HETEROGENEITY IN INOCULUM POTENTIAL AND EFFECTIVENESS OF ARBUSCULAR MYCORRHIZAL FUNGI

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Abstract. Arbuscular mycorrhizae are symbiotic associations among glomalean fungi and plant roots that often lead to enhanced water and nutrient uptake and plant growth. We describe experiments to test whether inoculum potential of arbuscular mycorrhizal (AM) fungal communities varies spatially within a broadleaf temperate forest, and also whether there is variability in the effectiveness of AM fungal communities in enhancing seedling growth. Inoculum potential of arbuscular mycorrhizal fungi in a temperate broad-leaved forest did not vary significantly among sites. Inoculum potential, measured as the extent to which the roots of red maple seedlings that had been germinated on sterile sand and then transplanted into the forest, were colonized by AM fungi, was similar in floodplain and higher elevation sites. It was as similar under ectomycorrhizal oaks as it was under red maples and other AM tree species. It was also similar among sites with deciduous understory shrubs with arbuscular mycorrhizae (spicebush, *Lindera benzoin*) and those with evergreen vegetation with ericoid mycorrhizae (mountain laurel, *Kalmia latifolia*). Where spicebush was the dominant understory shrub, inoculum potential was greater under gaps in the canopy than within the understory. Survivorship of transplanted red maple seedlings varied significantly over sites but was not strongly correlated with measures of inoculum potential.

In a greenhouse growth experiment, arbuscular mycorrhizal fungal communities obtained from tree roots from the forest had different effects on plant growth. Seedlings inoculated with roots of red maple had twice the leaf area after 10 wk of growth compared to the AM community obtained from roots of southern red oaks. Thus, although there appears to be little heterogeneity in inoculum potential in the forest, there are differences in the effectiveness of different inocula. These effects have the potential to affect tree species diversity in forests by modifying patterns of seedling recruitment.

Key words: Acer rubrum; *arbuscular mycorrhizae; inoculum potential; Maryland, USA;* Quercus falcata; *temperate forest; treefall gaps.*

Introduction

The effect of mycorrhizae, the symbiotic association among plant roots and fungi, on plant performance has been proposed to have far reaching ecological consequences, from increasing productivity of ecosystems to enhancing plant diversity (Grime et al. 1987, Francis and Read 1994, van der Heijden et al. 1998*a, b*). Arbuscular mycorrhizae (AM) are formed from the association of fungi from the order Glomales and most plant taxa (Allen 1991). In the functioning of mycorrhizae, plants are provided with phosphorus and a range of other benefits (Newsham et al. 1995) in exchange for carbon required by the fungus for growth and sporulation. Arbuscular mycorrhizae usually improve plant growth, although the level of growth enhancement can depend of the fungal community–host combination (Simmons and Pope 1987, Johnson et al. 1997, van der Heidjen et al. 1998*a, b,* Kiers et al. 2000), the prevailing environmental conditions (Johnson et al. 1997),

and even on the isolate of a particular fungal species (Morton and Bentivenga 1994).

In forests, seedling recruitment is a vital stage in the determination of forest structure and diversity (Ribbens et al. 1994, Clark et al. 1998). Seeds are dispersed without their mycorrhizal symbiont, and acquire a fungal symbiont where and when they germinate and develop roots. Colonization of seedling roots by AM fungi can enhance growth rates of seedlings (Brundrett 1991) and survival (Gange et al. 1993, Stahl et al. 1998, Kiers et al. 2000). Spatial and temporal variation in the inoculum potential of soils, defined as the potential for the growth of the fungi at the surface of its host (Garrett 1956), may therefore give rise to microsites that are more or less favorable for seedling growth and survival. Variation in the effectiveness of the AM fungal community in enhancing plant growth at different microsites could also influence the growth and survival of seedlings, independently of effects on inoculum potential (Johnson et al. 1997, van der Heijden et al. 1998*b,* Graham and Abbott 2000, Kiers et al. 2000). Heterogeneity in inoculum potential, or in the effectiveness of AM communities, could enhance the di-

versity of forests by increasing habitat heterogeneity (Tilman 1982) or through feedback processes (Bever et al. 1997). Our aim here is to test whether (a) the inoculum potential or (b) the effectiveness of AM communities are heterogeneous within a temperate broadleaf forest landscape, and therefore to determine whether variability in AM fungal communities has the capacity to affect forest diversity.

Factors leading to heterogeneity in inoculum potential in forests include all factors that influence the distribution of live and dead roots and other organic matter, and also any factors that influence the community composition of the fungi, fungal sporulation, and hyphal growth. Thus, in forests inoculum potential could be influenced by a bewildering array of soil and host plant characteristics. Heterogeneity in inoculum potential in soils has been observed at both small (from adjacent cores), and larger scales (among transects, Brundrett and Abbott 1995), over different soil types (Porter 1979, Klironomos et al. 1993, Klironomos 1995), gradients in disturbance (Koide and Mooney 1987, Alexander et al. 1992, Fischer et al. 1994, Boerner et al. 1996, Brundrett et al. 1996b), and vegetation types (Koide and Mooney 1987, Asbjornsen and Montagnini 1994, Brundrett et al. 1996a). To test whether heterogeneity in inoculum potential varies predictably with host tree or soil factors within a temperate broadleaved forest we used a bioassay. Seedlings of red maple (*Acer rubrum* L.), a tree species that commonly occurs at our study site (Parker and Tibbs, *in press*) and is widely dispersed (Clinton et al. 1994, Abrams 1998), were germinated in sterile soil without AM fungi. They were then transplanted into the field for 2 wk (Brundrett and Abbot 1994), after which colonization of their roots by AM fungi was assessed.

