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Quality of rooting environments and patterns of root colonization by arbuscular mycorrhizal fungi in strangler figs in a Mexican palmetto woodland

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Abstract Arbuscular mycorrhizal colonization in strangler figs, spore richness, and abundance of arbuscular mycorrhizal fungi were quantified in epiphytic and ground-rooted trees in a *Sabal* palmetto woodland that had marked heterogeneity in rooting environments for hemiepiphytic plants. An inoculation experiment was performed to assess whether low spore density could limit mycorrhizal colonization. There was no significant difference in mycorrhizal colonization among *Ficus* species, but epiphytic plants in nutrient-rich rooting environments had less mycorrhizal colonization than ground-rooted plants in low-nutrient soils. However, richness and abundance of spores was low, and to some extent, this limited the mycorrhizal colonization of strangler figs. Nevertheless, our results suggest intraindividual adjusting levels of root colonization in strangler figs in accordance with mineral availability. Such responses could maximize the cost–benefit balance of arbuscular mycorrhizal interactions throughout the development of strangler figs from epiphytic young plants to ground-rooted trees.

Keywords *Ficus* · Hemiepiphytic plants · Heterogeneous-rooting environment · Plasticity · *Sabal mexicana*

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Introduction

The mineral nutrient content of soils is one of the most important environmental factors affecting the performance of plants because of its heterogeneity and its effects on plants at various levels, from community structure to individual performance (Aikio 2000). Soil heterogeneity is especially important in tropical regions, where it has been estimated that the distribution of more than 30% of tree species is restricted by soil properties (Clark et al. 1999). The mineral nutrient content of soils is known to modulate intrinsic attributes in plants such as growth rate (Poorter 1989) and morphology (Schreeg et al. 2005). Furthermore, the outcomes of plant-associated interactions such as intra- and interspecific competition (Casper and Jackson 1997), herbivory (Boege and Dirzo 2004), and mycorrhizal colonization (Treseder and Vitousek 2001) are also affected.

Mycorrhizal interactions, especially arbuscular mycorrhizal (AM) interactions, occur in a wide variety of plants (Smith and Read 1997). For plants engaged in these interactions, the cost is in the form of organic compounds derived from photosynthesis (Fitter 1991), and the benefit provided by the AM fungi is improved uptake of water and minerals (Varma 1995), particularly phosphorus (Koide 1991). A substantial body of experimental evidence shows that root colonization by AM fungi is generally lower in nutrient-rich substrates than in nutrient-poor soils (Treseder 2004). This evidence supports the hypothesis that plants should invest more carbon in mycorrhizal fungi where nitrogen or phosphorous are limiting to plant growth because mycorrhizal fungi contribute to nutrient uptake by plants (Mosse and Phillips 1971). However, most of the evidence comes from experimental manipulation of the availability of mineral nutrients for plants (even under

field conditions), and very little is know from natural systems where the plant investment hypothesis could be tested.

In this paper, we propose the palm *Sabal mexicana* (Arecaceae) and its commonly associated strangler hemiepiphytic figs (*Ficus*, subgenus *Urostigma*) as a natural system for the in situ study of the modulation of AM interactions in heterogeneous rooting environments. This kind of palmetto woodland proliferates in perturbed areas with sandy soils of low mineral nutrient content (López and Dirzo 2007). In contrast, up to 9 kg of organic substrate accumulates in the stems of a single palm (López 2007). Therefore, primary hemiepiphytes that grow on *Sabal* palms face contrasting environments through their development: an organic-rich substrate when they are epiphytic and a poor sandy soil when anchored in the ground. Our main goal was to explore under natural conditions whether root colonization by AM fungi in strangler figs in the *Sabal* palmetto woodland could be modulated by the availability of mineral nutrients in the rooting environment.

We aimed to answer the following five questions: Is there a marked spatial heterogeneity in the mineral nutrient availability and biological properties of rooting environments for fig trees in the *Sabal* palmetto woodland? Are there interspecific differences in root colonization by AM fungi among strangler figs developing in the *Sabal* palmetto woodland? Does root colonization by AM fungi differ between contrasting ontogenetic stages of *Ficus* species? Is root colonization by AM fungi in the aerial substrate limited by the availability of infective AM structures? Is there evidence that root colonization by AM fungi in strangler figs is modulated by the quality of the rooting environment?

