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Arbuscular mycorrhizal communities in tropical forests are affected by host tree species and environment

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Abstract Arbuscular mycorrhizal (AM) fungi are mutualists with plant roots that are proposed to enhance plant community diversity. Models indicate that AM fungal communities could maintain plant diversity in forests if functionally different communities are spatially separated. In this study we assess the spatial and temporal distribution of the AM fungal community in a wet tropical rainforest in Costa Rica. We test whether distinct fungal communities correlate with variation in tree life history characteristics, with host tree species, and the relative importance of soil type, seasonality and rainfall. Host tree species differ in their associated AM fungal communities, but differences in the AM community between hosts could not be generalized over life history groupings of hosts. Changes in the relative abundance of a few common AM fungal species were the cause of differences in AM fungal communities for different host tree species instead of differences in the presence and absence of AM fungal species. Thus, AM fungal communities are spatially distinguishable in the forest, even though all species are widespread. Soil fertility ranging between 5 and 9 Mg/ha phosphorus did not affect composition of AM fungal communities, although sporulation was more abundant in lower fertility soils. Sampling soils over seasons revealed that some AM fungal species sporulate profusely in the dry season compared to the rainy season. On one host tree species sampled at two sites with vastly different rainfall, relative abundance of spores from *Acaulospora* was lower and that of *Glomus* was relatively higher at the site with lower and more seasonal rainfall.

Keywords Glomales · *Acaulospora morrowiae* · *Acaulospora mellea* · *Acaulospora foveata*

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Introduction

Arbuscular mycorrhizal (AM) fungi (order Glomales, division Glomeromycota) form a symbiotic relationship with most plant species (Allen 1991). The effect of mycorrhizal fungi on plant performance has been proposed to have far reaching ecological consequences, from increasing productivity of ecosystems to enhancing plant diversity (Janos 1980a; Grime et al. 1987; Gange et al. 1993; Francis and Read 1994; Bever et al. 1997; van de Heijden et al. 1998a, 1988b; Klironomos et al. 2000). 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 benefit plant growth, although the level of benefit can depend on the fungal community-host combination (Bever 1994; Johnson et al. 1997; van de Heidjen 1998a, 1998b; Kiers et al. 2000; Lovelock and Miller 2002), the prevailing environmental conditions (Johnson et al. 1997), and genotype (isolate) of a 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 symbiont at the time of germination. Spatial and temporal variation in the AM fungal community and the effectiveness of those fungi may therefore give rise to microsites that are more or less favorable for seedling establishment and growth (e.g., Alexander et al. 1992). Differences at this scale could be an important process in maintaining plant community diversity (Bever et al. 1997; Bever 1999).

Additionally, the diversity of fungal communities may also be maintained if different host tree species provide a range of environments for the fungal symbionts (Bever et al. 1996, 1997; Bever 1999). Heterogeneity of fungal communities in forests could be due to a wide array of soil and host plant characteristics (Abbott and Robson 1981; Klironomos et al. 1993; Klironomos 1995). But whether heterogeneity in AM fungal communities in tropical forests varies predictably with host or environmental factors is unknown. In this study we test whether host factors, soil type or rainfall influence the composition of indigenous AM fungal communities within old-growth forests in Costa Rica.

Tree species often are grouped on the basis of suites of correlated traits that constitute a life history strategy (Whitmore 1984). At one extreme of these groupings are long-lived, slow growing, large-seeded species with low photosynthetic rates and tissues that are often highly chemically defended. At the other end of the spectrum are short-lived, fast growing, small-seeded species that have high rates of photosynthetic carbon gain, and have tissues that are often less well defended. We hypothesize that because of enhanced nutrient demand and higher rates of photosynthetic carbon gain in short-lived tree species there may be potentially greater carbon availability for AM symbionts in these species that result in an assembly of communities of AM fungi that are different from those associated with long-lived host trees. In rainforest trees, detailed information about the physiology and ecology of many species is often not available. However, maximum lifetimes and growth rates of tree species have been estimated for a number of species in the La Selva Reserve in NE Costa Rica (Lieberman et al. 1985; Lieberman and Lieberman 1987). We used this information, together with that from other reports of tree species characteristics (Clark and Clark 1992), to choose 14 tree species that were either long- or short-lived for our study. We extracted spores from rhizosphere soil associated with mature individuals of these target tree species to test whether: (1) life history characteristics of host plants influences the AM fungal community, as represented by their sporulation pattern, and (2) different host tree species were associated with different AM fungal communities.

AM fungal communities are influenced by soil properties (reviewed in Brundrett 1991). Communities are responsive to pH, organic matter, tillage practices (Johnson et al.1992; Johnson 1993), and nutrient concentrations (Egerton-Wharton and Allen 2000). Although soils in tropical forests often are low in fertility, they also tend to be heterogeneous (Sollins et al. 1994). At La Selva the old-growth forest is distributed over two common soil types of varying fertility (Clark and Clark 2000). In this study we utilize this variability to test whether the AM fungal community differed across soil types by sampling AM fungal communities from one host tree, *Pentaclethra macroloba* (Willd.) Kuntze. *P. macroloba* is abundant in the reserve (Hartshorn and Hammel 1994) and is distributed across both soil types.

AM fungal communities may also be strongly influenced by the seasonality of rainfall (Brundrett 1991). At La Selva, there is a short drier season that occurs between December and March. We tested whether AM fungal communities were different between rainy and dry seasons. Central America has a strong east to west rainfall gradient, from 1.5 m on the Pacific coast to approximately 4.0 m on the Caribbean coast. We tested for difference in AM community composition in forests across this steep rainfall gradient. We controlled for the possible effect of host tree species by sampling the rhizosphere soil of a widely distributed species, *Ceiba pentandra* (L.) Gaertn.

