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Epiphytic and terrestrial mycorrhizas in a lower montane Costa Rican cloud forest

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Abstract The epiphyte community is the most diverse plant community in neotropical cloud forests and its collective biomass can exceed that of the terrestrial shrubs and herbs. However, little is known about the role of mycorrhizas in this community. We assessed the mycorrhizal status of epiphytic (Araceae, Clusiaceae, Ericaceae, and Piperaceae) and terrestrial (Clusiaceae, Ericaceae) plants in a lower montane cloud forest in Costa Rica. Arbuscular mycorrhizas were observed in taxa from Araceae and Clusiaceae; ericoid mycorrhizas were observed in ericaceous plants. This is the first report of intracellular hyphal coils characteristic of ericoid mycorrhizas in roots of *Cavendishia melastomoides*, *Disterigma humboldtii*, and *Gaultheria erecta*. Ericaceous roots were also covered by an intermittent hyphal mantle that penetrated between epidermal cells. Mantles, observed uniquely on ericaceous roots, were more abundant on terrestrial than on epiphytic roots. Mantle abundance was negatively correlated with gravimetric soil water content for epiphytic samples. Dark septate endophytic (DSE) fungi colonized roots of all four families. For the common epiphyte *D. humboldtii*, DSE structures were most abundant on samples collected from exposed microsites in the canopy. The presence of mycorrhizas in all epiphytes except *Peperomia* sp. suggests that inoculum levels and environmental conditions in the canopy of tropical cloud forests are generally conducive to the formation of mycorrhizas. These may impact nutrient and water dynamics in arboreal ecosystems.

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Introduction

The forest canopy has generally been considered a nutrient-poor environment for epiphytes, as canopy-dwelling plants have no connections to nutrients held in the forest floor nor to the vascular systems of their host trees (e.g., Madison 1977; Benzing 1987, 1990). Some epiphytes have evolved adaptations that provide efficient access to and retention of nutrients, such as litter-trapping leaf arrangements, slow growth rates, absorbent trichomes, ant-inhabited cavities, and mycorrhizas (Benzing 1987, 1990). Recent research with stable isotopes suggests that foliar nitrogen absorption by epiphytes is highly efficient and that "tight" nutrient cycling occurs within the canopy (Hietz et al. 1999, 2002).

Because of the physiological importance of mycorrhizas in nutrient-limited habitats (Smith and Read 1997), we would expect vascular epiphytes to be mycorrhizal. However, the results of previous studies suggest that many plant species that are commonly mycorrhizal when they grow terrestrially are inconsistently mycorrhizal when they grow epiphytically (e.g., Maffia et al. 1993; Nadarajah and Nawawi 1993). The juxtaposition of a mycorrhizal forest floor community with a non-mycorrhizal epiphytic canopy community is intriguing in neotropical cloud forests, where the vascular epiphyte community is more diverse and comprises a greater biomass than the terrestrial herbs and shrubs (Nadkarni 1984; Haber 2000). However, in most surveys of epiphyte mycorrhizas, roots were not sampled from the canopy but were collected either from fallen specimens of unknown origin or within a few meters of the ground (e.g., Bermudes and Benzing 1989; Lesica and Antibus 1990; Allen et al. 1993; Michelsen 1993; Gemma and Koske 1995).

We examined roots collected from canopy epiphytes and terrestrial plants in a lower montane cloud forest in Costa Rica. Taxa in three of the four families represented, namely Araceae, Clusiaceae, and Piperaceae, were expected to form arbuscular mycorrhizas (St. John 1980). Taxa in the fourth family, Ericaceae, were expected to form either arbutoid or ericoid mycorrhizas (Smith and Read 1997). In contrast to arbuscular mycorrhizas, ericoid mycorrhizas have enhanced abilities to mobilize nutrients from organic compounds (Cairney and Burke 1998; Chalot and Brun 1998). Thus, ericoid mycorrhizas may facilitate colonization into the canopy where light is relatively abundant, but where soils are highly organic and have low mineralization and nitrification rates (Vance and Nadkarni 1990; Ghosal et al. 1999; Nadkarni et al. 2002).

