Mycorrhiza (1994) 5:45–51

ORIGINAL PAPER

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Vesicular-arbuscular mycorrhizal inoculum potential affects the growth of *Stryphnodendron microstachyum* seedlings in a Costa Rican human tropical lowland

Abstract This study used a plant bioassay to investigate the vesicular-arbuscular mycorrhizal (VAM) inoculum potential of soil from three vegetation types (fern, secondary forest, and grass) in an abandoned pasture in the tropical humid lowlands at La Selva, in northeastern Costa Rica. Growth, measured as seedling height, number of leaves, and total (above- and below-ground) biomass, of *Stryphnodendron microstachyum* Poepp. et Endl. (Synon. *S. excelsum* Harms) seedlings was significantly lower when grown in soil inoculum from the fern areas than in soil inoculum from the forest and grass areas. However, *S. microstachyum* seedlings grown in the fern inoculum had significantly greater VAM colonization than seedlings grown in the forest and grass inoculum. In addition, roots collected from a dominant plant species from each of the three vegetation types showed that the fern (*Nephrolepsis biserrata*) had significantly greater mycorrhizal colonization than the tree (*Pentaclethra macroloba* (Willd.) Kuntze or the grass (*Brachiaria* spp.). The results of this study suggest that differences in mycorrhizal inoculum potential among vegetation types and its effects on seedling growth may have important implications for the restoration and management of degraded lands.

Key words Inoculum potential · Ecosystem restoration · *Stryhphnodendron microstachyum* Vesicular-arbuscular mycorrhizae

Introduction

Vesicular-arbuscular (VA) mycorrhizae play an important role in nutrient cycling, in particular, by facilitating plant uptake of phosphorus (Hayman 1983; Bolan 1991). The close link between nutrient cycling and ecological succession has stimulated interest in the potential importance of VA mycorrhizae in ecosystem restoration and in efforts to influence successional pathways.

Plant species from different successional communities exhibit varying degrees of dependency on VA mycorrhizae (Gange et al. 1990) and the capacity to regulate mycorrhizal colonization of their roots (Ratnayake et al. 1978; Koide and Li 1990). Mycorrhizal species composition and abundance may also change as succession proceeds (Hayman 1983; Hayman and Tavares 1985; Högberg and Piearce 1986). Furthermore, disturbance has been shown to affect the composition and function of mycorrhizal populations in the soil environment (Moorman and Reeves 1979; Hafeel and Gunatilleke 1988; Evans and Miller 1990; Fairchild and Miller 1990; Cuenca and Lovera 1991). These observations suggest that VA mycorrhizae-plant interactions may have an important role in influencing successional processes (Janos 1980a, 1985; Allen and Allen 1988; Allen et al. 1989; Gange et al. 1990; Perry and Amaranthus 1990).

VA mycorrhizal inoculation studies have shown that early mycorrhizal colonization may provide a competitive advantage for plant establishment and growth in the field (Reeves et al. 1979; Clarke and Mosse 1981; Koske and Polson 1984; Sieverding 1989). Several workers have demonstrated positive effects of VA mycorrhizal inoculation in the restoration of degraded lands in temperate regions (Reeves et al. 1979; Koske and Polson 1984; Perry and Amaranthus 1990; Sylvia 1990). Knowledge about the role of VA mycorrhizae in influencing ecosystem response to disturbance and successional pathways can provide important information for restoring and managing tropical degraded lands.

Assessment of mycorrhizal inoculum potential, defined here as the capacity of mycorrhizal propagules in the soil to colonize plant roots, provides a means to investigate the role of mycorrhizae in ecosystem processes across different habitats or microsites. Differences in mycorrhizal inoculum potential across vegetation

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types is hypothesized to affect the establishment and growth of plants and, consequently, to have implications for the restoration and management of those areas.

A bioassay was used to investigate the mycorrhizal inoculum potential of soil (and fine roots) collected from three successional vegetation types (fern, secondary forest, and grass) and its effects on seedling growth. The experiment was conducted in a shade house under controlled conditions in order to minimize potentially confounding effects of abiotic factors. *Stryphnodendron microstachyum* Poepp. et Endl. (Synon. *S. excelsum* Harms; "vainillo"), a leguminous, nitrogen-fixing tree species native to the region and characterized as an obligate mycotroph (Janos 1980b), was used as the test plant. *S. microstachyum* has soil-ameliorating properties (Montagnini and Sancho 1990) and exhibits relatively fast growth (Espinoza and Butterfield 1989), suggesting that it is a suitable species for restoring degraded tropical areas.