Materials and methods

Testing for the influence of life history of hosts, host tree and soil fertility

AM fungal spores were collected at the La Selva Biological Station (10°26'N, 83°59'W) of the Organization for Tropical Studies in NE Costa Rica in September and October 1999. La Selva is classified as a tropical wet forest with an annual rainfall of 4 m that is distributed fairly evenly throughout the year, with the exception of a very short dry season in September and a more prolonged dry season in February and March. All sampling was done in the 650 ha of forest that has not been disturbed for at least 200 years. To test for the influence of host tree life history characteristics and host tree on AM fungal community composition, we selected seven tree species with known or estimated maximum lifetimes that were either short (<150 years) or long (>150 years) (Leiberman et al. 1985; Lieberman and Lieberman 1987; Clark and Clark 1992; Table 1). Although *Virola sebifera* had an estimated maximum lifetime of only 130 years, we grouped it with the long-lived species after Lieberman et al. (1985) because of its relatively low estimated maximum growth rate. Using a database of tree species distributions (unpublished data of D. B. Clark and D. A. Clark) and the topographic and soil classification global information system (GIS) coverages, we located eight individuals of the 14 target tree species (seven short lived and seven long lived) within the undisturbed forest on the infertile Ultisols, avoiding steep slopes and watercourses. In the field we located the trees using GIS referenced grid posts. Individuals of the rarer species were selected first (e.g., *Dipteryx panamensis* and *Apeiba membranacea* are rare on Ultisols), followed by sampling of more common species (e.g., *P. macroloba* or *Laetia procera*) within the same general area. This approach led to widely distributed sampling points over the reserve. Distance between sampled trees always was >15 m. Our final data set consisted of 97, rather than 112 samples, because eight individuals of each species could not always be located and samples with less than ten live spores were omitted from the analysis.

Testing the influence of soil fertility, seasonality and rainfall

To test for the influence of soil fertility on AM fungal communities, we used the most common tree species on the reserve, *P. macroloba* (Mimosaceae). We sampled from eight individuals of *P. macroloba* on Ultisols and Inceptisols. These soils have approximately 5.7 and 9.0 Mg/ha total phosphorus in the top meter, respectively (unpublished data of D. B. Clark and D. A. Clark). To compare AM fungal communities between rainy and dry seasons, we selected a subset of six of the species used in the analysis of host and life history effects on AM communities (*Cecropia obtusifolia*, *Goethalsia meiantha*, *Stryphnodendron excelsum*, *P. macroloba*, *D. panamensis*, and *L. procera*). We

Table 1 Tree species and their estimated lifetime, maximum annual growth rate and common classification used in this study to assess the influence of life history and other species traits on AM fungal community structure

Tree species	Family	Common classification[a]	Lifetime[b]	Maximum annual dbh increment (mm)[b]
Short-lived				
Cecropia obtusifolia Bertol.	Cecropiaceae	Shade intolerant	<100[c]	
Goethalsia meiantha (D. Sm.) Burret	Tiliaceae	Canopy, shade intolerant	78	13.81
Casearia arborea (Rich.)Urban	Flacourtiaceae	Sub-canopy, shade intolerant	78	6.65
Cecropia insignis Liebm.	Cecropiaceae	Shade intolerant	<100[c]	
Stryphnodendron excelsum Harms	Mimosaceae	Canopy, shade intolerant	91	10.25
Hernandia didymantha Donn. Smith	Hernandiaceae	Canopy, shade intolerant	156	14.62
Simarouba amara Aubl.	Simaroubaceae	Canopy, shade intolerant	<120[c]	
Long-lived				
Pentaclethra macroloba (Willd.) Kuntze.	Mimosaceae	Canopy, shade tolerant	312	8.90
Dipteryx panamensis (Pitt.) Record	Fabiaceae	Canopy, shade tolerant	>200[c]	
Dendropanax arboreus (L.) Dcne. & Planch.	Araliaceae	Sub-canopy, shade tolerant	247	4.12
Virola sebifera Aubl.	Myristicaceae	Canopy, shade tolerant	130	7.31
Laetia procera (Poeppig) Eich.	Flacourtiaceae	Canopy, shade tolerant	286	4.64
Apeiba membranacea Spruce	Tiliaceae	Canopy, shade tolerant	338	5.88
Minquartia guianensis Aubl.	Olacaeae	Canopy, shade tolerant	280	2.58

[a] Lieberman and Lieberman (1987)
[b] Lieberman et al. (1985)
[c] estimated from Clark and Clark (1992)

resampled the rhizosphere soils of the eight individuals of each of these species in March 2000. To compare fungal communities over a rainfall gradient, while controlling for possible host tree effects, we collected soils from under eight individuals of the tree species *Ceiba pentandra* (L.) Gaertn, from both La Selva (rainfall of 4 m/year) and Palo Verde Reserve on the Pacific coast of Costa Rica (10°19'N, 85°18'W). Palo Verde is classified as tropical dry forest (Hartshorn 1983) with a highly seasonal rainfall of approximately 1.5 m annually (Coen 1983). At La Selva and Palo Verde *Ceiba pentandra* occurs on alluvial soils. It is a distinctively large tree that is rare at La Selva (0.01–0.1 stem/ha) and occurs only occasionally in Palo Verde (0.1–1 stem/ha) (Hartshorn 1983).

Sampling rhizosphere soils for spores

Three members of the field team arranged themselves around the base of the tree and collected fine roots using a small shovel, machete and pocket knife. Fine roots were located by following major roots from the bole of the tree (buttresses in some trees). Roots of the 14 tree species often were distinctive with respect to color, texture and odor. Each member of the field team then contributed approximately 200 cm^3 of soil from their excavation to a bulk soil sample for each tree (rhizosphere soil).

Isolation of spores, identification and enumeration of fungal morpho-species

Spores were isolated from 50 or 100 cm^3 of collected rhizosphere soils. Spores were extracted by wet-sieving to 45 μm followed by centrifugation in a 20/60% sucrose gradient (Daniels and Skipper 1982). The supernatant was washed in water and placed in petri dishes, from which spores were collected manually under a dissecting microscope. Preliminary groupings and identifications were made on fresh material, but all spores were mounted in Melzer's reagent to differentially stain wall structures of important diagnostic value (Morton 1998).