Worldwide, 30% of ericaceous genera occur in epiphytic habitats (Kress 1986) and members of the Ericaceae are common in forest canopies as disparate as the California redwoods (Sillett and Van Pelt 2000) and neotropical cloud forests (Luteyn 1989; Ingram et al. 1996). In our study area, terrestrial Ericaceae are generally restricted to exposed clearings in the dense forest, such as roadcuts and cliffs, whereas epiphytic Ericaceae are abundant and species-rich. For example, within the boundaries of the Monteverde Cloud Forest Preserve (MVCP), there are only two terrestrial ericaceous species but 28 epiphytic species (Haber 2000).

The objectives of this study were: 1) to assess the mycorrhizal status of vascular epiphytes collected from the forest canopy, 2) to compare mycorrhizal colonization of epiphytic and terrestrial Ericaceae, and 3) to explore potential relationships between mycorrhizal colonization and abiotic conditions, including position within the tree, canopy coverage, canopy soil depth, soil P concentration, and gravimetric soil water content.

Materials and methods

During May 2001, we sampled roots from epiphytic and terrestrial plants in the lower montane cloud forest within 6 km of the MVCP, Costa Rica (10° 18' N 84° 47' W). The epiphyte community is one of the most abundant and diverse recorded (Nadkarni 1984; Haber 2000). The canopy is exposed to frequent and intense mist throughout much of the year; mean annual precipitation is in the range of 1,850–8,000 mm (Clark et al. 2000). The upper tree canopy experiences greater extremes of temperature and more frequent and extreme wetting and drying cycles than the forest floor (Bohlman et al. 1995).

Our sample sites included a lower montane wet forest near the entrance of MVCP (site A, 1,460 m, 10° 18' N 84° 47' W), an elfin forest at La Ventana within MVCP (site B, 1,550 m, 10° 18' 5" N 84° 47' 5" W), a lower montane wet forest near the Santa Elena Reserve (site C, 1,700 m, 10° 20' 40" N 84° 48' 5" W), and a lower montane rain forest in La Estación Biológica (site D, 1,450 m, 10° 19' 25" N 84° 48' 40" W) (Haber 2000).

Root collection and mycorrhizal assessment

We examined roots from 43 plants, including 23 canopy epiphytes, 16 terrestrial plants, and four *Disterigma humboldtii* plants rooted in coarse woody debris on the forest floor. We gained access to the arboreal epiphyte collection sites via single-rope climbing techniques (Perry 1978) on established climbing trees. Epiphytes from the target families were present in and collected from five of the nine trees climbed [three *Ficus tuerckheimii* Standl. (Moraceae), one *Ocotea tonduzii* Standl. (Lauraceae), and one *Quercus corrugata* Hook. (Fagaceae)]. Epiphytes were collected from branch junctions and along branches 15–25 m from the ground and within 3 m of the central bole. Sections of plants and accompanying roots were collected and transported to the laboratory where roots were traced from plant stem to root tip within 24 h of collection. Unattached roots were discarded. Roots were either cleared immediately (10% KOH, room temperature, 5–7 days) or were preserved for up to 2 months (20°C) in 40–70% ethanol prior to clearing. *Clusia* (Clusiaceae) and *Stenospermation* (Araceae) roots were cleared for an additional 1–2 h in 3% H_2O_2 at 40°C. Cleared roots were acidified in 1% HCl and stained with 0.05% trypan blue (Phillips and Hayman 1970), except for a subsample of cleared terrestrial *Gaultheria erecta* roots that were embedded in Historesin (Leica Instruments, Heidelberg) (Dubrovsky et al. 2000), sectioned (2 μm), and stained with 0.05% toluidine blue for 5 min.