Materials and methods

Study site

This study was carried out near Tlalixcoyan, Veracruz (18° 49′N, 96°05′W), on the coastal plain of the Gulf of Mexico. The vegetation in the area is *Sabal* palmetto woodland (Miranda and Hernández 1963; Pennington and Sarukhán 1998), which develops on poor sandy soils that are occasionally flooded. This vegetation grows on tropical lowlands of relatively smooth topography and is increasingly being cut and converted to grasslands for cattle ranching. The converted terrains are typically subjected to dry-season fires or are abandoned, forming vegetation mosaics under different degrees of regeneration dominated by *Sabal* palm and this species is the main host of various species of strangler figs such as *Ficus obtusifolia*, *F. trigonata*, *F. padifolia*, *F. cotinifolia*, *F. lundelli*, and *F. pertusa* (López and Dirzo 2007). The mean monthly temperature of the area is 25.9°C, and the mean annual rainfall is 1,302 mm, predominantly between June and October (García 1988).

Characterization of rooting environments

Chemical composition

To evaluate the chemical composition of the soil and aerial substratum, we collected 20 soil cores (10×10×10 cm) in disturbed areas and in the riparian zone. We also collected the substratum deposited behind three remnant petioles of 20 palm trees by tying a polyethylene sheet around the stem of the palm tree and removing the remnant petioles above the sheet. The entire aerial substratum was then brushed out onto the sheet.

Soil pH was measured in a standard solution, 1:2 of soil–distilled water.

Total carbon was estimated based on the methods of Walkley and Black (Nelson and Sommers 1982). That is, 1 g of soil sample was transferred to a 250-ml Erlenmeyer flask, and 10 ml 1 N $K_2Cr_2O_7$ and 10 ml concentrated H_2SO_4 were added. After 30 min, 50 ml deionized water, 3 ml concentrated H_3PO_4, and 0.5 ml 1% diphenylamine indicator (Aldrich, 11,276-3) were added. The solution was then titrated with 1 M $FeSO_4$ to the endpoint where the solution turned green.

Total nitrogen was estimated using the micro-Kjeldahl method. That is, soil samples (200 mg) were digested with 4 ml of a digestion mixture (0.42 g Se, 14 g Li_2SO_4, 350 ml 30% H_2O_2, and 420 ml concentrated H_2SO_4) at 360°C for 2 h, after which enough water was added to make a final volume of 100 ml. An aliquot of the digest was mixed with 25 ml of alkali mixture (500 g NaOH and 25 g sodium disulphate in water, made up to 1,000 ml) and distilled. A total of 25 ml of the distillate was collected in a 50-ml beaker containing 5 ml boric acid indicator solution (20 g boric acid in water and 15 ml of pH 4.5 indicator solution diluted to 1,000 ml) and titrated with 0.01 M H_2SO_4 (Bremmer and Mulvaney 1982).

For phosphorus determination, 1 g soil was placed in a porcelain crucible and heated in a muffle furnace up to 550°C. The temperature was maintained at 550°C for 1 h, and then the samples were allowed to cool. After cooling, the organic P in the samples was extracted with 0.5 M H_2SO_4. Available P quantified using the ammonium molybdate method (Bray and Kurtz 1945).

Potassium was extracted from the soil by mixing 10 ml of 1 M ammonium acetate (pH 7.0) with a 10-g soil sample. Potassium was quantified in the filtered extract by flame photometry (Knudsen et al. 1982).

Biological properties

The biological properties examined in the rooting environments of the strangler figs were the density of spores of AM fungi (a component of the root colonization potential of AM fungi), ergosterol content, and the decomposition rate of plant litter.