In the first experiment inoculum potential was compared between lowland, floodplain soils, and soils from higher elevations. Low and higher elevation sites have markedly different soil characteristics, with lowland soils having higher fertility, levels of organic matter, and water availability, factors that could potentially influence the AM fungal community and the inoculum potential (Abbott and Robson 1991, Brundrett 1991). Because soil biogeochemical characteristics, including pH, level of organic matter, and mineral element concentrations are also influenced by the dominant tree species (Beatty 1984, Boerner and Koslowsky 1989, Finzi et al. 1998a, b), we also tested whether inoculum potential varied depending on the host tree species dominating the soil patch.

Light levels are highly variable in forests. Increased light levels in canopy gaps formed by tree fall or other disturbances enhance plant photosynthetic and growth rates (Orwig and Abrams 1995), soil water content, root density, and soil nutrient concentrations (Denslow et al. 1998). The conditions in forest gaps therefore may lead to increases in inoculum potential. In a second experiment, inoculum potential was compared among canopy gaps and within the understory in forest patches, with the understory dominated by an evergreen species or with a deciduous species. In both experiments we tested whether inoculum potential was correlated with the effectiveness of the inocula in enhancing survivorship of bioassay seedlings.

Equivalent inoculum potential at any given site may not necessarily imply similar effectiveness of inocula in stimulating plant growth (Johnson et al. 1992, 1997, Asbjornsen and Montagnini 1994, Graham and Abbott 2000, Kiers et al. 2000). Therefore at the same time as our field-based tests of inoculum potential, we also conducted a greenhouse experiment to test for differences in effectiveness of two AM fungal communities obtained from the forest.

MATERIALS AND METHODS

Assessment of inoculum potential in the forest

Seeds of red maple were collected from five maternal trees from the Smithsonian Environmental Research Center (SERC) property in Edgewater, Maryland, USA (~10 km SSE of Annapolis, 38°53′ N, 76°33′ W). The forest is a mixed deciduous forest with an overstory dominated by tulip poplar (*Liriodendron tulipifera*). A detailed description of the forest and its phenology can be found in Parker and Tibbs, *in press*. Soils are sandy loams and classified within the order Ultisols. They are Aquic and Typic Hapludults (Kirby and Matthews 1973).

Sources of AM fungal inocula in soils include spores, dead root fragments and other colonized organic matter, and the hyphal network supported by living mycorrhizae (Brundrett 1991). Inoculum potential of soils has been estimated using a variety of measures. The simplest indirect method has been to count the number of propagules, usually spores, but the amount of hyphae and living mycorrhizae have also been measured. Often these indirect measures have not been well correlated with the formation of mycorrhizae (Abbott and Robson 1991, Brundrett 1991). Another more direct method uses a bioassay, where the colonization of the roots of ''bait'' plants by arbuscular mycorrhizal fungi is interpreted as a relative measure of inoculum potential (Moorman and Reeves 1979). Serial dilutions of soils have been used to estimate the number of infective propagules (Porter 1979, Adelman and Morton 1995). But more recently, to avoid excessive disturbance of soils, researchers have favored using bait plants sown onto soil cores obtained from the field and cultivated in a greenhouse (e.g., Brundrett and Abbott 1994, 1995). In these assays percentage colonization of bait plant roots is assessed after a given period of time under conditions that are usually optimized for bait plant growth (light, water, and nutrient levels controlled). Here we have used bioassays, but have planted bait plants directly into the field. Our bait plants were seedlings of red maple, a tree species that is common and

widespread at our study site (Parker and Tibbs, *in press*). We chose to transplant bait plants directly into the forest where conditions are variable and light levels are low, rather than assess inoculum potential in soil cores in the greenhouse under controlled conditions. Transplanting into the field exposes plants to natural drainage and climatic conditions, and to the presence of living roots, mycorrhizae, and undisturbed hyphal networks. In addition, soils on the SERC property have high clay and silt content, and preliminary tests of water infiltration into potted soil cores was very low, resulting in high seedling mortality. By transplanting bait seedlings into the field we provide an estimate of inoculum potential that is experienced by seedlings germinating on the forest floor under the prevailing environmental conditions. Colonization in the 2-wk period of the bioassay is likely to be by the aggressive AM fungi within the community (Graham and Abbott 2000), and not necessarily by the whole AM community present (Brundrett and Abbott 1994).

Red maple seedlings were germinated in small pots (''cone-tainers,'' Hummert International, Earth City, Missouri, USA) on soil that had been previously sterilized in an autoclave at 120°C for 1 h. Seedlings were grown on the sterile sand in the greenhouse until they had developed two leaves in addition to their cotyledons. These seedlings were the ''bait'' plants that were transplanted out into the forest in the experimental design described below.

