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Host preferences of low-trunk vascular epiphytes in a cloud forest of Veracruz, Mexico

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Abstract: The diversity, abundance and frequency of vascular epiphytes on the lower trunk were compared between two host groups of a Mexican cloud forest: angiosperm trees (n = 72) and tree ferns (n = 28). The bark of the five most frequent host trees and the root mantle of the two tree ferns were analysed for their thickness, water content, water retention capacity and pH. A total of 55 epiphyte species and 910 individuals were found on the 27 host species. On hosts with a dbh range of 5–10 cm, epiphytes were significantly more diverse (4.3 ± 0.9 species per host) and more abundant (12.5 ± 2.2 individuals per host) on tree ferns than on angiosperm trees (1.9 ± 0.2 species per host and 3.9 ± 0.6 individuals per host). However, these differences were not significant for the dbh class of 10–20 cm, because epiphyte numbers increased on angiosperm trees with larger host size, but not in tree ferns. Most epiphyte species had no preference for any host group, but four species were significantly more frequent on tree ferns and two species on angiosperm trees. The higher epiphyte diversity and abundance on tree fern trunks of the smallest dbh class is attributed to their presumably greater age and to two stem characteristics, which differed significantly between host groups, the thicker root mantle and higher water retention capacity of tree ferns. These bark characteristics may favour germination and establishment of epiphytes.

Key Words: *Alsophila firma*, bark characteristics, *Cyathea divergens*, diversity estimators, *Peltapteris peltata*, root mantle, *Trichomanes*, tree ferns, water retention capacity

INTRODUCTION

Epiphyte–phorophyte relationships are not well understood (Benzing 1990, 1995). However, several authors reported favourable and unsuitable host species for epiphytes (Valdivia 1977, Zotz & Andrade 2002), and some host preferences for non-vascular epiphytes (Cornelissen & ter Steege 1989, González-Mancebo *et al.* 2003, Peck 1997, Went 1940), vascular epiphytes (Catling & Lefkovitch 1989, Díaz Santos 2000, Freiberg 1996, García-Franco & Peters 1987, ter Steege & Cornelissen 1989, Zimmerman & Olmsted 1992), and hemiepiphytes (Williams-Linera 1992). Host specificity, the exclusive presence of one epiphyte species on one host species, was rarely observed (Tremblay *et al.* 1998). The epiphyte–host relationship depends on specific host characteristics, for example tree architecture (Zotz & Andrade 2002), bark relief, water retention capacity (Callaway *et al.* 2002, Castro Hernández *et al.* 1999) and allelopathic components (Benzing 1990, Frei & Dodson 1972).

Since the microclimatic conditions on the lower trunk are relatively constant (Johansson 1974), the distribution of epiphytes should primarily depend on bark characteristics of the host trees. Many authors have studied angiosperm trees as host species (Benzing 1990, Lawton & Williams-Linera 1996, Zotz *et al.* 1999); however, tree ferns (Beever 1984, Johansson 1974, Medeiros *et al.* 1993, Moran *et al.* 2003, Oliver 1930, Pócs 1982) and other arborescent ferns, e.g. *Blechnum palmiforme* (Heatwole 1993) have been scarcely considered. Trunks of tree ferns offer an uncommon substrate for epiphytes (Hietz & Wolf 1996, Moran *et al.* 2003, Palacios-Rios & Mehltreter 1999), because dead leaves or their petiole bases may remain on the trunk

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(Page & Brownsey 1986), and aerial roots may form a root mantle, which covers the trunk gradually upwards and which can favour epiphyte establishment (Johansson 1974, Kelly 1985, Oliver 1930). To our knowledge, Oliver (1930) was the first, who mentioned a distinctive epiphyte flora on tree ferns, with some species excluded by and others confined to tree fern trunks. Examples for epiphytes nearly restricted to tree ferns are *Lycopodium novae-zealandicum*, *Tmesipteris tannensis*, *Trichomanes ferrugineum* and *T. venosum* in New Zealand (Oliver 1930), *Terpsichore asplenifolia*, *Trichomanes angustatum*, *T. capillaceum*, *T. polypodioides* in Mexico (Mickel & Beitel 1988), *Terpsichore liogieri* in Puerto Rico (Proctor 1989), and *Costaricia werckleana*, *Terpsichore lehmanniana* and *T. semihirsuta* in Central America (Moran & Riba 1995). The preceding examples were based on observations, but not on quantitative field studies. Moran *et al.* (2003) found that epiphytic ferns were more diverse and abundant on tree ferns than on angiosperms at four sites in Costa Rica, but did not distinguish among angiosperm host species and did not measure bark characteristics to explain these differences.

The aim of this study was to compare the epiphyte diversity and frequency between angiosperm trees and tree ferns under the same macroclimatic conditions in a cloud forest, where both host groups coexist (Tryon & Tryon 1982) and epiphytes are abundant (Aguirre-León 1992, Gentry & Dodson 1987). We further investigated if there exist host preferences, and if dbh (diameter at breast height, 1.30 m) or characteristics of the root mantle of tree ferns or the bark of angiosperms, such as thickness, water content, water retention capacity and pH could explain the host preferences of the epiphytes. Our hypotheses were that epiphytes would be more diverse and more abundant on (1) larger trees (larger dbh), on (2) tree ferns, on (3) host species with supposedly favourable bark characteristics, such as high water content and high water retention capacity, and that (4) some epiphytes will show specific preferences for one of the host groups.