Spore identifications were verified by examination of live and mounted reference material from the International Collection of Vesicular-Arbuscular Mycorrhizal Fungi (INVAM) (Morton et al. 1993). Because of the generally poor state of field material (spores differ in age and state of degradation), and the low relative abundance of some morphospecies, we chose to use a conservative approach to identifying species, and named only those with sufficient spores in good enough condition to be certain of identity. For example, only four live *Gigaspora* spores were found in all samples (although there were many dead ones). Variation placed them either in *G. margarita* or *G. rosea*, and so they were only identified only to genus. We grouped *Glomus* spores in various states of degradation into two "working" groups: *Glomus* "yellow-brown", a likely an amalgam of *G. ambisporum*, *G. geosporum*, *G. macrocarpum*, *G. mosseae*, and *G. clarum*; and *Glomus* "hyaline", which closely resembled *Paraglomus occultum*, but possibly was an amalgam of similar morphospecies (*Archeospora trappii, E. schenkii*, or *Paraglomus brasilianum*). Identification of *Glomus claroideum*, found at Palo Verde, is tentative because spores typical of the species were not found. *Entrophospora* sp. is pale yellow with a warty surface on the spores and sometimes very large warts, with closest similarity to *E. infrequens*. Other undescribed species are: *Acaulospora* sp.1, which could be a thin-walled reversible mutant of *A. morrowiae* (J. Morton, personal observation). *Acaulospora* sp.2 is similar to *A. morrowiae* (deep purple stain in Melzer's reagent), but is larger, pale yellow when live, with rough ornamentations, similar but distinct from those of *A. rehmii*.

Data analysis

Comparison of AM fungal species composition among all possible pairs of spores within soil samples was calculated using the Bray-Curtis (BC) dissimilarity coefficient (Bray and Curtis 1957) which is one of the most robust coefficients for the analysis of taxonomic composition data (Faith et al. 1987). Spore abundance data, using both numbers and volumes of spores of each species, were transformed to square roots to reduce the influence of occasional large abundance values of some taxa (Field et al. 1982). Spore volumes were estimated using diameters of spores of reference species in INVAM (Morton et al. 1993). For "working groups" diameters of all possible taxa in the group were averaged and the mean used to calculate spores volumes. The transformed abundance values for each taxon were standardized by the maximum sporulation measured for that taxon. This standardization equalizes the potential contributions of taxa to the overall dissimilarity in composition. Without standardization by taxon, the BC values are dominated by those taxa of high abundance (Faith et al. 1987).

In order to test the significance of taxonomic differences due to life history of hosts and host tree species, the BC matrix was subjected to analysis of similarities (ANOSIM) devised by Clarke (1993) using the computer program PRIMER 5 (Plymouth Marine Laboratory, UK; Clarke and Warwick 1994). We used the two-way nested ANOSIM with host trees species nested within life history. The advantage of the ANOSIM test is that it does not assume any underlying distribution to the data, and it avoids using the BC index directly to compare sets of assemblages. Instead, it is a non-parametric test, based only on the rank order of the matrix values.

Global non-metric multidimensional scaling (MDS; Kruskal 1964), an effective method available for the ordination of taxonomic composition data (Minchin 1987), provided a visual summary of the pattern of BC values for the comparison of spore composition of soil samples. It was chosen over other ordination techniques because no assumptions are made about the underlying distribution of the data. Each MDS was run with ten random starting configurations, and proceeded through 400 iterations for each of three dimensions. Sample points closest together on the resulting scatter plot represent host trees with the most similar AM fungal spore abundances. Each ordination has an associated ANOSIM test statistic, making interpretation of the plots unambiguous.

To understand the differences in species composition among host tree life history groupings and host trees, we calculated similarity percentages (SIMPER procedure from PRIMER 5; Clarke and Warwick 1994). The average BC dissimilarity between all pairs of samples within a group of samples (e.g., from the same host) was computed. The average then was broken down into separate contributions from each species. The SIMPER analysis gives an indication of the contribution of individual species to the similarity measured within sample groups and to dissimilarities measured among the sample groups. The SIMPER results indicate specifically which AM fungal taxa are responsible for the results obtained from the ANOSIM by comparing the average abundances of taxa for each life history and host tree.

Patterns of diversity among sites and environments were computed using a suite of diversity metrics: no. of species (S), species richness [$d=(S-1)/\log n$, where n is the total number of spores], the Shannon diversity index [$H'=-\Sigma_i p_i(\log p_i)$, where p_i is the proportion of the total number of spores for the ith species], and Pielou's eveness ($J'=H'/\log S$). These values were analyzed by ANOVA using the statistical computing package Data Desk 6.1 (Data Descriptions, N.Y.). In the analysis of the effect of host life history and host species, host species was considered a random effect and nested within life history (treated as a fixed effect). For analysis of the effect of soil type and sites with different rainfall, one-way ANOVA was used with soil type and site as fixed effects in the model. In the analysis of the effects of seasons on spore communities host and season were considered fixed effects in the model. Inspecting residual plots for normality was used to assess the suitability of ANOVA models.

Results

Effect of life history of hosts and host species

At La Selva 13 taxonomic groupings of AM fungi were identified, four of which were conglomerate groupings, thus this is an underestimate of AM fungal species diversity. In 100 cm^3 of rhizosphere soil, the mean number of spores was 55.4 (SE=5.9, n=97) and the mean number of species was 3.53 (SE=0.13, n=97). The mean number of AM fungal species per host tree species was 7.0 (SE=0.4, n=6–8). The identity of the host tree species or life history grouping of hosts had no significant effect on the total number of spores, spore volume, or the number of AM fungal species (S) or species diversity (H'). Species richness (R) of AM fungal communities tended to differ among host species ($F_{12,72}$=1.676, P=0.090) as did community eveness (J', $F_{12,72}$=1.850, P=0.055), but these differences were not significant.