For specimens of Araceae, Clusiaceae, and Piperaceae, at least 30 cm of root was examined (×400) for the presence/absence of vesicles, arbuscules, and dark septate endophytes (DSE). Further quantification of arbuscular mycorrhizal colonization followed McGonigle et al. (1990) with the following exceptions: root intersections were examined at ×400, and the maximum number of sightings scored for a single intersection was one, even if arbuscules, vesicles, and hyphae were all present. These intersections were also assessed for the presence of DSE hyphae and microsclerotia.

For ericaceous species, at least 24 cm of the finest roots (≤ 0.15 mm diameter) from each plant were examined. For each plant, 20 fields of view (×400) containing roots were randomly chosen for quantification. We estimated percent root length within each field of view covered by DSE hyphae and/or a mantle. In the first 10 of these fields of view, we also determined the proportion of cells containing ericoid mycorrhizal hyphal coils or DSE microsclerotia. If cells were obscured by a mantle, we searched along that same root for an area with visible cells. For each habitat (epiphytic or terrestrial), mean values for each fungal colonization type were computed by species and then converted into one of five colonization intensity levels: 0, no colonization; 1, <25%; 2, 26–50%; 3, 51–75%; 4, 76–100%.

Canopy coverage and soil analyses

At each root collection location, we visually estimated percent canopy coverage above the sampled plant (0–25%, 26–50%, 51–75%, 76–100%) and obtained soil samples for determination of gravimetric water content (Jarrell et al. 1999). We measured canopy soil depth at all epiphyte collection locations. At site A, seven soil samples were collected for determination of extractable-P. Five of these samples were obtained at epiphyte root collection sites (1–5 cm soil depth); the other two were obtained from the terrestrial Oa horizon below epiphyte collection sites. Samples were dried, sieved (2 mm), and analyzed for Bray I extractable-P (Olsen and Sommers 1982, A & L Analytical Laboratories, Modesto, Calif.).

Statistical analyses

Statistical tests were performed on data from taxa of the Ericaceae. We used three two-way ANOVAs to analyze effects of species and habitat on abundance of ericoid mycorrhizal hyphal coils, mantle, and DSE hyphae. We used a one-way ANOVA followed by a Tukey test to analyze the effect of canopy cover class on DSE hyphal abundance in epiphytic *D. humboldtii*. We evaluated the relationship between gravimetric soil moisture and mantle abundance on epiphytic ericaceous roots by simple linear regression. All tests were performed on colonization values for individual plants using SigmaStat 2.03 software (SPSS Inc. Chicago, Ill.).

Results

Arbuscular mycorrhizas

Vesicles and aseptate hyphae were observed in roots of *Anthurium pitteri*, *Clusia minor*, *C. rotundata*, *Clusia* sp. (Fig. 1), and *Stenospermation* sp. (Table 1). Colonization levels were surprisingly high in these taxa (26–75%, Table 1). Arbuscules were less common, but were observed in epiphytic *A. pitteri*, *C. rotundata* (Fig. 2), and *Clusia* sp. (Table 1). Arbuscular mycorrhizal colonization was not observed in *Peperomia* sp. or in any ericaceous species (Table 1).