Materials and methods

Site description

The study was conducted at the La Selva Biological Research Station of the Organization for Tropical Studies in northeastern Costa Rica, located at 10°26′N, 86°59′W and at 50 m mean elevation. The mean annual temperature is 24° C. Mean annual rainfall is approximately 4000 mm, with a maximum in July and a minimum in March (La Selva weather reports). The soils are derived from alluvially deposited volcanic materials (Fluventic Dystropepts), and are deep, well drained, and stone free. Soils have low to medium organic matter content, moderately heavy texture, and are generally acid and infertile (Sancho and Mata 1987).

The 10-ha study site had been converted from forest to grassland in the 1950s, and was grazed until 1980, after which it was left to regenerate naturally (Pierce 1992). Within the regeneration site, the predominant vegetation type was grass, interspersed with patches of fern and approximately 20-year-old secondary forest. The dominant species in the fern vegetation were *Hypolepsis repens* and *Nephrolepsis biserrata,* with few other plant species present. The grass vegetation comprised both native species (*Paspalum fasciculatum,* and *Cynodon*) and introduced species (*Brachiaria, Melinis minutiflora, Panicum maximum*). The dominant secondary forest species was *Pentachlethra macroloba* (Willd.) Kuntze, with some *Piper culebranum, Psidium guajava,* and species of the Melastomataceae family, with ferns and tree seedlings in the understory.

Soil analysis

The soils and VA mycorrhizal propagule abundance within the study site were characterized by establishing four 200- to 250-m transects. Along each transect, a sampling area representing each of the three dominant vegetation types (fern, secondary forest, and grass) was selected (4 transects × 3 vegetation types = 12 sampling areas). At each sampling area, five soil samples were collected with a trowel from the surface horizon, to an approximate depth of 15 cm in March 1991. Sampling was conducted by taking one sample from an arbitrarily chosen center point of the sampling area, and four additional samples approximately 7 m from the center in each of the cardinal directions. Soils were air dried and passed through a 2-mm sieve prior to analysis. Soils were analyzed for phosphorus on soil extracts prepared by mixing 4 g of soil with 20 ml of Mehlich's solution and analyzed on a Milton Roy Spectronic-501 spectrophotometer (Anderson and Ingram 1989). Total carbon and total nitrogen content were determined by dry combustion using a LECO CHN-600 elemental analyzer. The pH was measured on 1:2.5 mixtures of soil:deionized water with an Orion 701A digital analyzer. Exchangeable cation concentrations (Mg, Ca, K, and Al) were determined on the Mehlich extracts using a Thermo Jarrell Ash AtomScan-25 Inductively Coupled Plasma Spectrophotometer.

Mycorrhizal analysis

From each sampling area, entire root systems of five plants were excavated in March 1991 from the dominant plant species within each vegetation type: *Nephrolepsis biserrata* (fern), *Pentaclethra macroloba* (secondary forest) and *Brachiaria* spp. (grass). The roots were cleared with potassium hydroxide and hydrogen peroxide and stained with 0.05% trypan blue in lactoglycerol solution (Kormanik and McGraw 1982). Roots were analyzed for percent VA mycorrhizal colonization using the ±slide method (Giovannetti and Mosse 1980), in which 10 1-cm root segments were randomly selected from each root sample, and VA mycorrhizal colonization expressed as the percent of root segments colonized for each root sample. The average percent colonization of the five root samples from each sampling area was used for subsequent analyses.

Mycorrhizal spores in the soil were quantified using a wet-sieving technique (Gerdemann and Nicolson 1963) modified with centrifugation. Four soil samples approximately 15 cm deep were collected and pooled from each of the sampling areas along the four transects to produce four replicate 100-g (air dry weight) samples from each vegetation type. Each soil sample was agitated with a strong stream of water in a beaker, allowed to settle for 45 s, and decanted through three sieves (425 μm, 106 μm, and 45 μm). After repeating this procedure three times, the 45–106 μm and 106–425 μm fractions were combined and centrifuged with water for 3 min at 3000 rpm, followed by centrifugation with a 40% sucrose solution for 1 min at 3000 rpm. The supernatant (containing suspended spores) was poured through the 45-μm sieve and the spores washed thoroughly to remove the sucrose solution. The spores from each soil sample were placed into separate petri dishes, and the dishes coded to allow for blind scoring of the samples. The total number of VA mycorrhizal spores in each soil sample was determined under a dissecting microscope. The average number of spores of the four soil samples from each sampling area was used for subsequent analyses.

