranean-type climates (Brundrett and Abbott 1991). Root colonization was primarily EM with a small, but significant, level of colonization by Glomalean hyphae and vesicles (up to 25%; F=10.11; P=0.001).

Antisera illustrated the presence and seasonal shifts in abundance of Glomalean fungi in the rhizoplane (Fig. 2B, χ^2 P=0.066). *Acaulospora* prevailed during summer, while the cooler, moister conditions in autumn and winter promoted the proliferation of *Gigaspora* and *Scutellospora*. The abundance of *Glomus* remained relatively constant throughout the year. Brundrett and Abbott (1991) noted similar seasonal patterns of root colonization by Glomalean genera.

Mycorrhizas in *Q. agrifolia* conformed to the postulate of mycorrhizal succession in a temporal sequence (Fig. 2C). Ectomycorrhizal colonization (r=0.982, P=0.018) and the percentage of non-infected root (r=0.917, P=0.05) in *Q. agrifolia* increased significantly with plant age, while Glomalean colonization decreased significantly over time (r=–0.964, P=0.035). Ectomycorrhizal and Glomalean colonization units were rarely detected within the same root segment in *Q. agrifolia*; the relationship between observed and predicted dual Glomalean–EM association counts was not significant (χ^2 P>0.05).

Comparison of Glomalean and ectomycorrhiza inocula on plant productivity and nutrient status

Mycorrhizal type significantly influenced coast live oak seedling survival, productivity and nutrient status (Fig. 3). Survival was greatest in plants inoculated with *P. tinctorius* (100%) or AM (90%) and lowest in those receiving AM+EM inoculation (χ^2 P=0.001). Inoculation treatments affected root and stem, but not leaf (F=1.78, P=0.1748) dry matter accumulation (Fig. 3A). Specifically, plants inoculated with AM or EM were significantly larger (root F=5.414, P=0.0048; stem F=10.14, P=0.0001, total biomass F=4.642, P=0.0096), demonstrated a positive mycorrhizal dependency (AM 50.11%, EM 51.5%), and a higher foliar N (F=53.38 P<0.0001) and P (F=32.19 P<0.0001) status than non-inoculated or AM+EM inoculated plants. Interestingly, inoculation with AM resulted in the highest foliar N content while EM inoculum promoted the highest foliar levels of P (Figs. 3B, C, respectively). In contrast, seedlings receiving AM+EM inoculum exhibited a net negative mycorrhizal response (–12.01%), and foliar N and P levels that did not differ significantly from those in non-inoculated seedlings.

Differences between inoculation treatments were also manifest in significant shifts in root colonization patterns (F=71.18, P=0.001). The majority of root tips in EM-inoculated seedlings were ectomycorrhizal, although we noted some extraradical colonization by Glomalean hy-