Ericoid mycorrhizas

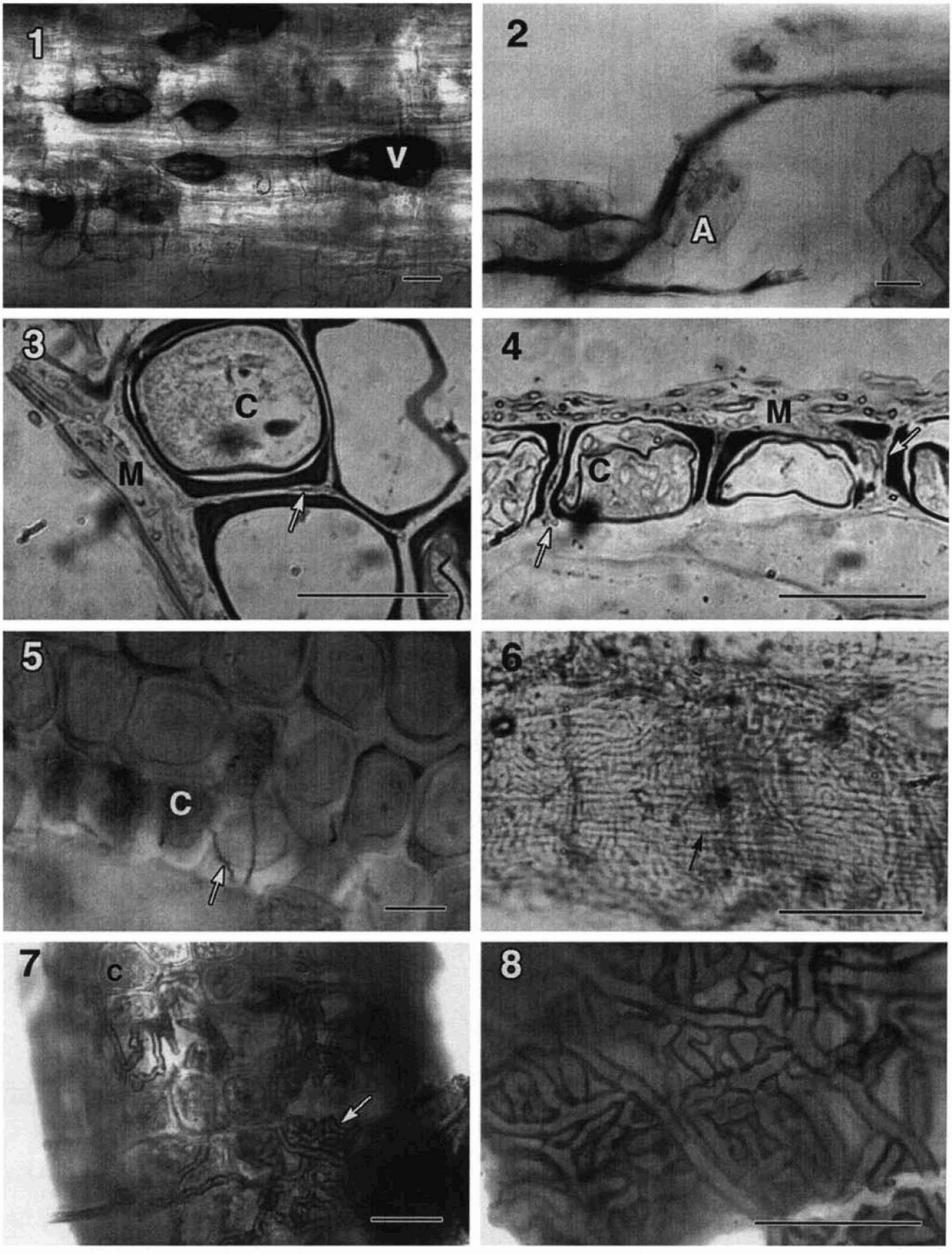
The morphology of epiphytic ericaceous roots was generally different from that of terrestrial ericaceous roots. The fine epiphyte roots (≤0.15 mm diameter) were infrequently branched and emerged directly from black, relatively thick (1 mm diameter) rhizomes. In contrast, terrestrial root systems were highly branched and gradually tapered to <0.15 mm diameter.

Typical ericoid mycorrhizal structures include intracellular hyphal coils formed by hyphae that have penetrated the external cell wall (Duddridge and Read 1982). We observed both dense (Fig. 3) and loose (Fig. 4) intracellular hyphal coils as well as hyphal penetration of the external cell wall (Fig. 5). Intracellular hyphal coils (Figs. 3, 4, 5) were present in roots of all ericaceous plants examined, regardless of habitat type (epiphytic, terrestrial, or coarse woody debris), position within the tree, canopy coverage, canopy soil depth, or gravimetric soil water content. Intracellular hyphal coil abundance did not differ significantly between epiphytic and terrestrial ericaceous plants (P 0.4, Table 1).