Inoculum potential

In order to assess the inoculum potential of the three dominant vegetation types and its influence on plant growth, VA mycorrhizal root colonization, seedling height and number of leaves, and biomass were compared over time for *S. microstachyum* seedlings grown in: (1) nonfumigated soil, which included fine root fragments, and (2) fumigated soil (described below), which included fine root fragments. The soil inoculum was collected to a depth of approximately 15 cm from sampling areas outside the experimental regeneration site supporting each of the three vegetation types in June 1991. The soil and fine roots were mixed thoroughly by cutting roots into small pieces and mixing by hand. Soils for the fumigated group were treated with methyl bromide gas with 2% chloropicrin at a concentration of 1 kg gas/45 l soil. Methyl bromide gas has been used effectively to eliminate viable mycorrhizal fungi (Janos 1980b). Transplanting to the nonfumigated soils occurred within 1 day after the soil and roots were collected from the field. Fumigated soils were allowed to stand at least 2 days before transplanting occurred to ensure complete volatilization of the gas.

Table 1 The vesicular-arbuscular (VA), mycorrhizal colonization (% VAM) of *Stryphnodendron microstachyum* seedlings grown in fern, forest, and grass soil inocula, the VA mycorrhizal colonization of dominant plant species collected from the fern (*N. biserrata*), forest (*P. macroloba*), and grass (*Brachiaria* spp.) vegetation, and the number of spores in soil collected from beneath these vegetation types. Standard deviation and sample size shown in parentheses. Matching lowercase letters indicate no significant difference at $P \leq 0.05$ across each row

	Fern	Forest	Grass
% VAM in soil inoculum	10.56a (11.6, 18)	0.20b (0.3, 18)	0.18b (0.5, 18)
% VAM of dominant plant species	*Nephrolepsis biserrata*	*Pentaclethra macroloba*	*Brachiaria* spp.
	0.42 a (0.1, 4)	0.10b (0.1, 4)	0.05b (0.1, 4)
Spores/100 g soil	25.5a (10.0, 4)	16.25a (6.1, 4)	10.25a (10.0, 4)

S. microstachyum seedlings not colonized by VA mycorrhizae were obtained by propagating seedlings from seed in a fumigated 50:50 sand:soil mixture in an enclosed shade house. At the age of 6 weeks, *S. microstachyum* seedlings of uniform size (approximately 7–9 cm in height, with 3–5 leaves) were transplanted to plastic cups (approximately 0.35 l) containing either nonfumigated or fumigated soil from each of the three vegetation types as described above. Each soil group contained 30 replicates. The fumigated soils received 100 ml of a microbial suspension prepared by soaking soil and roots from each vegetation type overnight in water and filtering the solution through a 45-μm sieve the following day. The filtrate served to replace soil microorganisms eliminated by fumigation (Janos 1980b).

Growth analysis

Seedling height and the number of leaves per seedling were recorded prior to each harvest. Three harvests of 10 seedlings from each soil group were conducted 49 days, 103 days, and 160 days after the transplant date. Visual observations of the roots verified that there had been no restriction of root growth. The roots were immediately cut off, rinsed with water, and preserved in individual bottles with FAA solution (90 ml 50% ethanol, 5 ml acetic acid, and 5 ml formalin). The stems and leaves were dried for 48 h at 70° C and weighed.

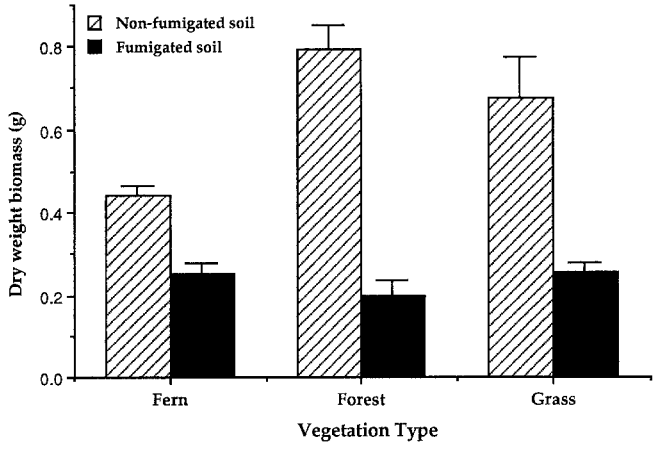

Fig. 1 Total biomass (above and below ground) of *S. microstachyum* seedlings grown in nonfumigated and fumigated soil inoculum collected from beneath fern, forest, and grass vegetation, 160 days after transplanting. The sample size for each treatment group was 6–10 seedlings. Significant differences between treatment groups are indicated by standard error bars