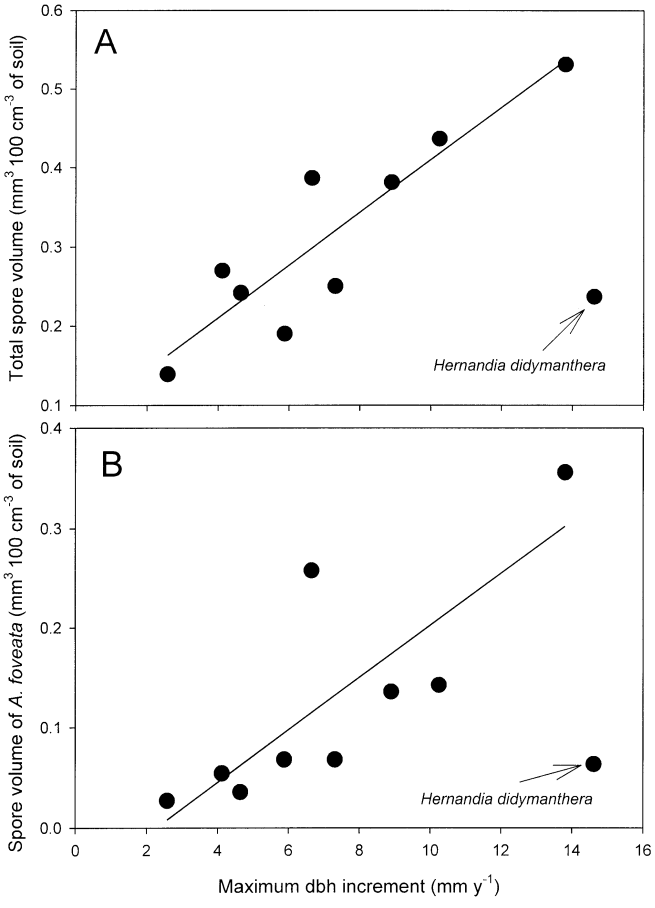

Fig. 1 Relationship between the estimated maximum annual diameter at breast height (*dbh*) increment and the total observed spore volume (**A**) and volume of spores of *Acaulospora foveata* (**B**) associated with the rhizosphere soil of ten species of tropical trees. One tree species (*Hernandia didymanthera*) was excluded from the regression. Regression equations are: $y=-0.576+0.00245\,x$, $r^2=0.79$ (**A**); $y=3.97+0.00248x$, $r^2=0.60$ (**B**)

Of the 4,794 spores examined, 96.8% were in the genus *Acaulospora* (Table 2). Approximately 62% of all the spores were *A. morrowiae* and 30% were *A. mellea*. On a volumetric basis, *A. foveata* was slightly more abundant than *A. mellea* (41.5% and 31%, respectively). Life history grouping of tree species had no significant effect on the community composition of the AM fungi, but there was a significant positive relationship between the estimated maximum growth rate of nine of the 14 trees species and the total volume of spores observed (Fig. 1A, r^2=0.79) and the volume of spores of *A. foveata* (Fig. 1B, r^2=0.60). Growth rates of four species were unavailable, and one species, *Hernandia didymanthera* was an outlier and therefore excluded from the regression.

Tree species had a significant effect on community composition (ANOSIM global R=0.184, P=0.001, Fig. 2).

Table 2 Relative abundance of AM fungal spores from La Selva Reserve, Costa Rica. Spores are from 100-cm^3 rhizosphere soil samples of five to eight individuals from 14 tree species. All samples were from old-growth forest on Ultisols

Arbuscular mycorrhizal fungal species	No. spores	% Spores	Spore volume mm^3	% Spore volume
Acaulospora morrowiae Spain & Schenck	2,957	61.68	0.669	16.02
Acaulospora mellea Spain & Schenck	1,429	29.81	1.292	30.96
Acaulospora foveata Trappe & Janos	137	2.86	1.731	41.45
Acaulospora sp.1	63	1.31	0.057	1.36
Acaulospora sp.2	30	0.63	0.043	1.03
Acaulospora tuberculata Janos & Trappe	17	0.35	0.073	1.76
Acaulospora spinosa Walker & Trappe	6	0.13	0.016	0.38
Scutellaspora pellucida (Nicol. & Schenck) Walker & Sanders	6	0.12	0.022	0.52
Scutellaspora castanea Walker	4	0.08	0.029	0.69
Gigaspora spp. (*margarita/rosea*)	4	0.08	0.069	1.64
Glomus "hyaline"	77	1.61	0.015	0.35
Glomus "yellow/brown"	62	1.29	0.154	3.70
Glomus tortuosum Schenck & Smith	2	0.04	0.006	0.15
Total	4,794		4.175	