In addition to the external hyphal wefts commonly associated with ericoid mycorrhizas (Duddridge and Read 1982), we observed mantles (7 μm thick) consisting of multiple layers of densely interwoven hyphae (≤1 μm width) that, once stained, obscured the cells below (Fig. 6). Mantles (Figs. 3, 4, 6) were present at intermittent intervals on ericoid mycorrhizal roots collected from primary forest, roadcuts, terrestrial sites,

Table 1 Fungal colonization of epiphytic (15–25 m) and terrestrial vascular plant roots from a lower montane cloud forest in Costa Rica. Letters and numbers in parentheses following species refer to site and number of plants examined. Sites: *a*, near the entrance of Monteverde Cloud Forest Preserve (MVCP); *b*, La Ventana in MVCP; *c*, near Santa Elena Reserve; *d*, La Estación Biológica. Abundance classes (*0*, no colonization, *1*, <25%, *2*, 26–50%, *3*, 51–75%, *4*, 76–100%, *nd*, not determined) represent % root length or % root cells (see methods) occupied by indicated structures. *AM* Arbuscular mycorrhizas, *DSE* dark septate endophytes, *E* epiphytic, *T* terrestrial, *H* hyphae (internal hyphae for AM, internal or external hyphae for DSE), *V* vesicles, *A* arbuscules, *M* microsclerotia

Species	Habitat	AM		Ericoid hyphal coils – % root cells colonized	Mantle abundance	DSE	
		Structures	Abundance			Structures	Hyphal abundance
Monocot							
Araceae							
Anthurium pitteri Engl. (a:1)	E	H, V, A	3	0	0	–	0
Stenospermation sp. (a:1)	E	H, V	2	0	0	H	1
Dicot							
Clusiaceae							
Clusia minor L. (a:1)	T	H, V	3	0	0	H, M	1
C. rotundata Standl. (a:1)	E	H, V, A	3	0	0	H, M	1
Clusia sp. (a:3)	E	H, V, A	3	0	0	H, M	1
Ericaceae							
Cavendishia capitulata J.D. Sm. (a:1; d:1)	E	–	0	3	2	H	1
C. capitulata (a:1)	T	–	0	2	1	H, M	2
C. melastomoides (Klotzsch) Hemsl. (a:2)	E	–	0	2	2	H, M	1
C. melastomoides (a:2)	T	–	0	3	4	H	1
Disterigma humboldtii (Klotzsch) Nied. (a:9)	E	–	0	2	3	H, M	2
D. humboldtii (a:2; b:2; c:2)	T	–	0	2	4	H	1
Gaultheria erecta Vent. (b:1)	T	–	0	1	3	–	0
Gonocalyx costaricense Luteyn (a:1)	E	–	0	3	nd	H, M	3
Sphyospermum buxifolium Poeppig & Endl. (d:1)	E	–	0	3	1	H, M	3
S. buxifolium (a:2; c:1)	T	–	0	2	4	H, M	2
Sphyospermum cordifolium Benth. (a:2)	E	–	0	2	3	H	1
S. cordifolium (c:2)	T	–	0	2	4	H	1
Piperaceae							
Peperomia sp. (a:1)	E	–	0	0	0	H, M	1


1
V
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epiphytic sites, and both sides of the Costa Rican continental divide. Mantles were not observed on Araceae, Clusiaceae, or Piperaceae roots, even when these were growing intertwined with ericaceous roots (Table 1). Mantle abundance did not differ significantly among ericaceous species (P 0.5), but was significantly lower on epiphytes than on terrestrial plants (Table 1, P 0.02). Mantle abundance on ericaceous epiphytes was inversely related to gravimetric water content (R^2 0.56, P 0.05). Mantle hyphae penetrated between epidermal root cells (Figs. 4, 5).