Root colonization

Root colonization of the entire root mass of harvested plants was assessed using the grid-line intersect technique (Giovannetti and Mosse 1980). After clearing and staining the roots as described above, the roots were cut into small pieces and spread evenly in a petri dish with a grid of 0.5-inch squares marked on the bottom. Petri dishes were coded to allow for blind scoring of the samples. The presence of a vesicle with a hyphal attachment was used as the criterion for VA mycorrhizal colonization. The percent of the total number of root-line intersections that were mycorrhizal was determined for each seedling using a MicroZoom II Microscope (Cambridge Instruments) at ×30–1000 magnification. Roots of seedlings grown in the fumigated soils were also scanned under the microscope to verify the absence of mycorrhizal colonization. Two seedlings from the fumigated soils were contaminated with mycorrhizae and were not included in the analyses. After mycorrhizal colonization was scored, the roots were rinsed with distilled water on Whatman No. 1 filter paper, dried for 4 days at 70° C, and weighed.

Statistics

One-way analysis of variance (ANOVA) was performed using SYSTAT to determine significant differences at the 95% level (SYSTAT 1989, Evanston, Ill.). Data for percent VA mycorrhizal colonization of *S. microstachyum* seedlings and of the dominant plant species collected from the field were subjected to arcsin transformations. Data on the number of spores in the soil were subjected to square-root transformations (Sokal and Rohlf 1981). Differences between treatments were confirmed using a Tukey test.

Results

S. microstachyum seedlings grown in the fern soil had significantly greater($P<0.01$) percent VA mycorrhizal colonization than seedlings grown in the forest or grass soils (Table 1). Similarly, roots collected from the dominant plant species within each vegetation type in the field indicated that fern roots supported significantly greater mycorrhizal colonization ($P<0.01$) than either the secondary forest or grass roots. In contrast, the numbers of spores present in the soils collected from beneath the fern, secondary forest, and grass vegetation were not significantly different ($P>0.05$).

The total biomass (above- and below-ground) of *S. microstachyum* seedlings grown in the nonfumigated forest and grass soils was significantly greater ($P<0.05$)

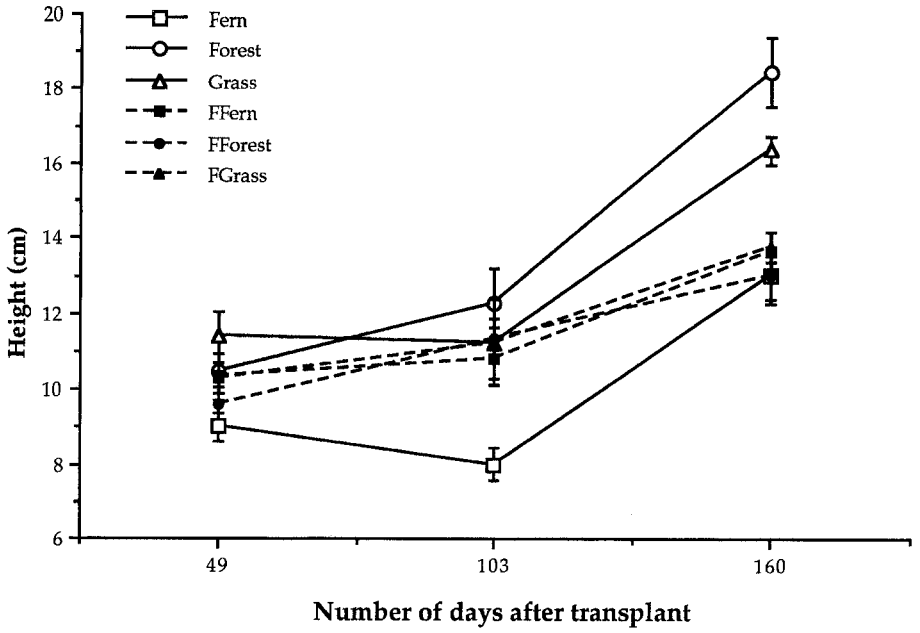

Fig. 2 Height of *S. microstachyum* seedlings grown in nonfumigated and fumigated soils collected from beneath fern, forest, and grass vegetation 49, 103, and 160 days after transplanting. The sample size for each treatment group was 6–10 seedlings. Significant differences between treatment groups are indicated by standard error bars. Fern, Forest, and Grass, indicate nonfumigated soil inocula; FFern, FForest, and FGrass, indicate fumigated soil inocula