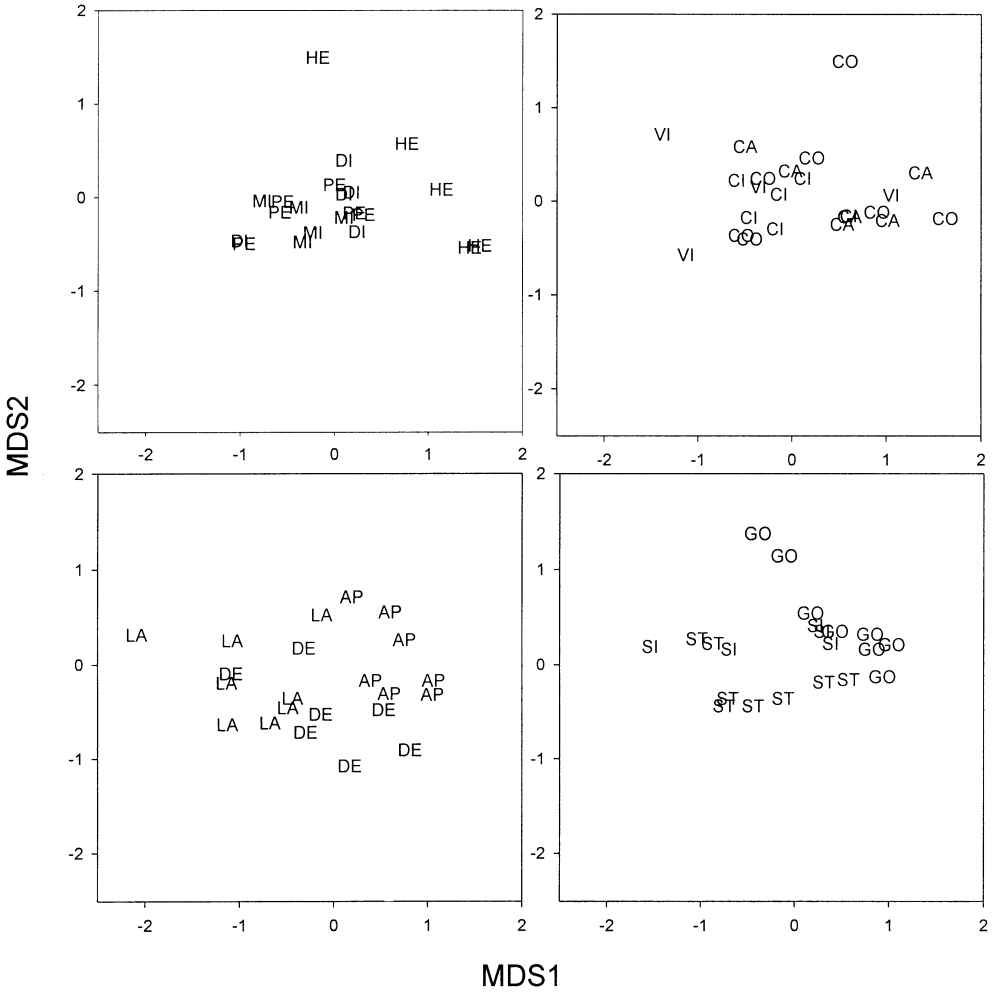

Fig. 2 Two-dimensional multidimensional scaling (*MDS*) of arbuscular mycorrhizal (AM) fungal communities associated with 14 host tree species growing in undisturbed forest on Ultisol soils at La Selva, NE Costa Rica. Tree species significantly affected communities of AM fungi (ANOSIM global R=0.184, P=0.001). AM fungal communities associated with three or four host species are represented per panel for clarity. Short-lived tree species are: *Cecropia obtusifolia* (*CO*), *Goethalsia meiantha* (*GO*), *Casearia arborea* (*CA*), *Cecropia insignis* (*CI*), *Stryphnodendron excelsum* (*ST*), *Hernandia didymantha* (*HE*), *Simarouba amara* (*SI*). Long-lived tree species are: *Pentaclethra macroloba* (*PE*), *Dipteryx panamensis* (*DI*), *Dendropanax arboreus* (*DE*), *Virola sebifera* (*VI*), *Laetia procera* (*LA*), *Apeiba membranacea* (*AP*), *Minquartia guianensis* (*MI*)

MDS of BC values showed significant differences in the AM fungal communities associated with tree species (Fig. 2, stress value for the two-dimensional MDS=0.17). In Fig. 2 the 14 host species are distributed over four panels for clarity. Differences among AM fungal communities associated with different host trees usually was due to differences in the relative abundance of the three most dominant taxa (Fig. 3). For example, *G. meiantha* had low abundance of *A. mellea* and high abundance of *A. morrowiae* spores, while *Stryphnodendron excelsum* had similar abundances of *A. mellea* and *A. morrowiae* spores. The AM fungal community associated with *Simarouba*

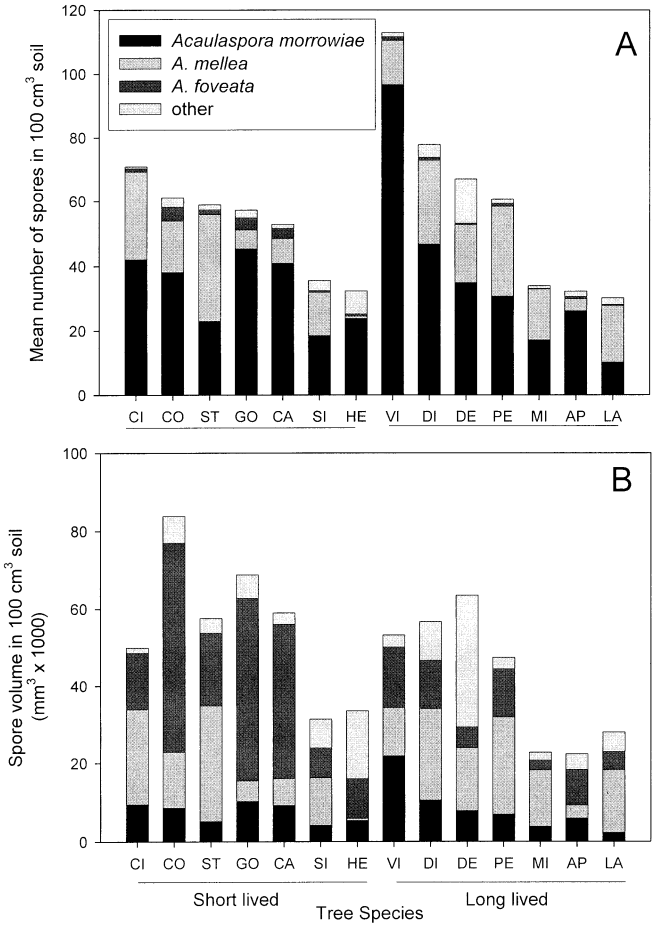

Fig. 3 Relative spore numbers (**A**) and spore volumes (**B**) of the three most abundant AM fungal species found in 100 cm^3 of rhizosphere soil of 14 host tree species growing in undisturbed forest on Ultisol soils at La Selva, north-east Costa Rica. Host tree species abbreviations as in Fig. 2

amara was different from that of other host trees because of the occurrence of yellow/brown *Glomus*, while the community of AM fungi associated with *Dendropanax arboreus* was distinct due to the relatively high abundance of *Glomus* "hyaline". *A. foveata* generally was more common in association with *Cecropica obtusifolia, G. meiantha* and *Casearia arborea*, while *A. mellea* spores had higher abundance in association with *Cecropia insignis, S. excelsum, D. panamensis* and *P. macroloba.*

Soil fertility, seasonal and rainfall comparisons

Tests of the influence of soil fertility on AM fungal communities, using the widely distributed host tree species *P. macroloba*, showed that lower fertility soils contained significantly more spores than high-fertility soils (61.7±SE 12.5 compared to 23.5±SE 3.9; $F_{1,12}$= 12.73, P=0.004). Soil fertility showed no significant effect on the composition of AM fungal communities (Fig. 4). But, on the recent and fertile alluvial soils on which *Ceiba pentandra* occurs within La Selva, samples had a higher relative abundance of *A. spinosa*, *A. scrobiculata*, and *Glomus* spp., fungal species that are uncommon on older Inceptisols and Ultisols (compare Table 2 with Table 3).