Dark septate endophytes

DSE hyphae (2–4 μm width) and microsclerotia were common in ericaceous species, particularly epiphytic Ericaceae (Figs. 7, 8), but were present also in *Stenospermation* sp., *C. minor*, *C. rotundata*, *Clusia* sp., and *Peperomia* sp. (Table 1). As noted in other systems (Urcelay 2002), DSE were often present on roots colonized by arbuscular mycorrhizal or ericoid mycorrhizal fungi (Table 1, Fig. 7). We observed typical DSE structures including loose wefts of runner hyphae (Fig. 7), partial mantles (Fig. 8), and microsclerotia (Table 1). Among epiphytic *D. humboldtii*, the highest DSE colonization levels were associated with samples collected from sites with the least canopy coverage (P 0.04).

Canopy coverage and soil analyses

Epiphytes were present in and collected from microsites with 26–100% cover. Within the study area, terrestrial Ericaceae are restricted to forest openings; thus, terrestrial ericaceous plants were collected from only one canopy coverage class (0–25%). The depths of canopy soils varied according to position within the tree. Canopy soils were thickest at branch junctions (1- to >50 cm), less thick along nearly horizontal limbs (0.5–5 cm), and absent on vertically oriented branches. Gravimetric soil water content was lower in canopy soils (0.67 g H_2O per g dry soil, range 0.31–1.14) than in terrestrial soils (0.82 g H_2O per g dry soil, range 0.42–1.24). Extractable-P levels were low in canopy soils (3 ppm, range 1–4 ppm) and in the terrestrial Oa horizon (8 ppm, range 3–17 ppm).

Fig. 1 Vesicles (*V*) in epiphytic *Clusia* sp., whole mount, trypan blue

Fig. 2 Arbuscules (*A*) in epiphytic *Clusia rotundata*, whole mount, trypan blue

Fig. 3 Dense ericoid mycorrhizal coils (*C*), mantle (*M*), and extensions of mantle hyphae between root cells (*arrow*) in terrestrial *Gaultheria erecta*, longitudinal section, toluidine blue (5 min)

Fig. 4 Loose ericoid mycorrhizal coils (*C*), mantle (*M*), and extensions of mantle hyphae between root cells (*arrows*) in terrestrial *G. erecta*, longitudinal section, toluidine blue (5 min)

Fig. 5 Ericoid mycorrhizal coils (*C*) and hyphal penetration of the external cell wall (*arrow*) in terrestrial *G. erecta*, whole mount, trypan blue

Fig. 6 Surface view of hyphae (*arrow*) comprising a mantle on terrestrial *G. erecta* whole mount, trypan blue

Fig. 7 Ericoid mycorrhizal coils (*C*) and dark septate endophyte (DSE) hyphae (*arrow*) on epiphytic *Disterigma humboldtii*, whole mount, trypan blue

Fig. 8 DSE partial mantle on epiphytic *D. humboldtii*, whole mount, trypan blue

Discussion

Mycorrhizal associations benefit both plant host and fungus. Although we did not assess the effects of the observed fungal associations on plant host and fungus, we refer to these associations as "mycorrhizas" when we observed structures typical of AM and ericoid mycorrhizas in plant families known to be mycorrhizal.

Arbuscular mycorrhizas

Previous reports have suggested that arbuscular mycorrhizas generally are absent or rare in epiphytes (Bermudes and Benzing 1989; Allen et al. 1993; Nadarajah and Nawawi 1993). However, we found abundant vesicles and hyphae and occasional arbuscules in epiphytic Araceae and Clusiaceae roots. Lesica and Antibus (1990) also observed epiphytic arbuscular mycorrhizas in this region. Thus, conditions in the canopy of this lower montane cloud forest may be particularly conducive to the colonization of epiphytes by arbuscular mycorrhizal fungi.

Three factors that may facilitate arbuscular mycorrhizal colonization are low P concentration, elevated moisture level, and the presence of potential biotic spore dispersers. We believe that all three factors may function in the canopy at this study site. The non-ericaceous epiphytes we examined were rooted along branches in shallow soils containing low levels of extractable-P. Moderately low concentrations of extractable-P have been associated with enhanced levels of arbuscular mycorrhizal colonization (Bolan et al. 1984).