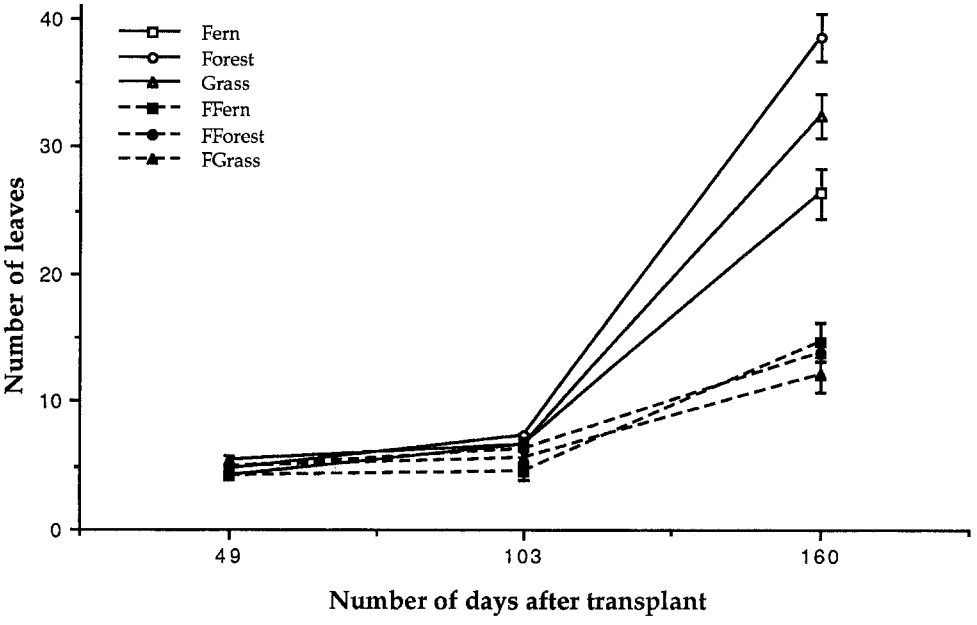

Fig. 3 Number of leaves of *S. microstachyum* seedlings grown in nonfumigated and fumigated soil inoculum collected from beneath fern, forest, and grass vegetation 49, 103, and 160 days after transplanting. The sample size for each treatment group was 6–10 seedlings. Significant differences between treatment groups are indicated by standard error bars. Fern, Forest, and Grass, indicate nonfumigated soil inocula; FFern, FForest, and FGrass, indicate fumigated soil inocula

than that of seedlings grown in the fumigated fern soil for all three harvests (Fig. 1). There was no significant difference in the biomass of seedlings grown in the nonfumigated forest and grass soils. The total biomass of *S. microstachyum* seedlings grown in the nonfumigated forest and grass soils was significantly greater ($P<0.05$) than the respective seedlings grown in the fumigated soils for all three harvests. Seedlings grown in the nonfumigated fern soil had significantly greater ($P<0.05$) biomass than seedlings grown in the fumigated fern soil in the second and third harvests. There was no significant difference in the biomass of seedlings grown in the fumigated soils among the three vegetation types. Root:shoot ratios, leaf weight ratios and root weight ratios reflected the same trends as the biomass data, and are not presented here.

The height of seedlings grown in the nonfumigated fern soil was significantly ($P<0.05$) than the height of seedlings grown in the nonfumigated forest and grass soils in the second and third harvests (Fig. 2). The height of seedlings grown in the fumigated fern soil was significantly lower than the height of seedlings grown in the nonfumigated fern soil for the second harvest, but by the third harvest there was no significant difference. Seedlings grown in the nonfumigated fern soils had significantly fewer leaves than seedlings grown in the nonfumigated forest soil (third harvest) or nonfumigated grass soil (first harvest; Fig. 3). Seedlings grown in the fumigated soils from all three vegetation types had significantly fewer leaves than seedlings grown in the nonfumigated soils by the third harvest.