Seasonal comparison of AM fungal spores from six host tree species within the La Selva reserve revealed substantially more spores in the dry season than in the rainy season (Table 4). Additionally there were seasonal differences in the relative abundance of species of the AM fungal communities, showing seasonal differences in sporulation of AM fungal species. *A. mellea* dominated in the dry season, accounting for 71% of all spores compared to 36% in the rainy season. Community evenness (*J'*) of spores was consequently reduced in the dry season compared to the wet season (Table 4). However, season had no significant effect on community species richness (*d*) or diversity (*H'*).

Table 3 Relative abundance of arbuscular mycorrhizal spores extracted from 100 cm^3 of rhizosphere soil under *Ceiba pentandra* growing on alluvial soils on both the wet Caribbean lowlands of Costa Rica at La Selva (rainfall 4 m/year), and from the drier Pacific coast at Palo Verde, Costa Rica (rainfall 1.5 m/year)

Fungal species	La Selva				Palo Verde			
	No. spores	% Spores	Spore volume mm^3	% Spore Volume	No. spores	% Spores	Spore volumemm^3	% Spore volume
A. mellea	144	27.80	0.130	24.98	23	4.29	0.024	1.99
A. morrowiae	94	18.15	0.022	3.47	68	11.22	0.016	1.30
A. scrobiculata	70	13.5	0.062	12.20	110	18.15	0.100	8.47
A. spinosa	30	5.79	0.078	15.11	24	3.96	0.064	5.34
Acaulospora sp.1	20	3.86	0.018	3.46	2	0.33	0.002	0.15
A. foveata	4	0.66	0.050	9.69	4	0.66	0.050	10.57
Scutellaspora spp	0	0	0	0	24	3.96	0.100	8.51
Glomus claroideum	74	14.28	0.064	11.00	0	0	0	0
Glomus "hyaline"	48	9.65	0.024	1.83	18	2.97	0.004	0.29
G. tortuosum	20	3.86	0.062	11.90	0	0	0	0
Glomus "yellow/brown"	12	2.31	0.030	5.73	114	18.81	0.284	24.06
Entrophospora sp.	0	0	0	0	216	35.64	0.538	45.59
Total	518		0.478		606		1.180	

Table 4 Comparison of the arbuscular mycorrhizal spore community in wetter (September and October) and drier periods (March) of the La Selva Reserve, Costa Rica. Spores are from 100-cm^3 rhizosphere soil samples from five to eight individuals of six tree species. All samples were from old-growth forest on Ultisols

	Rainy season	Dry season	*F*	*P*
Total number of spores in 100 cm^3 of soil	107.4±14.2	149.8±12.0	4.673	0.0337
Species richness (*d*)	0.715±0.050	0.634±0.035	NS	
Pielou's evenness (*J'*)	0.660±0.027	0.571±0.031	5.114	0.0265
Spores of *A. morrowiae* as percentage of total spores	55.9	23.4		
Spores of *A. mellea* as a percentage of total number of spores	36.5	70.6		

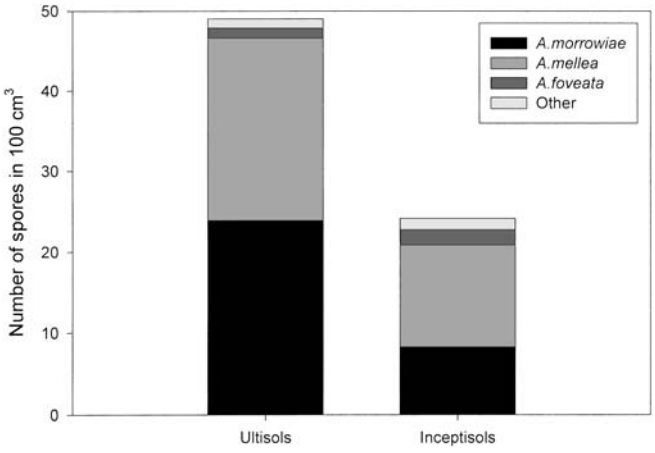

Fig. 4 Relative abundance of spores of AM fungal species across two soils with different fertility within the La Selva Reserve, northeast Costa Rica. The Ultisols have approximately 5 Mt/ha phosphorus, while Inceptisols have 9 Mt/ha phosphorus in the top 1 m

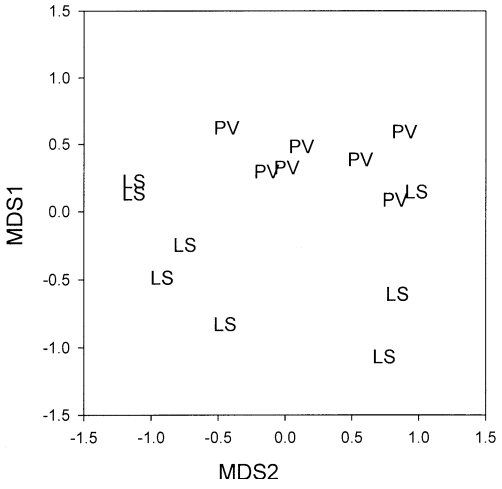

Fig. 5 Two-dimensional MDS of AM fungal communities collected from 100 cm^3 of rhizosphere soil from trees of *Ceiba pentandra* growing on alluvial soils at La Selva (*LS*, rainfall 4 m/year) and at Palo Verde (*PV*, rainfall 1.5 m/year), Costa Rica. Communities from the two sites differed significantly (ANOSIM global R=0.236, P=0.039)

By sampling soils under the tree species *Ceiba pentandra*, and thus controlling for tree species effects on the AM fungal community, we tested whether communities of AM fungi varied across a rainfall gradient. Communities differed significantly between the dry and wet forest sites (ANOSIM global R=0.236, P=0.039, Fig. 5, stress value for the two-dimensional MDS=0.12). In the drier site at Palo Verde, spores of *Glomus* and *Entrophospora* species were more common than they were at La Selva, the higher rainfall site (Table 3).