Experiment 1. Effects of lowland and upland soils and adult species identity.—On 15 June 1998, seedlings of red maple ''bait'' plants were transplanted into the forest in (1) either upland sites or floodplain sites or (2) under the canopy of red maples that have arbuscular mycorrhizae (Schultz and Kormanik 1982, Brundrett and Kendrick 1987, Berliner and Torrey 1989) or under other species that were within 15 m of the red maple. In the upland sites, ''other'' species were grouped into two groups: (1) a mix of trees that are known to have arbuscular mycorrhizae (Schultz and Kormanik 1982, Simmons and Pope 1987, Berliner and Torrey 1989), including *Liriodendron tulipifera* L. (tulip poplar) and *Liquidambar styraciflua* L. (sweet gum), and (2) *Quercus falcata* Michx. (southern red oak). Oaks are ectomycorrhizal, and soil beneath oak crowns has reduced pH and lower concentrations of calcium and phosphorus compared to red maples and other AM tree species (Finzi et al. 1998*a, b*). In the floodplain habitat where oaks are less common, there was only one group of allospecifics consisting of *Fraxinus pennsylvanica* Marshall (green ash) and sweet gum. Eleven red maple seedlings were planted under the canopy of four adults of either con- or allospecifics. A total of 220 seedlings were transplanted.

Experiment 2. Effects of understory composition and canopy gaps.—Seedlings of red maple were transplanted on 31 July 1998 into the forest in sites dominated by the deciduous understory shrub *Lindera benzoin* (spicebush), which has arbuscular mycorrhizae, or in understory dominated by evergreen *Kalmia latafolia* (mountain laurel), which has ericoid mycorrhizae. In each of these forest types six canopy gaps with paired understory sites were selected. Gaps in the canopy were chosen if direct sunlight was illuminating the foliage of the understory shrubs at midday. Gaps were <15 m in diameter and were usually caused by a branch fall from the canopy rather than by tree fall. Eight seedlings of red maple were transplanted under the canopy gap and in the understory at each location, giving a total of 192 seedlings transplanted in this experiment.

After 2 wk all surviving seedlings were collected and the number of surviving seedlings was recorded. Two weeks was the time period chosen for the bioassay because it is sufficient time for preliminary colonization of roots (Brundrett and Abbott 1994). Colonization of roots by AM fungi has a trajectory where there is a near linear increase in colonization (Bethlenfalvay et al. 1982, Brundrett et al. 1985) to a plateau that is usually reached within 4–6 wk (Moorman and Reeves 1979, Bethlenfalvay et al. 1982, Brundrett et al. 1985, Torrisi et al. 1999, Graham and Abbott 2000). In a study where seedlings of leeks were transplanted under an established conspecific, similar to the approach we used here, there was abundant colonization of seedling roots within 1 wk (Brundrett et al. 1985). Plants that died within the first 2 d after transplanting were replaced. Roots of the collected seedlings were washed and stored in 70% ethanol before staining and mounting to assess percentage colonization by arbuscular mycorrhizal fungi. Roots were cleared and stained using the methods of Kormanik and McGraw (1982), but substituting methyl blue in 0.05% acidified glycerol for the phenol component. Approximately ten 1-cm sections of roots of each seedling were then mounted in polyvinyl alcohol. Percentage colonization of roots was assessed for ~100 fields of view for each sample at 100× magnification (see Carling and Brown 1982, Morton and Bentivenga 1994). Roots were scored as colonized by AM fungi based on the presence of structures within the roots (hyphae, arbuscules, or vesicles) and/or when extraradial hyphae were present with evidence of entry and/or exit points at the root surface. Colonization of roots by hyphae was the majority of colonization observed.

Experiment 3. Testing the effects of different inocula on seedling growth and mineral element concentrations.—Plants were inoculated with arbuscular mycorrhizae using two different inocula. Inocula were coarsely chopped roots and adhering soil obtained from the base of three adults of either red maple or southern red oaks. To collect roots for inocula we followed primary roots at the base of the tree to finer branching roots, which we then removed with a knife. Twenty-eight red maple seedlings that were germinated on sterilized sand were transplanted to D' pots (Hummert International) filled with sterilized soil (50:50 sieved forest soil and

sand sterilized in an autoclave at 120°C for 1 h) mixed with the chopped root inocula (10% of pot volume). Seven control plants for each of the red maple and oak inoculum treatments were inoculated with roots inocula, but after the roots had been sterilized in an autoclave. To reintroduce the soil microbial community to control plants (excluding the AM fungi), a filtrate obtained from the living roots, made by washing the roots in water and passing the solution through a 25-μm mesh filter to remove AM fungal spores, was applied to control plants.

Plants were grown in the glasshouse at SERC for 10 weeks under light levels similar to those in the forest understory during the summer. Maximum light levels during growth were 60 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (mean 30 $\mu mol \cdot m^{-2} \cdot s^{-1}$), temperatures ranged between 20 and 32°C and relative humidity varied between 55% and 90%. Plants were watered daily and their position in the glasshouse changed weekly.