To evaluate the density of spores of AM fungi, we collected ten soil samples from each soil type and ten samples of the epiphytic substrate in the *Sabal* palms. Spores were extracted from 100 g of soil or aerial substrate by passing the soil or aerial substrate through 250-, 125-, and 52-μm sieves. Then, the material recovered from the 125- and 52-μm sieves was centrifuged, separately, with 20 ml 60% glucose solution for 5 min at 3,000 rpm (Daniels and Skipper 1982). We then recovered the suspended spores from the middle layer of the supernatant, rinsed them with tap water, and stored them at 4°C. Spores were sorted into morphospecies, then counted and mounted with a mixture of polyvinyl alcohol and Melzer reagent for identification at the generic level.

Ergosterol content, an indirect measure of active fungal biomass (Zhao et al. 2005), was evaluated in 12 of the aerial substrate samples and in ten samples of each soil type from the disturbed areas and the riparian zones. Each sample consisted of 4 g soil extracted in 12 ml methanol for 2 h with constant shaking. The samples were then centrifuged for 5 min at 10,000 rpm, and the liquid phase of each was filtered through 0.45-μm nylon syringe filters. We then injected the solution into a 20 μl loop of a high-performance liquid chromatograph, using methanol as the mobile phase at a rate of 1 ml/min. The solid phase was a C18 column of length 30 cm. Samples were run at room temperature, and eluted products were registered with a UV detector at 280 nm. Under these conditions, ergosterol was eluted at a retention time of 19.5 min. The area under the ergosterol peak was transformed into grams of ergosterol per gram of dry soil using a standard curve based on commercial ergosterol (Aldrich E200-0) over the concentration range 0.25–10 μg/ml in methanol.

To estimate the dry mass of soil in each sample, we took four replicate subsamples (each 4 g wet weight) from each sample. These were dried for 72 h at 60°C and then weighed again to estimate the water content of each soil sample.

Litter decomposition was evaluated experimentally with decomposition nylon mesh (0.5 mm) bags (40×50 mm). In each bag, we placed a fragment (35×45 mm) of a dry leaf from *Piper auritum* (a pioneer species common to many tropical forest) and a commercially available wooden toothpick. We used this combination of a soft readily decomposable leaf of *P. auritum* and a piece of wood to ensure we could quantified the decomposition rate even in a scenario of very low microbial activity (sandy soils in perturbed areas) and still being readily comparable to the decomposition rate in sites with a high microbial activity (riparian soils). The whole content of each bag was weighed, and the bags were sealed with silicone. Bags were randomly placed in 20 sites of each of the three rooting environments and left for 4 weeks before being collected. The remaining content of each bag was dried at 60°C for 72 h and weighed to estimate the percentage mass loss.

Interspecific and intraspecific variation in root colonization by AM fungi

We collected fine roots (<3 mm in diameter) from ground-rooted trees and epiphytic plants of the hemiepiphytic species *F. obtusifolia*, *F lundelli*, and *F. cotinifolia*. In total, we collected roots from 42 individuals: seven of each species from each environment (ground-rooted and epiphytic). Roots were fixed in 4% acetic acid and were then treated with 10% KOH for 24 h at room temperature and 5% HCl for 10 min to remove root pigments (Koske and Gemma 1989). Clear roots were then stained in glycerol acid solution (50% glycerin, 40% distilled water, and 10% lactic acid) with 0.05% trypan blue for 24 h and then rinsed and stored in glycerol acid solution. For each individual tree, we mounted 30 segments of roots, each 1 cm long, in polyvinyl alcohol and gently squashed them between two microscope slides. We then recorded the presence of AM structures (hyphae, vesicles, and arbuscles) in 90 fields under a light microscope (three fields per root segment; McGonigle et al. 1990).

Spore inoculation in epiphytic plants

To determine if AM infection in epiphytic plants of *Ficus* species was limited by the inoculum potential of the AM fungi, we experimentally increased the abundance of spores of AM fungi. This experiment was undertaken under natural conditions at the study site using epiphytic plants of *F. padifolia*. To increase the abundance of spores in the rhizosphere of epiphytes, we extracted spores in sieves as detailed above and recovered the mud trapped in the 128- and 52-μm sieves from a total of 10 kg of soil collected from the rhizosphere of ground-rooted *F. padifolia* trees at the study site. We then added distilled water to a volume of 1,000 ml. In the field, we selected 40 epiphytic *F. padifolia* plants and applied one of three treatments to each plant. Twenty plants were inoculated with spores (mud), ten plants received water but no spores, and ten plants were marked as controls. Plants were inoculated by placing a 1-g ball of cotton wool soaked in the mud (or distilled water) in the rhizosphere of the epiphytic *F. padifolia* plants. Three

months later, fine roots were extracted from the 40 plants and processed as described above to evaluate root colonization by AM fungi.