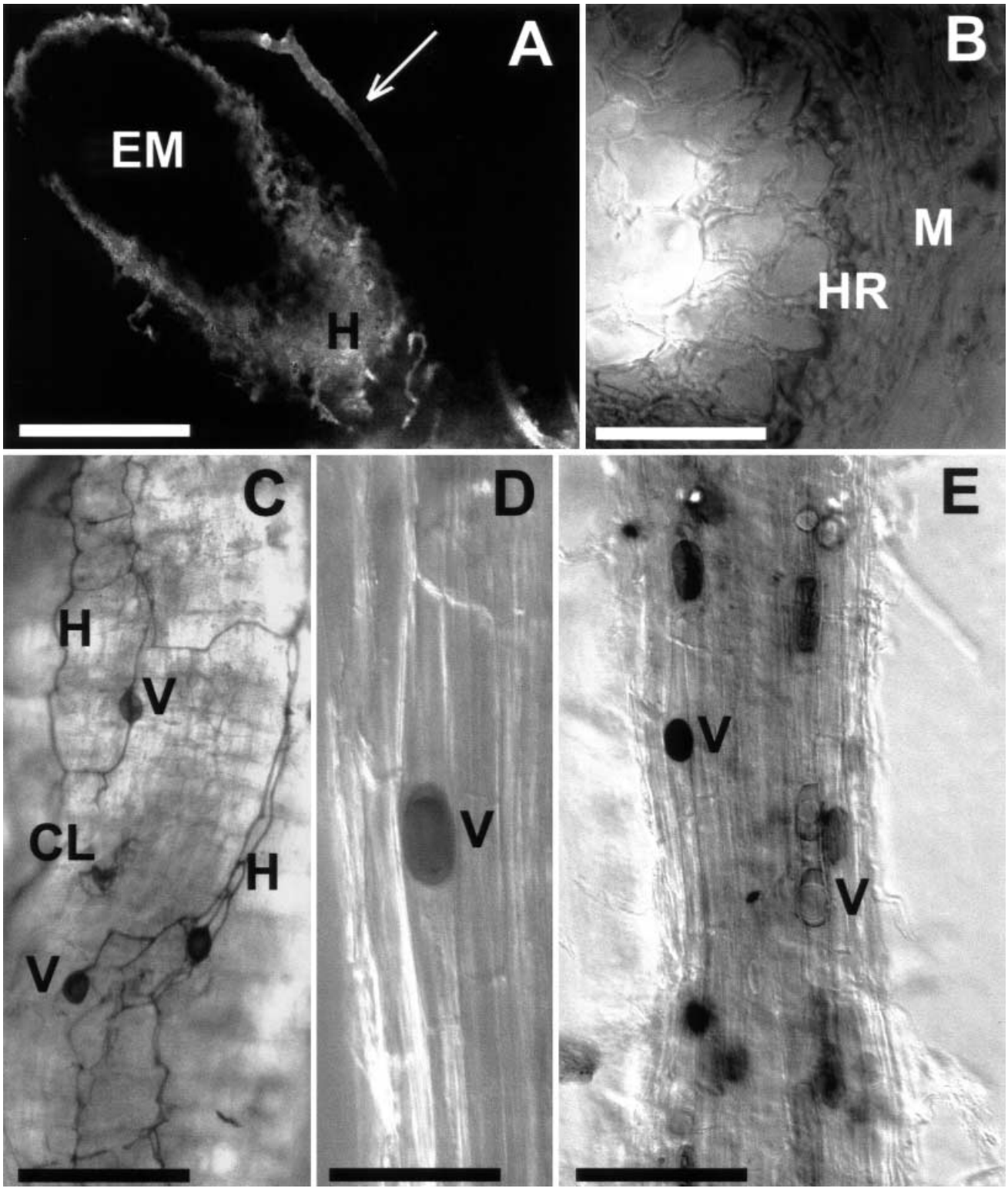

Fig. 1A–E Light and confocal microscope images of mycorrhizas in *Quercus agrifolia* roots. **A** Ectomycorrhizal root tip (*EM*) with dense hyphae (*H*) and immunofluorescently detectable extraradical Glomalean hyphae (*arrow*) loosely associated with the root. **B** Transverse section of fresh root tip showing dense hyphal mantle (*M*), and Hartig net (*HR*) with elongated cortical cells and beaded intercellular hyphae. **C–E** Distribution of intraradical vesicles (*V*), hyphae (*H*) and hyphal coil (*CL*) of Glomalean fungi within an oak root

phae (*Scutellospora*, Fig. 4A, B). Root colonization in AM-inoculated plants was dominated by Glomalean hyphae (*Glomus*, *Gigaspora*) with a low abundance of vesicles. This was similar to the occupancy of *Q. agrifolia* roots by Glomalean fungi under field conditions (Fig. 2).

Roots of seedlings from the mixed inoculum treatment were highly colonized by both EM and Glomalean