The year-round mist characteristic of the lower montane cloud forest may facilitate development of a mycorrhizal epiphyte community, either directly through support of arbuscular mycorrhizal hyphae, or indirectly through maintenance of a vigorous and abundant vascular epiphyte community. Although canopy soils are chemically similar to the O horizon of the forest floor below (Vance and Nadkarni 1990), they are subject to more frequent and severe drydowns (Bohlman et al. 1995). The frequency and severity of drydowns may be tempered by cool and humid conditions in the cloud forest. Data from a comparison of three Venezuelan forests (Rabatin et al. 1993) suggest that the most plentiful arbuscular mycorrhizal colonization and most diverse arbuscular mycor-

rhizal fungal community are associated with the wettest of these forests. In a survey of epiphytes on fallen branches within the MVCP, Lesica and Antibus (1990) found mycorrhizas only in samples from moist microsites. Samples collected from relatively dry bare branches were non-mycorrhizal. We did find mycorrhizas on epiphytes collected from bare branches; however, due to safety considerations, we were restricted to collecting within 3 m of the central bole and did not sample epiphytes from exposed branch tips.

Biotic spore dispersal may be critical in areas where the dense canopy can limit wind dispersal of arbuscular mycorrhizal spores (Allen 1991). However, many potential biotic spore dispersers such as worms, ants, wasps, birds, and rodents (McIlveen and Cole 1976; Janos and Sahley 1995; Mangan and Adler 2000) are present in the Costa Rican cloud forest canopy (Nadkarni and Longino 2000; Hanson 2000; Young and McDonald 2000; Langtimm 2000) In particular, mycorrhizal spores have been found in feces of four scansorial mice species in the MVCP (Langtimm 2000). Thus, spore dispersal may be supported by multiple vectors in this study area.

Of the four families surveyed, only Piperaceae lacked both arbuscular and ericoid mycorrhizal structures. Non-mycorrhizal epiphytic Piperaceae have been reported from MVCP (Maffia et al. 1993; Lesica and Antibus 1990), La Selva, Costa Rica (Lesica and Antibus 1990) and Ethiopia (Michelsen 1993). In contrast, arbuscular mycorrhizas were observed in terrestrial Piperaceae at MVCP (Maffia et al. 1993), and from epiphytes growing close (0.4–3 m) to the ground in Malaysia (Nadarajah and Nawawi 1993), Hawaii (Gemma and Koske 1995), and Ecuador (Bermudes and Benzing 1989). However, we cannot assume an inverse relationship between arbuscular mycorrhizal colonization of Piperaceous species and distance from the ground because no study has examined roots of a single species of Piperaceae collected from a wide range of heights.

Ericoid mycorrhizas

Ericoid mycorrhizas are common in many areas dominated by organic soils, and epiphytic habitats are no exception. We observed intracellular hyphal coils typical of ericoid mycorrhizas in ericaceous plants growing in epiphytic sites and in coarse woody debris on the forest floor. Ericoid mycorrhizas have been detected previously in ericaceous epiphytes collected from felled trees in Ecuador (Bermudes and Benzing 1989), fallen branches in Costa Rica (Lesica and Antibus 1990), and from within 3 m of the ground in Hawaii (Gemma and Koske 1995). Thus, unlike many other epiphyte families, Ericaceae may be consistently mycorrhizal in a variety of habitats, including tree canopies.

We observed both loose and dense intracellular hyphal coils within the same section of a root. McLean et al. (1998) noted similar variation in intracellular hyphal coil density following inoculation of *Epacris impressa* Labill. roots by a single fungal isolate. Thus, such variation may be indicative of differences in colonization stage.