Colonization as a function of soil quality

We used the results of a natural experiment testing root colonization by AM fungi in three contrasting rooting environments to address whether *Ficus* plants can modulate the intensity of their AM interactions in response to soil quality. This experiment included epiphytic plants and ground-rooted trees in disturbed areas and in riparian zones. The riparian zones, which are flooded every year, receive a substantial input of organic matter, which potentially makes the soils in this zone richer than those in disturbed areas. Therefore, to compare root colonization by AM fungi in grown trees of *Ficus* species (*F. cotinifolia*, *F. obtusifolia*, and *F. trigonata*) in the perturbed area and the riparian zone, we sampled roots of 20 ground-rooted trees (see above) in riparian zones and estimated colonization by AM fungi as detailed above.

Statistical analysis

We used multivariate analysis of variance (MANOVA) to compare the soil mineral nutrient concentration between environments (aerial substrate and soil from disturbed areas and riparian zones). Spore counts in each rooting environment were compared using the Kruskal–Wallis test. We used a one-way analysis of variance (ANOVA) to compare ergosterol content, decomposition rate, and the effect of added spores on root colonization between the different rooting substrates. Interspecific and intraspecific variation in root colonization by AM fungi in contrasting rooting environments were analyzed with a two-way ANOVA, with species and rooting environments as main factors. When appropriate, normality and homoscedasticity of residuals were checked, and transformation was applied if needed. All statistical analyses were done with the R language and environment for statistical computing (R-Development-Core-Team 2005).

Results

Characterization of rooting environments

Chemical composition

The MANOVA test on the mineral nutrient content of rooting environments was highly significant (Pillai=0.96; df=1, 38; F_{approx}=269.3; df=5, 34; P<0.001). The corresponding ANOVA and the Honestly Significantly Different Tukey post-hoc tests showed significant differences (P<0.01) among the three rooting environments in all soil chemical properties but potassium, which was higher in the aerial substratum than in the two soil environments. The highest values for all chemical attributes were observed in the aerial substratum (Table 1), whereas the soil in disturbed areas had the lowest values.

Organic carbon was more than seven times more concentrated in the riparian zones and more than 40 times more concentrated in the aerial substratum than in the soil in disturbed areas. Similarly, phosphorus was more than seven and 11 times more concentrated in the riparian zone and the aerial substratum, respectively, than in the soil in disturbed areas.

Biological properties

We also observed that the abundance of spores of AM fungi differed significantly between the aerial substrate and the soil environments (Fig. 1) according to the Kruskal–Wallis rank-sum test (χ^2=19.5; df =2; P<0.001). On average (±standard deviation), the abundance of spores of AM fungi in the aerial substrate was 42±10 spores per 100 g of dry substrate. On the other hand, the abundance of spores in the soil was 327±75 and 307±95 spores per 100 g of dry soil in the disturbed areas and riparian zones, respectively. There were 13 and 11 species in soils from the disturbed areas and riparian zones, respectively (ten species of *Glomus*, one species of *Gigaspora*, one species of *Acaulospora*, and one unidentified species). All species found in the riparian zone were also present in disturbed areas. In contrast, we found only four species of AM fungi (two species of *Glomus*, one species of *Gigaspora*, and an unidentified species) in the aerial substrate, and only two of these species (*Glomus* and *Gigaspora*) were shared with the soils.