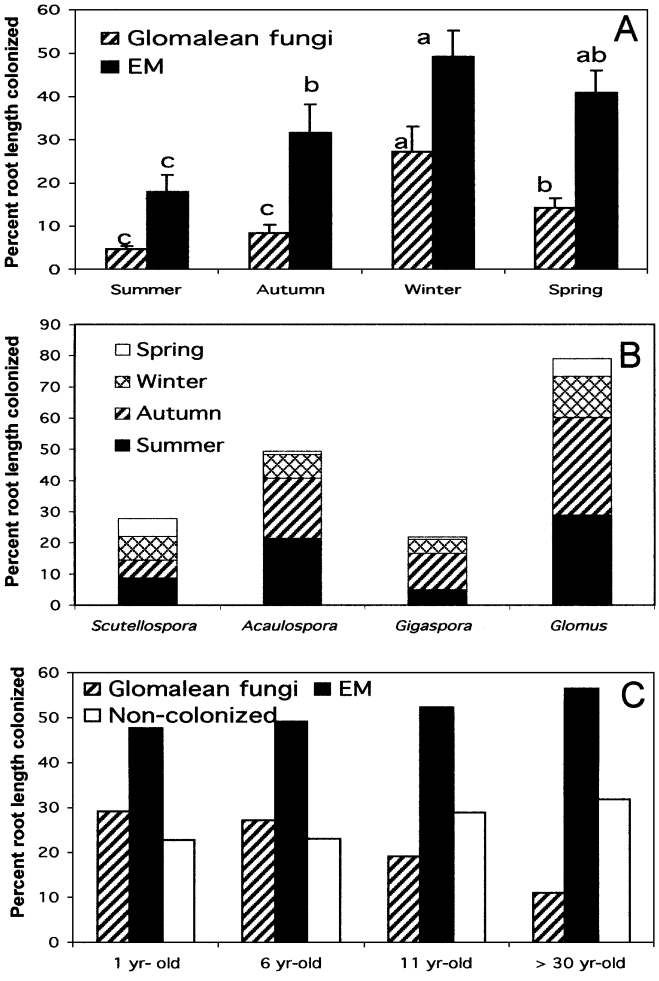

Fig. 2A–C Percentage of root length colonized in *Q. agrifolia*. **A** Seasonal fluxes in EM and Glomalean colonization. **B** Percentage extraradical colonization apportioned by Glomalean genus and season. **C** Variation in EM and Glomalean colonization over the host ontogenetic sequence.. *Vertical bars* indicate the standard error of the means. Values within each graph with the same letter do not differ at $P<0.05$ by Fisher's LSD test (*EM* ectomycorrhiza)

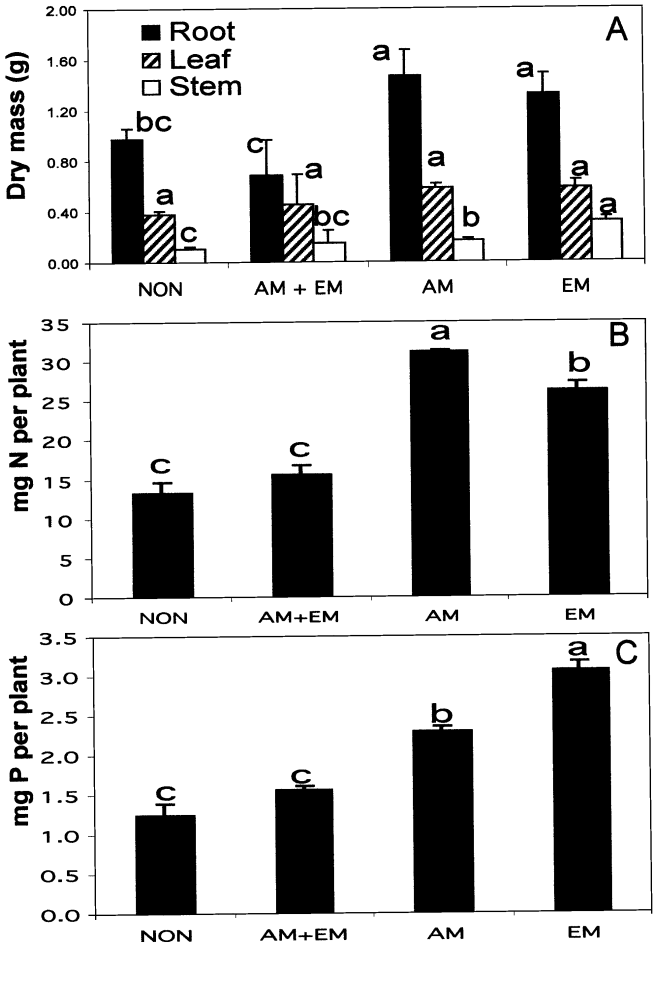

Fig. 3A–C Inoculation of *Q. agrifolia* seedlings with ecto- (*EM*) or arbuscular (*AM*) mycorrhizas, combined EM+AM inoculum, and in comparison with non-inoculated (*NON*) plants. **A** Dry mass accumulation apportioned to root, stem and leaves. **B, C** Mean foliar N and P content per plant, respectively. *Vertical bars* indicate the standard error of the means. Values within each graph with the same letter do not differ at $P<0.05$ by Fisher's LSD test

fungi. Particularly striking was the reduced density of EM root tips (38% versus 52% of root length colonized, Fig. 4A). The percentage of root length colonized by Glomalean fungi was also significantly reduced (22% versus 12%, Fig. 4A). Glomalean hyphae of the genus *Glomus* predominated (Fig. 4B). Moreover, the proportion and abundance of EM and Glomalean fungi in AM+EM inoculated plants were similar to those noted in field seedlings on both a seasonal basis (Fig. 2A), and in 1-year-old seedlings (Fig. 2C). Thus, the observed host responses were most likely due to differences in the mycorrhizal biota and not cultural conditions.