During the experiment growth was measured weekly as the increase in leaf area using an allometric relationship established between leaf width and leaf area for the size range of leaves of the experimental plants: for leaves 0.5–3.5 cm wide, leaf area = −1.0218 + 2.1545[leaf width], $r^2 = 0.952$, $N = 87$ leaves. At the end of the experiment plants were harvested and separated into component parts. A small sample of root (~10 cm) was collected and placed in 70% alcohol for assessment of AM colonization. Plant parts were then dried in an oven at 60°C for 1 wk, after which they were weighed. Dry tissue was then analyzed for elemental concentrations using Inductively Coupled Plasma-Atomic Emission Spectroscopy (ICP) analysis at the Agricultural Analytical Services Laboratory of the University of Pennsylvania. Small samples of ground leaf tissue was also used for analysis of both $\delta^{13}C$ and $\delta^{15}N$ isotopic composition. Samples (0.5–0.8 mg dry mass) were weighed into tin boats and then combusted at 1020°C in a Carlo Erba NC 2500 Elemental Analyzer (CE Instruments, Milan, Italy) in a He stream in the presence of zero grade oxygen. N_2 and CO_2 were separated on a molecular sieve column prior to entering the Conflo II Interface on a DeltaPlusXL gas source isotope ratio mass spectrometer (Finnigan MAT, Bremen, Germany). Standard deviations for $\delta^{13}C$ for standard materials and homogenized samples were ±0.1/mL and, for $\delta^{15}N$, ±0.4/mL. Differences in fractionation of ^{13}C isotopes are correlated with variations in the ratio of the CO_2 concentration inside the leaf (C_i) to CO_2 outside the leaf (C_a) (Farquhar and Richards 1984). More-negative $\delta^{13}C$ values indicate a lower C_i/C_a ratio, and thus lower instantaneous water use efficiency during photosynthesis (i.e., water transpired/CO_2 fixed). Differences in $\delta^{15}N$ isotopic composition indicate plants are accessing different sources of nitrogen (Handley et al. 1993).

Relative growth rate (RGR) of plants was calculated as (ln[final dry mass] − ln[initial dry mass])/10 wk.

Net assimilation rate (NAR) was calculated as ([final dry mass − initial dry mass]/10 wk)/([final leaf area − initial leaf area]/[ln(final leaf area) − ln(initial leaf area)]). Initial leaf area was estimated using the allometric relationship between leaf width and area for each plant (see *Materials and methods: Experiment 3,* above). Initial dry mass was estimated for each plant using an allometric relationship established between leaf area and plant mass ([plant dry mass] = 0.0348 + 0.002913[leaf area], $r^2 = 0.64$, $N = 28$ plants). Average initial leaf area was 5.36 ± 0.39 cm^2 (mean ± 1 SE, $N = 28$ plants), and average initial dry mass was 0.050 ± 0.001 g, $N = 28$ plants). Leaf mass ratio (LMR) was calculated as leaf dry mass/final dry mass, leaf area ratio (LAR) as final leaf area/final dry mass, and specific leaf area (SLA) as final leaf area/leaf dry mass.

Data analysis

The influence of habitat (upland or floodplain), and the identity of the adult tree (conspecific, AM allospecific, or oak allospecific) under which seedlings were planted, on percentage colonization of root length of test seedlings was assessed by analysis of variance (ANOVA). Habitat and adult identity were fixed effects, and replicate adult tree was considered a random effect, nested within adult identity, in the model. Two analyses were performed because of the unbalanced design (i.e., there was only one group of allospecifics in the floodplain habitat). In the first analysis the data for upland ''oaks'' were omitted, and thus the effect of adult identity (allospecifics or conspecifics) could be compared in both habitats. In the second analysis the floodplain data were omitted and thus the effects of two groups of allospecifics (oaks and other AM species) could be compared. The effect of habitat and adult identity on survivorship of seedlings was tested using chi-square tests on upland vs. floodplain data without the allospecific ''oaks,'' and separately on upland data including the ''oaks.''

The influence of understory species composition and canopy gaps on percentage colonization of seedling roots was assessed using ANOVA. Here understory species composition and canopy gaps were considered as fixed effects. Replicate canopy gap-understory pairs were considered a random effect nested within the understory species composition.

The effect of two different inocula on seedling growth was also analyzed using ANOVA. Inoculum source (red maple or oak) and whether the inocula were alive or dead (i.e., sterilized) were fixed effects in the model. Data were transformed (square root transformation for percentage root colonization, or log transformed for other variables) to meet the constant variance criteria of ANOVA models. Adequacy of the ANOVA models was determined by inspecting residual plots. A multivariate analysis of variance (MANOVA)

TABLE 1. Fate of red maple test seedlings transplanted into upland and lowland forest sites in Maryland under the canopy of different trees.

A) Root colonization by fungi (percentage root length)

Site	Red maple		Other AM species		Oaks	
	Mean	1 SE	Mean	1 SE	Mean	1 SE
Upland	31.7[a]	2.4	37.2[a]	2.5	29.0[a]	3.4
Floodplain	40.1[a]	2.6	31.2	3.4	...	...