Table 1 Chemical characterization of rooting environments of epiphytic and ground rooted *Ficus* species in the *Sabal* palmetto woodland. Values are means (±standard deviations) based on 20 samples in each rooting environment

	Ground soil		Aerial substrate
	Disturbed area	Riparian zone	
pH	3.8 (±0.3)	5.8 (±0.7)	6.2 (±0.9)
C (%)	1.0 (±0.5)	8.3 (±6.1)	43.4 (±8.0)
Nitrogen (%)	0.1 (±0.1)	1.3 (±0.3)	1.4 (±0.3)
Phosphorous (mg/g)	2.2 (±1.2)	15.7 (±12.1)	25.5 (±14.4)
Potassium (meq/100 g)	1.1 (±1.4)	0.6 (±0.3)	1.7 (±1.0)

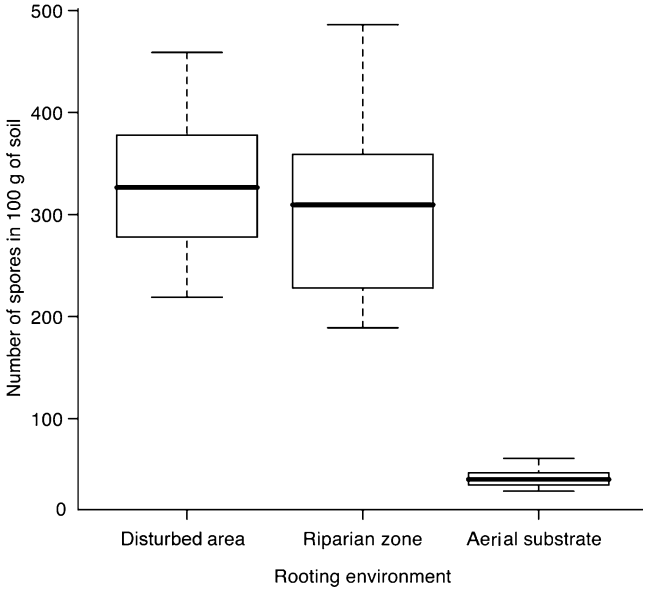

Fig. 1 Number of spores of AM fungi in 100 g of soil (median [*thick line*], first and third quartile [*box limits*], and minimum and maximum values [*whiskers*]) in three contrasting rooting environments in the *Sabal* palmetto woodland

Ergosterol content (Fig 2a) and the decomposition rate of plant litter (Fig. 2b) also showed significant differences between rooting substrates (F=8.5, df=2, 29, P<0.001 and F=14.9, df=2, 47, P<0.001, respectively). Both attributes were higher in the aerial substrate (P<0.001) than in the soils from disturbed areas, and in the case of the decomposition rate, there was no significant difference between the aerial substrate and soil from the riparian zone.

Interspecific and intraspecific variation in mycorrhizal colonization

The plants of *Ficus* species used to investigate inter- and intraspecific variation included *F. cotinifolia*, *F. lundelli*, and *F. obtusifolia* in only two rooting environments (aerial substrate and soil in disturbed areas). Species and the interaction between species and rooting environment had no significant effect on root colonization by AM fungi (F=1.03, df=2, 36, P<0.367 and F=0.10, df=2, 36, P=0.90, respectively). Colonization of epiphytic plants (Fig. 3) was 6.9±7.11 (mean±standard deviation), whereas it was 63.0± 11.8 for ground-rooted plants. This difference was highly significant (F=346.0; df=1, 36; P<0.001). Spores and vesicles were rarely observed during this study, and their incidence in roots is in less than 1% of the observed fields.

Spore inoculation in epiphytic plants

On average, we deposited 970±56 spores (recovered from soil) in the rhizosphere of each of the 20 plants that received mud recovered from the 128- and 52-μm sieves. This represents almost three times the number of spores counted in 100 g of soil in the same area (see above). We observed that root colonization by AM fungi was not significantly different between the control plants (4.1± 3.1%, mean±standard deviation) and those that received a ball of cotton wool with distilled water (3.7±2.5%; P=0.64, Fig. 4). In contrast, we observed a significant increase (F=5.05; df=2, 37; P=0.008) in the percentage of root colonization by AM fungi in plants that received mud with spores (13.2±3.2%). However, this increase in colonization