Discussion

The mycorrhizal associations in *Q. agrifolia* display a number of attributes that may influence the establishment of seedlings and development of oak woodlands. From the results presented, it is clear that there are marked differences in root colonization patterns by Glomalean and ectomycorrhizas over the lifespan of coast live oak, that Glomalean and EM fungi interact within the same root system, and that the relative abundance of each mycorrhizal type within the roots alters plant productivity and nutrient acquisition.

Oak seedlings (1-year-old) were commonly associated with both Glomalean and EM fungi. The detection of Glomalean hyphae, vesicles and EM root tips in *Q. agrifolia* corroborates earlier studies of mycorrhizas in the

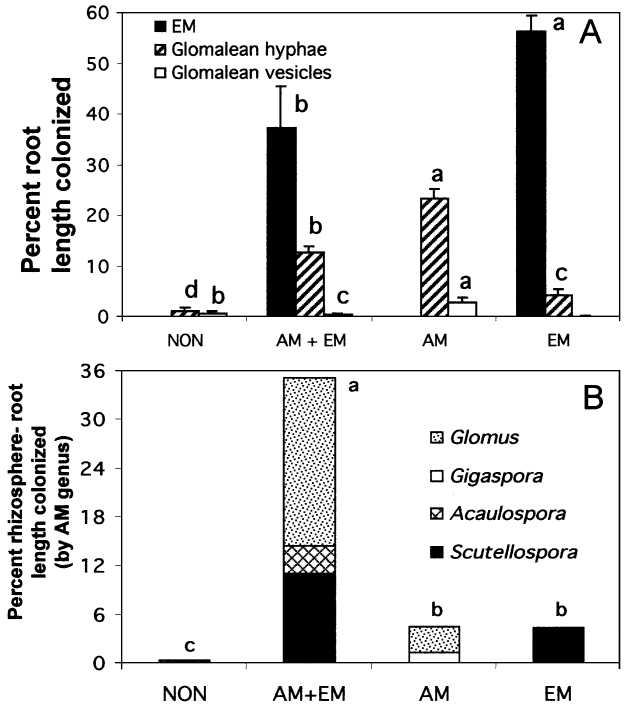

Fig. 4A, B Percent root length colonized following inoculation of *Q. agrifolia* seedlings with ecto- (*EM*) or arbuscular (*AM*) mycorrhizas, combined EM+AM inoculum, and in comparison with non-inoculated (*NON*) plants. **A** Intraradical colonization. **B** Extraradical colonization apportioned by Glomalean genus. *Vertical bars* indicate the standard error of the means. Values within each graph with the same letter do not differ at $P<0.05$ by Fisher's LSD test

Fagaceae (Henry 1933; Grand 1969; Williams and Aldon 1976) and dual mycorrhizal associations in general (e.g., Cázares and Trappe 1993). The detection of hyphal coils in *Q. agrifolia*, however, is particularly important and upholds an earlier observation of arbuscules in *Eucalyptus* (Chilvers et al. 1987). Both arbuscules and coils may be sites of carbon and mineral nutrient transfer (Giovanetti et al. 1994) and their presence indicates possible mutualistic functioning by Glomalean fungi alone or in concert with EM in *Q. agrifolia*, as occurs in *Eucalyptus* (Lapeyrie and Chilvers 1985; Chen et al. 2000). The positive growth and mineral nutrient (N) benefits to oak seedlings inoculated with AM alone supports this proposal. However, oaks inoculated simultaneously with both mycorrhizal types performed poorly by comparison. Root colonization data illustrate the causal nature of this relationship.

Glomalean and EM fungi extensively colonized, interacted and competed for space within the same root system. Because mycorrhizas constitute a significant sink (30%) for the host's net primary productivity (Finlay and Söderström 1992), it follows that a high fungal load and associated demand for photosynthates likely resulted in carbon depletion from and reduced growth in the host plant (Nylund and Wallander 1989; Lodge and Wentworth 1990). Thus, simultaneous Glomalean–EM associations create a negative impact in the oak plant. Since 1-year-old field seedlings demonstrated a similarly high Glomalean and EM fungal load, it is possible that coexistent mycorrhizal types constitute a cost, rather than a benefit, during the establishment of young oaks and potentially impede their establishment. However, the progressive shift to predominantly EM colonization with increasing plant age suggests that mycorrhizal associations become beneficial over time, especially for the acquisition of P. Oaks are generally regarded as obligately EM (Trappe 1962) and could, therefore, be expected to benefit from an increasing abundance of these fungi within the roots (Smith and Read 1997).