Table 2 Nutrient concentrations in soils collected from beneath fern, secondary forest, and grass vegetation within the regeneration site. The sample size for all analyses was 20. Matching lower case letters indicate no significant difference at $P \leq 0.05$

	Nutrient							pH
	C (%)	N (%)	P (mg/kg)	Ca (cmol/kg)	Mg (cmol/kg)	K (cmol/kg)	Al (cmol/kg)	
Fern	4.4a	0.50a	2.5a	0.41a	0.32a	0.19a	5.8a	46b
Forest	4.4a	0.47a	1.3a	0.38a	0.42a	0.19a	5.8a	4.7ab
Grass	4.5	0.48a	1.9a	0.56a	0.66b	0.28a	5.8a	4.8a

Chemical analysis of the soil samples indicated that the concentrations of exchangeable P, Ca, and K and total N in the fern, secondary forest, and grass soils were not significantly different ($P > 0.05$). Only exchangeable Mg in the grass soils was significantly higher ($P < 0.05$) than the forest and fern soils. The pH for the fern soils was significantly lower than the grass soil ($P < 0.05$), but was not significantly different ($P > 0.05$) from the secondary forest soil (Table 2).

Discussion

Mycorrhizal propagule abundance, mycorrhizal inoculum potential, and growth of the test plant *S. microstachyum* were found to vary among soils from the three dominant vegetation types within the regeneration site. The significantly higher VA mycorrhizal root colonization of *S. microstachyum* seedlings grown in the fern soil as compared to seedlings grown in the forest and grass soils suggests that the fern soil has a greater mycorrhizal inoculum potential. The significantly lower biomass of seedlings grown in the fumigated soil as compared to the nonfumigated soils, and the lack of significant difference in seedling biomass among the three vegetation types for the fumigated soils, suggests that growth differences may be related to mycorrhizal interactions. However, the consistently poorer growth performance of seedlings grown in the fern soil as compared to seedlings grown in the grass and forest soils suggests that the mycorrhizae-plant associations formed in the fern soil may be less effective at enhancing plant growth than those which formed in the forest or grass soils.

The occurrence of VA mycorrhizae in ferns has been extensively documented (Cooper 1976; Iqbal et al. 1980; Haefeel and Guantilleke 1988; Gemma et al. 1992). The relatively high inoculum potential of fern soil may be a result of the dense rhizomatous mat typical of fern vegetation, as the greater surface area for contact between the seedling and fern roots could facilitate the transfer of VA mycorrhizal colonization. Hafeel and Gunatilleke (1988) hypothesized that the thick root mat of ferns in a *Pinus* spp. plantation in Sri Lanka increased the degree of VA mycorrhizal colonization and spore production as compared with the natural forest. The fern soil inoculum potential may be further accentuated by the greater mycorrhizal propagule abundance in the form of colonized root fragments observed in the fern soil. In addition, the slow rate of root turnover in ferns may have contributed to their high rates of mycorrhizal colonization by allowing a build up of colonization to occur (D. P. Janos, personal communication).

The relatively low inoculum potential of the grass and forest soils may be related to the mycorrhizal dependency of species within these vegetation types. Grasses are commonly facultative mycotrophs (Miller 1987), and are hypothesized to be the most independent of mycotrophic plants (Baylis 1975), and thus to tolerate low fertility in spite of low mycorrhizal colonization (Janos 1980a). Mycorrhizal dependency of obligate plant species is hypothesized to decrease after maturity (Janos 1980a), possibly accounting for the lower mycorrhizal colonization observed in the roots of the secondary forest vegetation.

The inverse relationship between inoculum potential and *S. microstachyum* seedling growth may reflect differences in the infectivity and effectivity of mycorrhizal species among the fern, forest, and grass soils. VA mycorrhizal species composition has been hypothesized to vary across habitats and microsites (Sieverding 1989; Janos 1992). Different mycorrhizal species may also vary in their capacity to colonize plant roots (infectivity) and to enhance phosphorus uptake or provide other benefits to the host plant (effectivity; Hayman 1983). Mycorrhizal species in soils supporting fern vegetation may be more effective at colonizing plant roots, while less effective at enhancing phosphorus uptake, resulting in a lower capacity of fern soil inoculum to stimulate seedling growth in the initial stages of plant development. In addition, specificity between the mycorrhizal species and *S. microstachyum* may have contributed to the differential seedling growth response if mycorrhizal species in the fern vegetation established more beneficial associations with *S. microstachyum* than mycorrhizal species in the grass and forest vegetation (Hayman 1983; Sieverding 1989).