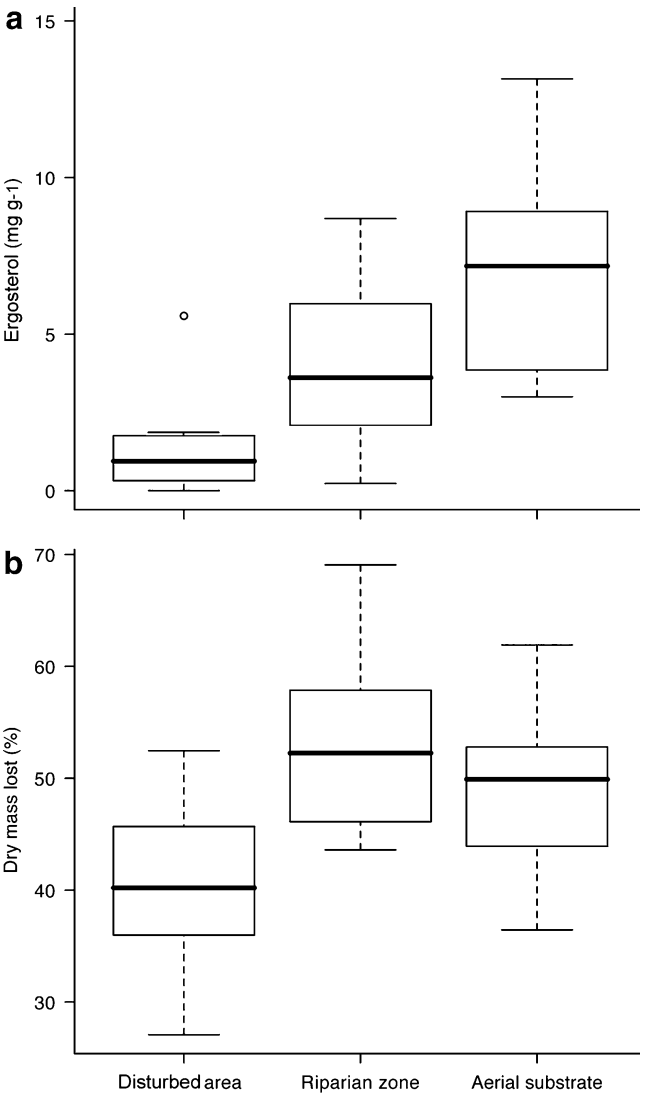

Fig. 2 Biological properties of three contrasting rooting substrates for strangler figs in the *Sabal* palmetto woodland. **a** Ergosterol content (median [*thick line*], first and third quartile [*box limits*], 1.5 time interquartile range below and above the first and third quartile [*whiskers*], respectively, and outliers [*small circles*]). **b** Decomposition rate of plant litter after four weeks under natural conditions (median [*thick line*], first and third quartile [*box limits*], and minimum and maximum values [*whiskers*])

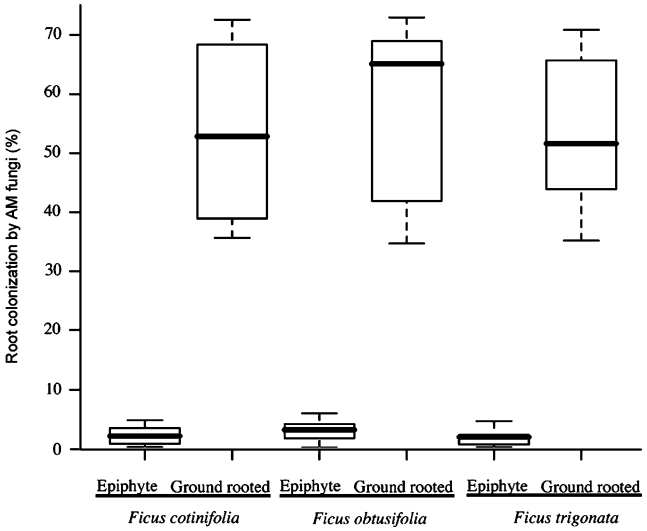

Fig. 3 Root colonization by AM fungi (median [*thick line*], first and third quartile [*box limits*], and minimum and maximum values [*whiskers*]) of *Ficus cotinifolia*, *F. obtusifolia* and *F. trigonata* as epiphytic plants (aerial rooting substrate) and ground rooted trees in the *Sabal* palmetto woodland, $n=7$ for all cases