The observed increase in EM colonization and concomitant decline in Glomalean colonization over time suggests that age-related changes result in the competitive exclusion of Glomalean fungi in *Q. agrifolia*, as they do in *Eucalyptus* (Chilvers et al. 1987) and *Populus* (Lodge and Wentworth 1990). A number of mechanisms have been proposed to explain this shift (detailed in Chen et al. 2000). For example, the susceptibility of roots to colonization by AM fungi may decline with host age (Chen et al. 2000). In addition, suberization of the root or the development of the EM mantle may physically constrain Glomalean colonization to new root tips (Chilvers et al. 1987). Alternatively, molecular recognition and signaling molecules at the fungus–root interface may act to suppress colonization (Gianinazzi-Pearson 1996). Apart from these mechanisms, our root colonization data imply that carbon limitation also controls succession. Björkman (1942) and others (Jasper et al. 1979; Chilvers et al. 1987; Lodge and Wentworth 1990) have suggested that soluble carbohydrate supply to the roots selectively controls mycorrhizal colonization. Although AM fungi are rapid colonizers of individual roots and early recipients of carbon, the gradual increase in the abundance of EM root tips over time possibly constitutes a more powerful sink for carbon than AM fungi localized within root segments (Lapeyrie and Chilvers 1985). Because older EM roots (2-year-old), as well as new root tips, also comprise a significant carbon sink (Al Abras et al. 1988), domination of the carbon pool by EM fungi might only be expected to increase with host age.

Based on this and previous studies of dual associations, there appears to be a limit on the number of mycorrhizas or symbionts that may be sustained within a host's root system. One or two mycorrhizal types appear to be the threshold in a suite of plant families (e.g., Fagaceae, Myrtaceae, Betulaceae, Pinaceae). The three-way interactions between tropical leguminous tree species, *Rhizobium* and mycorrhizal fungi are also instructive because they similarly demonstrate the presence of one or two symbionts within a root system. Such combinations include EM and AM, EM and *Rhizobium*, AM and *Rhizobium*, or *Rhizobium* alone (Högberg 1982; Newbery et al. 1988; Frioni et al. 1999; Moyersoen and Fitter 1999), and *Frankia* and AM in *Casuarina* (Reddell et al. 1986). Because similar patterns occur among a diversity of plant taxa and ecosystems, it is possible that carbon limitation represents a more general mechanism to limit the number

of symbionts within a particular root system in order to balance the cost:benefit relationship of symbiont to host.

Finally, the responses of oaks to AM fungi alone yield clues about the patterns of oak establishment in natural systems and the fate of woodlands in ecosystems currently undergoing conversion to Mediterranean annual grasslands. In a manner comparable to *Eucalyptus* (Chilvers et al. 1987) and *Pseudotsuga* (Smith et al. 1998), coast live oak seedlings were responsive to AM as well as EM inocula, suggesting that this host species is receptive to a wide range of fungi and will host either type of mycorrhiza, depending on the spatial heterogeneity in fungal inoculum (Chilvers et al. 1987; Brundrett and Abbott 1995). For example, when EM inoculum levels are high, oak seedlings show strong colonization by EM fungi. However, if EM inoculum levels are low or absent, oaks will readily host, and benefit from, Glomalean fungi based on their high inoculum potential. It follows that edaphic constraints (Lodge 1989; Bever 1994; Moyersoen and Fitter 1999; Van der Heijden et al. 1999) most likely have a greater control over oak establishment in grasslands than simply the type of mycorrhiza present.

The concordance between experimental and descriptive components in this study support a causal relationship between mycorrhizal type and host plant productivity, and a possible role for both Glomalean and ectomycorrhizas in maintaining or initiating the spatial and temporal structure of oak woodlands, because differences in mycorrhizal colonization patterns altered the cost:benefit relationship of mycorrhizas to the host plant. Such integration of mycorrhizal functioning into the coast live oak community further supports the paradigm of plant–mycorrhiza interactions as regulators of the plant community (Read 1991; Trappe and Luoma 1992).

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