B) Maple seedling survival

Site	Seedling status	Red maple		Other AM species		Oaks	
		No.	%	No.	%	No.	%
Upland	live	36	73.5	41	93.2	33	70.2
	dead	13	26.5	3	6.8	14	29.8
Floodplain	live	35	79.6	29	42.0	...	...
	dead	9	20.4	21	58.0	...	...

Notes: Trees were red maples, other species with arbuscular mycorrhizae ("Other AM species"), or southern red oaks with ectomycorrhizae ("Oaks"). Different superscript lowercase letters within a row indicate significantly different means ($P < 0.05$).

RESULTS

Site and host species on inoculum potential and seedling survivorship

Two weeks after red maple seedlings were transplanted into the forest, the percentage colonization of seedling roots by AM fungi did not differ significantly between upland and floodplain habitats (Table 1). In upland habitats, the species of adult under which seedlings were planted also had no influence on the percentage colonization of seedling roots. In the floodplain habitat, percentage colonization of red maple seedling roots tended to be higher when they were planted on the mounds of conspecifics compared to those planted

TABLE 2. Fate of red maple test seedlings transplanted into Maryland forest with understory dominated by either *Lindera benzoin* (spicebush) or *Kalmia latifolia* (mountain laurel).

A) Root colonization by fungi (percentage root length)

Site	Spicebush		Mountain laurel	
	Mean	1 SE	Mean	1 SE
Gap	31.9[a]	2.7	19.2[b]	2.0
Understory	20.5[bc]	2.5	23.1[c]	2.0

B) Maple seedling survival

Site	Seedling status	Spicebush		Mountain laurel	
		No.	%	No.	%
Gap	live	39	81.2	48	100
	dead	9	18.7	48	100
Understory	live	38	79.2	0	0
	dead	10	20.8	0	0

Notes: Seedlings were planted under gaps in the forest canopy or within the understory. Different superscript lowercase letters within a row indicate significantly different means ($P < 0.05$).

under allospecifics (habitat × species effect, $F_{1,6} = 4.63$, $P = 0.075$).

Red maple seedlings planted out in the forest for 2 wk had higher mortality in floodplain habitats than in upland habitats ($\chi^2 = 5.524$, $P = 0.0188$, Table 1). In the floodplain, mortality was mainly due to seedlings being pushed over by running water or debris, or due to wilting, possibly caused by a fungal pathogen. Within the floodplain more maple seedlings died when they were planted under allospecifics than when planted on the mounds that occur under red maple adults ($\chi^2 = 5.117$, $P = 0.0237$). In contrast, in the upland habitats maple seedlings tended to have higher mortality under conspecifics and oaks than under allospecific AM species ($\chi^2 = 9.631$, $P = 0.0081$). In the upland seedlings were largely killed by an unidentified invertebrate that severed the stem at the base, and also due to digging by small mammals.

Effects of understory dominants and canopy gaps on inoculum potential and seedling survivorship

Seedlings planted in canopy gaps where spicebush was dominant tended to have higher levels of root colonization by arbuscular mycorrhizal fungi than those in the understory, but root colonization of seedlings where mountain laurel was dominant was lower in gaps than in the understory (species × gap interaction, $F_{1,10} = 24.26$, $P = 0.0006$). In the understory there was no significant effect of the dominant species in on percentage root colonization, which averaged ~20% after 2 wk.

Mortality of seedlings of red maple was much lower in sites dominated by mountain laurel than at sites dominated by spicebush (Table 2, $\chi^2 = 28.43$, $P < 0.0001$). The presence of canopy gaps did not influence survivorship of red maple seedlings. Over all sites, survivorship was weakly negatively correlated with per-

TABLE 3. Percentage of root length colonized by arbuscular mycorrhizal fungi, and growth and biomass partitioning of red maple seedlings, after 10 weeks of growth in a greenhouse (mean ± 1 SE, $N = 6$–7 plants).

| | Red maple root inocula | | Oak root inocula | |
Measure	Living	Dead	Living	Dead
Root colonization in 10 wk	85.7 ± 2.2[a]	14.3 ± 2.3[b]	80.5 ± 2.8[a]	9.1 ± 1.2[b]
Final leaf area (cm^2)	32.9 ± 2.3[a]	17.6 ± 2.8[b]	16.2 ± 3.0[b]	12.1 ± 1.2[b]
Total biomass (g)	0.127 ± 0.016[a]	0.099 ± 0.010[ab]	0.066 ± 0.011[b]	0.079 ± 0.007[b]
Relative growth rate (g·g^{-1}·wk^{-1})	0.084 ± 0.011[a]	0.066 ± 0.010[ab]	0.025 ± 0.012[b]	0.042 ± 0.009[b]
Net assimilation rate (g·m^{-2}·wk^{-1})	4.55 ± 0.75[a]	4.79 ± 0.76[a]	1.32 ± 0.73[b]	3.34 ± 0.76[ab]
Leaf mass ratio (g/g)	0.567 ± 0.018[a]	0.444 ± 0.039[b]	0.500 ± 0.022[ab]	0.412 ± 0.030[b]
Leaf area ratio (cm^2/g)	2.72 ± 0.19[a]	1.73 ± 0.16[b]	2.46 ± 0.27[a]	1.56 ± 0.13[b]
Specific leaf area (m^2/g)	4.77 ± 0.21[a]	3.88 ± 0.08[a]	4.86 ± 0.38[a]	3.78 ± 0.07[b]

Notes: Seedlings were inoculated with live or dead (sterilized in an autoclave) coarsely chopped roots and adhering soil of mature red maple or southern red oak trees. Different superscript lowercase letters within a row indicate significantly different means (ANOVA with Bonferroni correction, $P < 0.05$).

centage colonization of seedling roots (Spearman rank correlation, $r_S = -0.392$, $N = 44$ plants, $P < 0.05$).