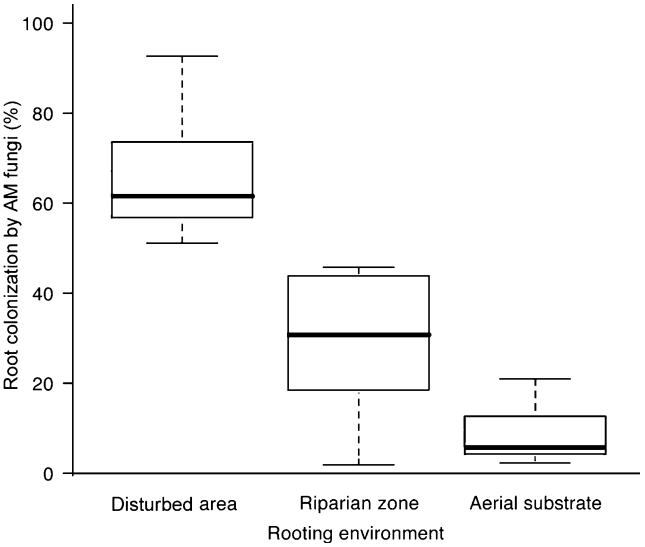

Fig. 5 Root colonization by AM fungi (median [*thick line*], first and third quartile [*box limits*], and minimum and maximum values [*whiskers*]) in *Ficus* trees in three contrasting rooting environments in the *Sabal* palmetto woodland

after spore inoculation was in marked contrast to the observed colonization of ground-rooted plants (60±7%).

Mycorrhizal colonization

The ANOVA model showed significant differences ($F=217.4$; $df=2, 59$; $P<0.001$) in the percentage of root colonization by AM fungi in the three rooting environments (Fig. 5). These differences accounted for 88% of the observed variability. The post-hoc test of Tukey showed significant differences among the three sites.

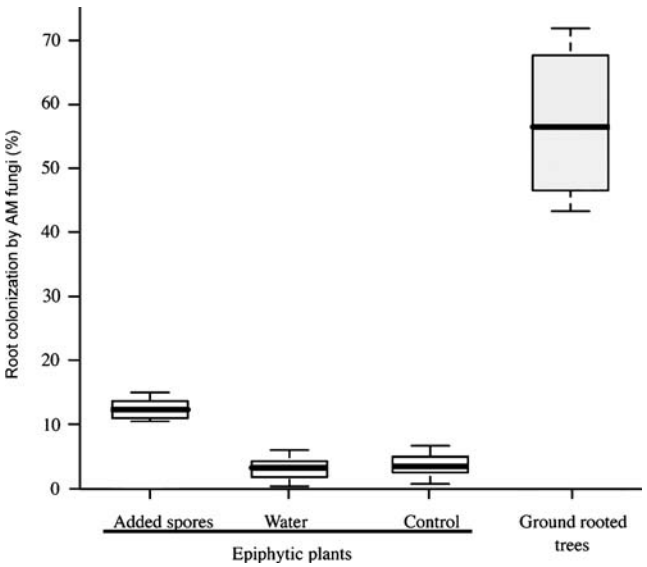

Fig. 4 Root colonization by AM fungi (median [*thick line*], first and third quartile [*box limits*], and minimum and maximum values [*whiskers*]) in spore-inoculated epiphytic plants of *Ficus padifolia* and naturally colonized ground-rooted trees in the *Sabal* palmetto woodland

Discussion

Our observations showed that root colonization by AM fungi in strangler figs varied mainly between developmental stages associated with contrasting rooting environments (epiphytic plants vs ground-rooted trees) rather than between species. This is not surprising, as phylogenetically close species (subgenus *Urostigma*), with the same habit (hemiepiphytic), growing in a common environment are expected to display similar strategies. Epiphytic plants took root in a mineral-rich, slightly acidic substrate and showed low levels of root colonization by AM fungi, whereas ground-grown trees grew in a strongly acidic, mineral-poor soil and showed high levels of root colonization. This is in agreement with the vast literature showing that adding fertilizers to soil reduces root colonization by AM fungi (Treseder 2004). Nevertheless, the main contribution our study makes to increasing understanding in this field is to show a natural scenario where plants of several *Ficus* species face a marked shift in the quality of their rooting environment during their development and to show how this affects plant–AM interactions as predicted by the plant investment hypothesis (Mosse and Phillips 1971).