Discussion

The AM fungal community at La Selva

Diversity of the AM fungal community is moderate to low (Brundrett 1991; Morton et al. 1995), and very low compared to the diversity of the tree species. There are 350 species of trees at La Selva and 1,864 species of vascular plants (O. Vargas, personal communication). In comparison a temperate grassland with plant diversity of approximately 40 plant species yielded 37 AM fungal species (Bever et al. 2001), leading Bever and co-authors to hypothesize that a range of host plants providing variable environments for AM fungi are essential for maintenance of the diversity of the AM fungal community. Although the number of AM fungal species at La Selva is certainly underestimated in this study, due to: (1) the poor condition of field material which hampers identification, (2) our conglomerate taxa (*Glomus* "hyaline" and *Glomus* "yellow/brown"), which could easily double or triple the estimated fungal diversity when more fully explored (Stutz and Morton 1996; Brundrett et al. 1999), (3) the restricted number of environments from which we collected (we did not sample under all potential hosts, in the swamps, across all soil types and depths, or on slopes or stream valleys), and (4) the restricted temporal sampling. But whether the ratio of plant to AM fungal species will reach the 1:1 ratio apparent in grasslands, and whether there are factors that limit local AM fungal diversity are yet to be discovered. Dispersal by rodents and other small mammals, and the activity of microarthopod consumers are likely to be important in regulating local AM fungal species diversity (e.g., Janos et al. 1995).

The AM fungal species recovered from La Selva soils were overwhelmingly dominated by *Acaulospora* species, with very few spores of *Glomus* species. This community

composition is atypical compared to that in other tropical regions, where *Glomus* species tend to be dominant (Musoko et al. 1994; Cuenca and Meneses 1996; Johnson and Wedin 1997; Guadarrama and Alvarez-Sanchez 1999; Picone 2000; Zangaro et al. 2000; Husband et al. 2002; but see Janos and Trappe 1982). Picone (2000) also showed higher relative abundance of *Acaulospora* species in AM fungal communities on the Caribbean slope of Nicaragua and Costa Rica (37% of all spores). Dominance of *Acaulospora* species may be partly controlled by the fairly even distribution of rainfall throughout the year. But other factors could also be important.

High relative abundance of *Acaulospora* in the La Selva forest could be due to unique characteristics of the type of forest at La Selva. Most notably, the leguminous tree *P. macroloba* accounts for 15% of all stems above 10 cm diameter at breast height (Hartshorn 1983). However, reports of AM fungal species richness from temperate forests also found high abundances of *Acaulospora* (and *Scutellospora*) species, and low abundance of *Glomus* spores (Helgason et al. 1998; Merryweather and Fitter 1998a, 1998b), suggesting that vegetation types with long-lived trees may have distinctive AM fungal floras. Although the biology of individual AM species is poorly understood, Sieverding (1989) reports that isolates of the most common species found in the La Selva forest soils (i.e., *A. mellea, A. morrowiae*), and one of the other less common species (*S. pellucida*) were not effective growth promoters of tropical agricultural plant species. Additionally, *Glomus* species were more commonly associated with pastures than forests (Picone 2000). *Acaulospora* and *Scutellospora* species may be more effective symbionts for slow-growing, woody species in resource-limited environments than are *Glomus* species.

Spore numbers are not always correlated with the proportion of root length colonized by most genera, especially *Acaulospora* and *Glomus* (Merryweather and Fitter 1998a, 1998b). Their results highlight a limitation of using relative abundance of AM fungal spores collected from the field as indicators of the relative abundance of AM species in an AM fungal community: (1) not all species of the community may be sporulating at the time of sampling, and (2) sporulation may not proportionally represent all the species colonizing roots. In spite of these limitations, relative differences among communities of spores provides a useful tool for investigating the ecology of AM fungal communities.

Effects of life history of hosts and host tree species

The life history trait tree species longevity did not have a significant effect on AM fungal communities. Life histories of tropical trees are complex (Clark and Clark 1992; Rees et al. 2001) and tree lifespan may not correlate strongly with the traits that influence host-AM fungi interactions. However, estimated maximum growth rates of tree species were correlated with the volume of AM spores observed. Thus, allocation of carbon to sporulation of fungal symbionts could be influenced by tree species growth rates or productivity. Moreover, the greater volume of *A. foveata* spores observed associated with faster growing species could also indicate that particular species of AM fungi are sensitive to host tree species physiological characteristics.

Although AM fungal communities did not differ among our life history groupings, different host tree species harbored distinct AM fungal communities (Figs. 2 and 3). For example, the high abundance of *A. foveata* spores with some host tree species (*G. meiantha, Cecropia obtusifolia*, and *Casearia arborea*), and the high abundance of *A. mellea* with other tree species (*P. macroloba, S. excelsum, Cecropia insignis,* and *D. panamensis*) suggest that host species do offer differential environments for AM fungal sporulation. In a tropical forest in Mexico, Allen et al. (1998) found no effect of host species on AM fungal communities, but their level of replication may have been too low (n=3) to detect differences. In tropical moist forest in Cameroon (Musoko et al. 1994) and Panama (Husband et al. 2002), in temperate forests in Yorkshire (Merryweather and Fitter 1998b), and in temperate grassland ecosystems (Johnson et al. 1992; Bever et al. 1996; Eom et al. 2000) host plants have been shown to significantly affect the composition of the AM fungal community. Despite host tree species effects on fungal communities, common AM fungal species are distributed widely in local plant communities (Musoko et al. 1994; Bever et al. 1996; Johnson et al. 1992; Cuenca and Meneses 1996; Eom et al. 2000; Picone 2000), so that all plants recruited into the forest are likely to be exposed to the dominant sporulating AM fungal species.

Many underlying causes could be responsible for differences in AM communities associated with various host trees. Tree species differ in growth rates and also in phenology [e.g., Hazlett (1987) for *P. macroloba* and *G. meiantha*]. Root morphologies are also distinctive and trees deploy their roots in different regions of the soil profile (Pavlis and Jenik 2000). For example, *G. meiantha*, both *Cecropia* species, *P. macroloba, S. excelsum* and *D. panamensis* all have abundant roots found very close to, or on the soil surface, while those of *Minquartia guianensis* and *Apeiba membranaceae* are deployed deeper in the soil profile (C. E. Lovelock, personal observation).