Effectiveness of inocula obtained from different sources in plants grown in the greenhouse

The source of inocula, either from oaks or red maples, had a significant effect of growth and biomass allocation in red maple seedlings (MANOVA, Wilks' lambda for inoculum source, $\lambda = 0.4574$, $P = 0.0353$, Table 3). At the end of the experiment ~80% of root length were colonized in inoculated plants. Roots of control plants that were inoculated with sterilized roots were colonized by AM fungi (average of 10% of root length), probably due to contamination of pots with airborne spores in the greenhouse. Percentage colonization of roots was significantly, but only slightly, greater using root inocula obtained from red maples than oaks (main effect of inocula, $F_{1,23} = 5.676$, $P = 0.0258$).

Despite this similar level of root colonization with the different inocula, different inocula resulted in dif-
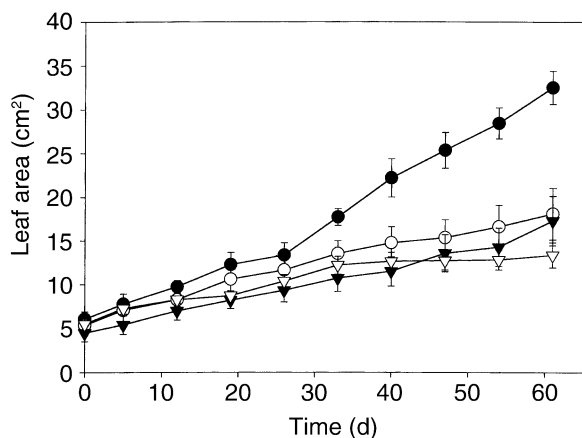

FIG. 1. Leaf area growth of red maple seedlings over 10 wk. Seedlings had been inoculated with live (circles) or dead (triangles) chopped roots and adhering soil of mature red maple (closed symbols) or southern red oak trees (open symbols). Values are means ± 1 SE; $N = 6$–7 seedlings/treatment.

fering growth patterns (Fig. 1, Table 3). In plants inoculated with red maple roots, growth of leaf area was approximately double that of plants inoculated with oak roots (Fig. 1). The final leaf area (main effect of inocula, $F_{1,23} = 20.803$, $P = 0.0001$) and relative growth rate was also higher (main effect of inocula, $F_{1,23} = 15.265$, $P = 0.007$). Plants inoculated with oak roots had low rates of leaf area growth similar to those of controls. Higher growth rates in plants inoculated with red maple roots than in those inoculated with oak roots were associated with higher levels of net assimilation (Table 3, main effect of inocula, $F_{1,23} = 9.544$, $P = 0.0052$), and to a lesser extent due to greater allocation of biomass to leaves (leaf mass ratio, main effect of inocula, $F_{1,23} = 3.148$, $P = 0.0893$). The source of inocula did not alter the specific leaf area or the leaf area ratio, although these variables were greatly altered depending on whether inocula were live or dead (main effect of live/dead for SLA, $F_{1,23} = 18.288$, $P = 0.0003$, and for LAR, $F_{1,23} = 22.983$, $P = <0.0001$).

Mineral element concentrations within plant tissue were also influenced by the source of the inocula, and whether the inocula were living or dead (Table 4). Concentrations of P, Cu, and Zn were significantly higher in seedlings inoculated with living inocula than with sterilized inocula. When inocula were obtained from oak roots, P concentrations in plants were higher than in plants inoculated with red maple roots (main effect of inocula, $F_{1,23} = 8.14$, $P = 0.0090$). Leaf N concentrations, C/N ratios, and whole plant concentrations of Ca, Mg, Mn, Fe, B, and Al were not significantly affected by any treatment.

We also assessed the isotopic fractionation of both C and N in seedling leaves (Table 4). Inoculation with live inocula from either source did not affect the $\delta^{15}N$ signal. $\delta^{15}N$ had a mean of -1.4, and ranged between -4 and $+2$, values that are consistent with atmospherically derived nitrogen (Hogberg 1997). In contrast, $\delta^{13}C$ was lower in plants inoculated with oak roots than those inoculated with red maple roots (main effect of inocula, $F_{1,23} = 6.245$, $P = 0.0200$). More negative $\delta^{13}C$ values indicate lower instantaneous water use ef-

TABLE 4. Elemental concentration and carbon and nitrogen isotopic composition of red maple seedlings after 10 weeks of growth (mean $\pm$ 1 SE, N = 6–7 plants).