In addition to intracellular hyphal coils typical of ericoid mycorrhizas, we unexpectedly observed mantles as well as finger-like projections of mantle hyphae extending between epidermal cells suggestive of a Hartig net. Extensive external hyphae, mantles, or mantles in conjunction with Hartig nets have been reported on ericoid mycorrhizal plants from the USA (Smith et al. 1995; Wurzburger and Bledsoe 2001), Ecuador (Bermudes and Benzing 1989), Canada (Xiao and Berch 1996), and Italy (Bergero et al. 2000). These reports include plants grown in vitro (Bergero et al. 2000), in the greenhouse (Smith et al. 1995), and collected from the field (Bermudes and Benzing 1989; Xiao and Berch 1996; Wurzburger and Bledsoe 2001). Further work is needed to determine whether the association between these mantle-forming fungi and the plant host is mycorrhizal.

Other members of the Ericales (e.g., *Arbutus*, *Arctostaphylos*, *Pyrola*) form arbutoid mycorrhizas consisting of intracellular coils, external hyphal development ranging from a loose weft of hyphae to a mantle, and an intermittent to well-developed Hartig net (Robertson and Robertson 1985; Massicotte et al. 1993). Although this combination of characters is similar to our observations, it would be premature to classify our observations as "arbutoid mycorrhizas", or to designate the hyphal projections between cells as a "Hartig net". Phylogenetic analyses indicate that the reduced ericoid mycorrhizal condition evolved from an arbutoid mycorrhizal ancestor prior to evolution of the vacciniid and *Gaultheria* taxa represented in this study (Cullings 1996; Cairney and Ashford 2002). In addition, several features may distinguish our observations from structures associated with arbutoid mycorrhizas. The mantle we observed was intermittent along plant roots and the hyphal projections between plant cells was generally not as extensively branched as those associated with arbutoid Hartig nets (Robertson and Robertson 1985; Massicotte et al. 1993). This lack of branching in conjunction with the relatively thick cell walls of the epidermal root cells may preclude the efficient transfer of materials characteristic of a Hartig net (DJ Read, personal communication).

Unlike the sparse hyphal weft typically associated with ericoid mycorrhizas, a mantle may create a barrier to direct passage of water and nutrients between the soil and plant root. Our results indicate mantle abundance may be influenced by environmental factors. Mantle abundance was highest on ericaceous roots collected from terrestrial habitats and was negatively correlated with gravimetric soil moisture content on ericaceous roots collected from epiphytes. However, taxonomic identity of the mycobiont(s) may also play a role. For example, Bergero et al. (2000) found that formation of an extensive hyphal net on *Erica arborea* grown in vitro was limited to colonization by a particular fungal isolate.

Dark septate endophytes

DSE refers to an assemblage of fungi that form characteristic inter- and intracellular structures, including a superficial net of hyphae, penetration into the cortical layer, microsclerotia and, occasionally, a partial mantle (Jumpponen and Trappe 1998). Consensus has not been reached on whether this association is mycorrhizal; effects of DSE colonization may be contingent upon both host and fungal genotypes (Jumpponen 2001). However, the range of plant responses to colonization by DSE is not unlike the range of responses to colonization by various mycorrhizal types (Jumpponen 2001).

Although DSE have not been reported previously in any of the species described in this study, they have been reported in taxa from at least 114 families worldwide (Jumpponen and Trappe 1998). DSE are common in stressful habitats such as arctic (Jumpponen and Trappe 1998) or alpine environments (Read and Haselwandter 1981), and the acidic organic soils of the California pygmy forest (Wurzburger et al. 2001). Similarly, we observed abundant DSE hyphae on ericaceous roots from potentially stressful epiphytic habitats.

The inverse relationship between canopy coverage and DSE abundance in epiphytic *D. humboldtii* may be a response to changes in water and/or light levels. Similar increases in abundance have been noted in other mycorrhizal associations in response to drought (Augé 2001) and to increased light levels (Whitbeck 2001). The melanins in DSE hyphae may provide additional protection against desiccation (Jumpponen and Trappe 1998).

In conclusion, the abundant mycorrhizal structures on epiphytic roots examined in this study indicate significant mycorrhizal presence in the canopy of this lower montane cloud forest. Thus, mycorrhizal activity may influence nutrient and water uptake by canopy epiphytes as well as terrestrial neotropical cloud forest species.

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