Another possible explanation for the different growth rates of seedlings grown in the fern, forest, and grass soils is the ability of *S. microstachyum* seedlings to regulate mycorrhizal colonization of its roots. *S. excelsum* is characterized as an obligate mycotroph (Janos 1980a). Obligate mycotrophs are hypothesized to have

a poor capacity to regulate mycorrhizal colonization of their roots (Janos 1985). If *S. microstachyum* is adapted to relatively low VA mycorrhizal inoculum conditions in its natural habitat, it may be less able to regulate colonization of its roots, which may allow mycorrhizal colonization to exceed optimum levels for plant growth under the conditions of high inoculum potential present in the fern soils.

A final factor which may affect seedling growth in the fern soil inoculum is allelopathic interactions, a phenomenon which has been documented for several fern species and geographic regions (Bohm and Tryon 1967; Munther and Fairbrothers 1980; Rice 1984). Phytotoxins leached from dead, standing bracken fronds and transferred by the soil medium was found to cause herb suppression (Gliessman and Muller 1972, 1978). Allelopathic chemicals have been shown to influence soil microorganisms (Rovira 1969), and both ecto- and endo-mycorrhizae appear to be sensitive to allelochemicals in litter and soil organic material (Perry and Choquette 1987). However, *Pteridium aquilinum* (bracken fern) did not affect the rate or degree of mycorrhizal colonization nor the foliar phosphorus concentration of black cherry seedlings (Horsely 1992). If phytotoxins are produced by the fern vegetation, they may influence VA mycorrhizal colonization and subsequent plant growth, possibly through effects on plant regulatory mechanisms as determined by membrane permeability and root exudation.

Although rapid VA mycorrhizal colonization of roots may be expected to provide a competitive advantage to seedlings, the degree of mycorrhizal colonization is not necessarily positively correlated with seedling growth (Hayman 1983; Saif 1987). It has been suggested that a growth depression may occur if the costs of mycorrhizal colonization to the host plant outweigh the benefits provided by the mycorrhizal symbiont (Snellgrove et al. 1982; Bethlenfalvay et al. 1983; Koide and Elliott 1989). The mycorrhizal associations of seedlings grown in the fern soils may have posed a greater photosynthetic cost to the plant as compared with the mycorrhizal associations of seedlings grown in the forest or grass soils, possibly due to the high infectivity and low effectivity of VA mycorrhizal species, the inability of *S. microstachyum* seedlings to maintain VA mycorrhizal colonization of its roots within the optimum range for plant growth, or the presence of allelopathic interactions. However, the relatively short duration of this experiment precludes determination of whether the *S. microstachyum* seedlings may eventually benefit from the symbiosis once sufficient photosynthetic capacity is established to support the higher levels of colonization.

This study suggests that it may be important to consider differences in the VA mycorrhizal inoculum potential across vegetation types, and its influence on plant establishment, growth, and competitive interactions, in designing restoration and management strategies for degraded areas. In sites where inoculum potential is low, reforestation efforts may be facilitated by inoculating seedlings with VA mycorrhizae prior to transplanting to the field. However, for certain plant species, such as *S. microstachyum,* inoculation does not appear to be necessary, and may even reduce plant growth rates during the early stages of establishment. Excessively high inoculum potential in some successional communities may require other measures to ensure successful initial establishment and growth of transplanted seedlings, particularly if the VA mycorrhizae species are relatively ineffective, if plant species transplanted to the site are adapted to conditions of low mycorrhizal inoculum potential, or if phytotoxins interfere with the establishment of plant-mycorrhizal associations.

Acknowledgements Funding for this research was provided by a grant for ecological research from the Andrew W. Mellon Foundation to the Yale University School of Forestry and Environmental Studies. The authors would like to thank David Janos for his assistance during the initial design of the project and review of the final manuscript, and Kristiina Vogt for valuable discussions in synthesizing the results of the study and review of the final manuscript. The authors also thank Graeme Berlyn, Janine Bloomfield, James Bryan, Peter Palmiotto, and Whendee Silver-Beissinger for their careful review of the manuscript and helpful comments, and Dena Rebozo, Martha Rosemayer, Kathy Richardson, Ricardo Russo and Dwight Baker for their technical assistance in the field and lab.

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