Measure	Red maple root inocula		Oak root inocula	
	Living	Dead	Living	Dead
Whole plant				
P (%)	0.356 ± 0.017[a]	0.065 ± 0.005[b]	0.393 ± 0.016[a]	0.084 ± 0.006[b]
K (%)	1.18 ± 0.03[a]	0.96 ± 0.03[b]	1.12 ± 0.05[ab]	1.10 ± 0.07[ab]
Cu concentration (mg/kg)	56 ± 11[a]	8 ± 1[b]	54 ± 6[a]	10 ± 1[b]
Zn concentration (mg/kg)	64 ± 5[a]	36 ± 2[b]	79 ± 4[a]	42 ± 3[b]
Leaves				
N (%)	2.09 ± 0.12[a]	2.06 ± 0.09[a]	2.48 ± 0.11[a]	2.09 ± 0.15[a]
C/N ratio	26.4 ± 1.5[a]	26.5 ± 1.3[a]	21.6 ± 1.1[a]	26.2 ± 2.0[a]
$\delta^{13}C$	−31.72 ± 0.25[a]	−30.84 ± 0.18[b]	−31.87 ± 0.25[ab]	−31.84 ± 0.22[ab]
$\delta^{15}N$	−1.25 ± 0.23[a]	−1.07 ± 0.45[a]	−1.97 ± 0.48[a]	−1.26 ± 0.78[a]

Notes: Seedlings were inoculated with live or dead (sterilized in an autoclave) chopped roots and adhering soil of mature red maple or southern red oak trees. ANOVA with different superscript lowercase letters within a row indicate significantly different means (Bonferroni correction, $P < 0.05$).

ficiency during photosynthesis (i.e., more water transpired per mole of CO_2 fixed), which can be due to lower maximum rates of photosynthesis (Farquhar and Richards 1984).

DISCUSSION

Heterogeneity in inoculum potential

From the view of a seed landing on the forest floor, there would appear to be few sites that are better than others with respect to the probability of colonization by arbuscular mycorrhizal fungi. Higher inoculum potentials in gaps with spicebush may reflect greater carbon resources available for fungal growth both in the established plants and the seedlings in this environment, due to greater light availability and higher rates of photosynthetic carbon fixation (Orwig and Abrams 1995; L. Schreeg, *unpublished data*). Increased levels of soil moisture in gaps (Uhl et al. 1988, Denslow et al. 1998) may also encourage fungal growth. Lower colonization of bait seedling roots in gaps with mountain laurel could be due to mountain laurel's comparatively low rates of photosynthetic carbon gain even in gaps where light availability is enhanced (L. Schreeg, *unpublished data*), or perhaps to a combination of factors that include low densities of herbs and low soil moisture levels at mountain laurel sites (L. Schreeg and R. Miller, *unpublished data*).

In floodplain sites inoculum potential tended to be higher under maples compared to other species. This could be due to the higher density of roots and organic matter on red maple mounds. Less frequent inundation within the mound at the base of floodplain red maples compared to flatter areas (Golet et al. 1993) may also favor fungal growth. That inoculum potential is higher in gaps with spicebush and tended to be higher on the mounds of red maples in the floodplain may result in some benefits to seedlings at these sites, but conditions are also generally more favorable for plant growth in gaps and on mounds. Thus, the positive effects of

slightly higher inoculum potential may be relatively small compared to the effects of increased light levels and less frequent inundation.

There appears to be no predictable variation in inoculum potential under canopies of different host trees species, despite differences in soil characteristics. Across vegetation types percentage colonization of bait plants has been found to be positively correlated with water content, soil organic matter, pH, and levels of NH_4^+ and K (Klironomos et al. 1993, Brundrett et al. 1996a). Our results from within the SERC forest demonstrate that within the understory, small-scale heterogeneity in inoculum potential within a patch is as high as between patches, as has been observed in other forests (Brundrett and Abbott 1995).

Surprisingly, inoculum potential of arbuscular mycorrhizae was similar even in cases where the forest was dominated by plants that form ecto- and ericoid mycorrhizae. Brundrett and Abbott (1995) suggest that ecto- and arbuscular mycorrhizae occupy separate soil volumes that are distributed on a finer scale than the occurrence of the host tree species. For example, red maple roots, or roots of other AM species, would be intermixed but patchily distributed within those of oaks or mountain laurel, thereby making arbuscular mycorrhizae ubiquitous with respect to all but the smallest seedlings. We have found numbers of live AM fungal spores to be similar in soils sampled under oaks and red maples (C. E. Lovelock, *personal observation*). Dispersal of spores and hyphae by animals, in water flow, and by wind can also contribute to homogeneity of inoculum in forests (Brundrett 1991). Differences in inoculum potential seem to be detectable on a large scale when comparing vegetation types (Koide and Mooney 1987, Asbjornsen and Montagnini 1994, Fischer et al. 1994, Brundrett et al. 1996a) and soil types (Porter 1979, Klironomos 1995), and where disturbance is a factor, for example, during dune stabilization (Cordiki and Rincon 1997) or due to logging or clearing

of vegetation by humans (Alexander et al. 1992, Fischer et al. 1994, Brundrett and Abbott 1995, Boerner et al. 1996, Brundrett et al. 1996b) or other animals (Koide and Mooney 1987).