Tree species can also differentially alter fertility and other physical and chemical characteristics of soils (van Breemen 1998 and references therein), which in turn can affect AM community structure. Detailed studies of how individual tropical tree species influence their soil environment are rare. However, for *Simarouba amara* soil phosphorus levels are elevated under the canopy of female trees compared to adjacent sites (Rhoades et al. 1994). This may play a role in the higher relative abundance of *Glomus* spp. under this tree species compared to other host trees. Cuenca and Menedes (1996) found the abundance of *Glomus* species were

correlated with fertility (measured as available phosphorus and exchangeable magnesium and potassium). But in tropical deciduous forests in Mexico, soil textural differences rather than fertility were attributed to differences in community structure of sporulating AM fungi (Allen et al. 1998). The large legumes in this study (e.g., *D. panamensis, P. macroloba,* and *S. excelsum*) are likely to enhance soil N concentrations that may in turn influence the AM fungal community (Eom et al. 2000; Egerton-Warburton and Allen 2000). Soil pH is also known to influence the relative abundance and effectiveness of AM fungal species (Howeler et al. 1987; Sieverding 1989; Moutoglis and Widden 1996), but as yet we do not know how soil pH varies with host tree species. Biotic variables, such as the abundance of fungal grazers (Klironomos and Kendrick 1996), or fungal parasites (Daniels and Menge 1980; Janos 1983; Lee and Koske 1994), also could influence the fungal communities associated with individual tree species.

Soil fertility

Assessment of the AM fungal community associated with *P. macroloba* over a doubling in phosphorus concentrations from Ultisol to Inceptisol soils did not significantly alter the AM fungal species composition, although total numbers of spores were greater in the lower fertility Ultisols. The similarity in AM community composition observed over the soil fertility gradient associated with *P. macroloba* could suggest that host variables, such as physiology, morphology, litter quality or phenology may have a greater impact on the fungal community than absolute differences in soil type or fertility (Eom et al. 2000). More abundant sporulation in low fertility soils is observed in many studies, possibly because colonization of roots is higher under these conditions (Allen 1991; Brundrett 1991), but lower rates of spore decomposition could also be responsible.

AM communities at La Selva from the more recently deposited, fertile alluvial terraces (associated with host tree *Ceiba pentandra*) differ from AM communities in the older, less fertile soils within the reserve (Ultisols and Inceptisols; C.E. Lovelock, unpublished data). The most recent alluvium and older soils differ in texture, which may also contribute to AM fungal community differences.

Seasonality and rainfall

Despite the limited duration of the dry season at La Selva, sporulation was enhanced in the dry season compared to the rainy season. Peaks in sporulation were observed in other locations where rainfall is fairly evenly distributed throughout the year (e.g., Singapore, Louis and Lim 1987). Picone 2000, working in Nicaragua and Costa Rica measured greater abundance of large-spored fungal species in the wet season but no differences in spore numbers among seasons in other species. In more seasonal tropical forest sites, seasonal differences in sporulation and fungal community structure were more dramatic (Musoko et al. 1994;, Guadarrama and Alvarez-Sanchez 1999; Mangan and Adler 2002; but see Allen et al. 1998 for an exception). Seasonal differences in abundance of spores could in part be due to reduced predation of spores during drier weather. Seasonality in spore abundance may result in: (1) seasonal changes in inoculum potential [although this was not observed by Brundrett and Abbott (1994)], or (2) seasonal changes in the AM fungal community to which germinating seedlings are exposed, which could impact seedling recruitment.

Rainfall at La Selva is higher and less seasonal than that at Palo Verde and many other tropical areas. *Entrophospora* and *Glomus* species sporulated more commonly at the drier and more seasonal Palo Verde site in association with the shared host species, *Ceiba penandra*. Other soil and plant factors also vary across these sites, and therefore these data are only preliminary indicators of rainfall effects. Amount and duration of rainfall clearly may be important, as indicated by the dominance of small-spored species, especially *Glomus*, in arid biomes (Stutz and Morton 1996; Stutz et al. 2000; Egerton-Warburton and Allen 2000). Causal factors favoring *Glomus* in dry-seasonal environments could be the totipotency of diverse propagules of *Glomus* (Beirmann and Linderman 1983) allowing rapid colonization of host plants from hyphae during fleeting periods of high water availability, or other poorly understood life history traits. Another hypothesis, given the high levels of parasitism observed in spores (Daniels and Menge 1980; Janos 1980b; Lee and Koske 1994) is that higher levels of fungal parasitism and predation may occur in locations with higher rainfall, similar to that observed for plant herbivores (Coley and Barone 1996), and that possibly *Acaulospora* species are less susceptible to predation and parasitism than are *Glomus* species. In Puerto Rican forests, Gonzalez and Seastedt (2001) found a higher abundance of soil fauna in wet tropical forest compared to dry forests. The factors that regulate the composition of AM fungal communities at broad spatial scales are still unknown and require further investigation.

Conclusions

Within the La Selva forest distinctive AM fungal communities are detectable at the scale of individual host trees, despite common fungal species being widely distributed. Spatial variation in AM fungal communities could be an important factor contributing to the maintenance of tree diversity in forests, because differences in the effectiveness of AM fungal communities could influence seedling recruitment, a key process in the maintenance of diversity in forests (Ribbens et al. 1994; Clark et al. 1998; Wright 2002; Husband et al. 2002). In a model developed by Bever et al. (1997) negative feedback of AM fungal communities on some host plants relative to

others could result in the maintenance of plant diversity. Results with tree seedlings have shown that different AM fungal inocula can have different effects on growth (Kiers et al. 2000; Lovelock and Miller 2002). Whether this is due to AM fungi or other microorganisms in the inocula, particularly pathogens (e.g., Mills and Bever 1998; Packer and Clay 2000) are not known. Our results suggest that in order for AM fungal communities to affect recruitment, variation in relative abundance of the same few dominant AM fungal species must be capable of differently altering seedling recruitment and growth. Van der Heijden et al. (1998a, 1998b) and Bever (1999, 2001) show in experiments with herbaceous species that the composition of the AM fungal community can alter plant community structure and productivity. We hypothesize that AM fungi are having similar impacts in tropical forests.

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