The observed difference in phosphorus content (more than 11-fold) between rooting environments in our study site, coupled with the difference in pH, magnifies the contrast in mineral availability faced by the strangler figs,

as phosphorus will be less available to plants in the strongly acidic soils than in the near-neutral aerial substrate (Murrmann and Peech 1969). Notwithstanding the fact that the aerial substrate is rich in organic matter, which potentially makes nutrients less available to plants, we found high levels of ergosterol, an indirect measurement of fungal biomass (Zhao et al. 2005), and a higher decomposition rate. Thus, nutrients are readily released from the organic matter in the epiphytic substrate and rendered available for plants.

In accordance, the low levels of root colonization by AM fungi in epiphytic plants of *Ficus* species suggest that AM interactions may not be cost effective for these plants, as the aerial substrate is nutrient rich (Putz and Holbrook 1989). However, such low levels of root colonization by AM fungi could simply be a consequence of reduced opportunities for root colonization in the aerial substrate. This idea is supported by the fact that epiphytic strangler figs showed a threefold increase in root colonization by AM fungi when inoculated with spores (on average from 4.1 to 13.2%). Nevertheless, root colonization in inoculated epiphytic plants (13.2%) remained low compared with root colonization in ground-rooted trees (60%). Because we ended the inoculation experiment after 3 months, it could be argued that the observed increase in root colonization by AM fungi is time limited and that we underestimated the root colonization of epiphytic plants by AM fungi. Although our understanding on the dynamic of root colonization in seedlings of tropical trees is limited, there is evidence for seedlings of species such as *Guazuma ulmifolia*, *Leucaena leucocephala*, and *Ceiba pentandra* reaching above 25% root colonization 3 months after inoculation (Allen et al. 2003). With no assessment on the effect of the mycorrhizal potential of the utilized inoculum, we cannot disentangle whether low colonization in the experimental epiphytic plants is still limited by the availability inoculum or this is a consequence of the high mineral nutrient availability in the epiphytic substrate on the palms as would be predicted by the plant investment hypothesis (Mosse and Phillips 1971).

In addition, when we compared grown trees of similar size growing in contrasting rooting environments (riparian zones and perturbed areas), we observed the same expected pattern as predicted by the plant investment hypothesis (Mosse and Phillips 1971): low length of root colonized by AM fungi in rich soils. Therefore, our findings show that hemiepiphytic *Ficus* species growing in the *Sabal* palmetto woodland are facultative mycorrhizal trees (see Janos 1980) adjusting levels of root colonization they support in accordance with mineral availability. As such, strangler figs seem to maximize the cost–benefit balance of AM interactions throughout their development, from epiphytic young plants to ground-rooted trees, and this could have significant consequences for both ecological and evolutionary aspects of strangler fig biology.

Our findings are in complete agreement with those found in a similar system in the Llanos of Venezuela (*Copernicia* palms–*Ficus*), where there is also a marked contrast in rooting environments between epiphytic and ground-rooted plants (Putz and Holbrook 1989). It seems that contrasts in nutrient availability between aerial substrates and soil is a common characteristic of most tropical forests (Nadkarni et al. 2002) because of the accumulation of organic matter (Alvarez-Sanchez and Guevara 1989) and microbial activity (Wardle et al. 2003). Because the hemiepiphytic habit is widely distributed in tropical forests and plants with this habit, mainly *Ficus* species, have been reported to colonize up to 20% of tree stems in some tropical forests (Prosperi et al. 2001), our finding that AM interactions in hemiepiphytic *Ficus* species could be modulated by changes in the soil quality is relevant for a broad range of tropical ecosystems.

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