Seedling survivorship of red maples bait plants was similar to that observed in the first weeks of growth of naturally occurring populations of red maple seedlings in other broad-leaved eastern American forests (Streng et al. 1989, Jones et al. 1994, Jones and Sharitz 1998). Contrary to our expectations, over all sites seedling survivorship was weakly negatively correlated with inoculum potential, perhaps indicating initial seedling survivorship for red maples is independent of colonization by AM fungi, and that seedlings are able to maintain themselves on seed reserves for an extended time (Allsopp and Stock 1995, Zangaro et al. 2000). The weak negative correlation between survival of seedlings and inoculum potential could also occur because conditions that favor growth of mycorrhizal fungi and colonization of roots could also be the most suitable for pests and diseases. In additional, colonization with AM fungi imposes a carbon cost on the seedlings (Johnson et al. 1997) that could compromise survival. Differences in survivorship of seedlings under different adult trees, particularly between red maples and other non-ectomycorrhizal species that form AM, and between sites with spicebush and those with mountain laurel, suggest a high degree of heterogeneity in the suitability of the forest floor for red maple recruitment, and also high variability in the causes of seedling mortality in different sites.

Variability in effectiveness of inocula measured in the greenhouse

Tests for differences in inoculum potential under oaks and red maples in the field found that inoculum potential of the two AM fungal sources was equivalent. Growth of seedlings for 10 wk with inocula from these two sources also found that percentage colonization of roots by AM fungi obtained from roots of red maples and oaks was similar. Seedling growth under this particular set of experimental conditions showed significant differences in the effectiveness of the inocula in promoting growth. Leaf area of plants inoculated with red maple roots was double that of plants inoculated with oak roots. Enhancement of growth in plants inoculated with red maples roots is likely due to greater net assimilation rate per unit leaf area, and to a lesser extent due to an increased proportion of biomass invested in leaf area. More positive $\delta^{13}C$ values in plants inoculated with maple roots indicate higher instantaneous water use efficiency during photosynthesis (i.e., less water transpired per mole of CO_2 fixed), which can be due to higher maximum rates of photosynthesis or lower stomatal conductance at similar photosynthetic rates (Farquhar and Richards 1984). More positive $\delta^{13}C$ in plants inoculated with maples roots could indicate higher maximum rates of photosynthesis, corroborating

the higher values of net assimilation rate observed in these plants. Higher $\delta^{13}C$ in plants inoculated with maples roots could also indicate that the AM community from the red maple root inocula was more effective in facilitating water uptake.

The large difference in the size and net assimilation rates between plants inoculated with red maple and oak roots could not be attributed to reduced nutrient levels in oak inoculated plants, which tended to have higher concentrations of P. Differences in $\delta^{15}N$ can indicate of reduced or altered functioning of nutrient uptake processes in plants without symbionts (Handley et al. 1993), but $\delta^{15}N$ values were similar in plants inoculated with live red maple or oak roots. The mechanism by which growth is enhanced with red maple inoculum is not clear but could be due to differences in the relative nutrient delivery and carbon demands of the AM fungal communities in each inoculum (Tinker et al. 1994, Graham and Abbott 2000).

Plant size after the first season of growth has been positively correlated with survivorship in red maple and other tree seedlings (Jones and Sharitz 1998). Thus, seedlings inoculated with the fungal community associated with red maple roots may have a greater long term survivorship than those recruiting under oak trees, suggesting that the AM fungal community at any given site in the forest could have an impact on recruitment and species distributions, which could in turn enhance forest tree diversity (Grime et al. 1987, Connell and Lowman 1989, McGonigle and Fitter 1990, Johnson et al. 1992, Gange et al. 1993, Francis and Read 1994, Bever et al. 1996, 1997, van der Heijden et al. 1998b, Mills and Bever 1998, Kiers et al. 2000). In the case of red maple, more favorable inocula and a significant growth advantage for seedlings recruiting under or near red maple adults could lead to clumping of red maples. In forest of the southeastern USA the opposite trend has been observed (Streng et al. 1989), perhaps suggesting that other factors interact with, and can override, the positive benefits of a ''good'' inoculum (Bever 1994, Mills and Bever 1998, Packer and Clay 2000). Further more, we used chopped roots as inocula in our experiment, not the bulk soil from under red maples and oaks. In omitting the bulk soil we may have omitted components of the microbial community from the red maple sites that could reduce plant growth (Packer and Clay 2000). Therefore, our results must be viewed as preliminary.

We have found that within a forest, inoculum potential of arbuscular mycorrhizal fungi is uniform within the understory, irrespective of dominant host tree species and the type of mycorrhizae present. Some variation in inoculum potential was found at different microsites (e.g., canopy gaps vs. understory in spicebush and mountain laurel dominated sites). These effects could be due to a range of factors, including enhanced light availability and higher rates of photosynthetic carbon gain in gaps, and differences in the density of

herbaceous flora between mountain laurel and spice-bush dominated sites. More prominent were differences in the effectiveness of inocula that resulted in large differences in seedling size in a very short time. Enhanced size of seedlings could have an effect on recruitment (Jones and Sharitz 1998), therefore, different sites within the forest may be better for growth of certain species depending on the community of AM fungi present.

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