STUDY SITE

The study was carried out in a 7-ha cloud forest fragment, located in a gorge in San Andrés Tlalnelhuayocan, near Xalapa, Veracruz, Mexico (19°30′56″N, 96°59′50″W; altitude 1500–1600 m asl). The study site is about 200 m from the forest edge. Annual precipitation is 1514 mm with a drier period from November to April, and a mean annual temperature of 17.9 °C (García 1981). The altitude and climate define the vegetation as a montane cloud forest (Hamilton *et al.* 1995). The forest is a complex system with a mean canopy height of 30 m and with primary tree species, including *Quercus* spp. (Fagaceae), *Liquidambar styraciflua* (Hamamelidaceae) and *Clethra mexicana* (Cyrillaceae), in addition to many shrubs and vines (Zamora & Castillo-Campos 1997). To date, there have been 81 vascular epiphyte species recorded on the upper trunk and tree branches in this forest fragment and 101 species including the surrounding landscape. Orchidaceae, Bromeliaceae and Polypodiaceae are the families with the highest diversity and abundance (Flores-Palacios & García-Franco 2001).

METHODS

We tagged all 100 living trees with a dbh $\geq$ 5 cm along four transects of 30 m length and 5 m width (total area 600 m^2). Transects were 100 m distant from each other and ran perpendicular to a permanent creek on a SW-facing slope with 40–50° inclination. For each tree, we recorded the following data: species name (or morphospecies, especially for juvenile individuals, which could not be identified to species level), dtb (diameter at trunk base), dbh and distance from the creek. The taper of the trunk was determined as the difference between dtb and dbh.

In November 1999, at the end of the rainy season, we surveyed all trunks for epiphytes on a section from the ground to a height of 1.5 m. Epiphyte diversity (number of species) and abundance (number of individuals) were recorded on each tree trunk ($n = 100$). As measure of abundance, we applied the concept of 'stands' *sensu* Sanford (1968), i.e. clearly delimited patches of the same species, because the delimitation of individuals was impossible for several fern species with long-creeping and ramifying rhizomes. Epiphyte frequencies are reported as the number of hosts on which each species occurred (Appendix 1). Jackknife 1 was used as non-parametric estimator of species richness (Chazdon *et al.* 1998, Palmer 1990, 1991) and its standard deviation was calculated with the formula given in Burnham & Overton (1978) and Gimaret-Carpentier *et al.* (1998). Species are listed, following the classification system of Mabberley (1997). Species vouchers were deposited at XAL, the Herbarium of the Instituto de Ecología, A. C. in Xalapa.

We confirmed the uniform distribution of both host groups with increasing distance from the creek, running a Kolmogorov–Smirnov Goodness-of-Fit test for continuous data (Zar 1999). Relationships between dbh, number of species, number of individuals and bark characteristics were explored using Spearman rank correlation.

To compare both host groups for their suitability as epiphyte substrate, considering bark characteristics, mean dbh, and tapering of the trunk, we ran the Mann–Whitney rank sum test. Since transects included several angiosperm tree species with less than five individuals, we

Table 1. Characteristics of host species, two tree ferns (marked *) and five angiosperm trees in a Mexican cloud forest. Mean ± SE. Different superscripts indicate significant differences, Mann–Whitney, $P < 0.05$.

Host species	Number of trees	Basal area ($m^2\ ha^{-1}$)	Mean number of epiphytes per tree: Species	Individuals
Alsophila firma (Baker) Conant*	15	3.1	3.6 ± 0.7	10.8 ± 1.9
Cyathea divergens Kunze*	13	3.7	5.2 ± 0.7	16.8 ± 2.2
Arachnothryx capitellata (Hemsl.) Borhidi	12	1.2	2.3 ± 0.3	5.8 ± 1.0
Clethra mexicana DC.	8	11.9	4.1 ± 0.5	9.9 ± 2.0
Bernardia interrupta (Schltr.) Müll. Arg.	6	3.8	2.8 ± 1.1	8.3 ± 3.6
Liquidambar styraciflua L.	6	7.7	2.5 ± 1.0	5.5 ± 2.2
Styrax glabrescens Benth.	6	1.2	3.7 ± 0.8	9.8 ± 4.2
Other 20 spp.[1]	34	8.6	2.7 ± 0.4	7.0 ± 1.6
All tree ferns*	28	6.8	4.3 ± 0.5^a	13.6 ± 1.5^a
All angiosperms	72	34.4	2.9 ± 0.2^b	7.3 ± 0.9^b
All hosts	100	41.2	3.3 ± 0.2	9.1 ± 0.8

[1] *Alchornea latifolia* Sw. (1 individual), *Carpinus caroliniana* Walt. (1), *Citharexylum mocinnii* D.Don (1), *Eugenia* sp. (1), *Icacorea compressa* (Kunth) Standl. (2), *Inga* sp. (1), *Oreopanax capitatus* (Jacq.) Decne. & Planch. (1), *Picramnia* sp. (4), *Prunus serotina* Ehrenb. (1), *Quercus leiophylla* A.DC. (2), *Rapanea myricoides* (Schltdl.) Lundell, (1), *Senecio* sp. (4), Sp. A (1), Sp. B (1), Sp. C (1), Sp. D (3), *Symplocos coccinea* Bonpl. (2), *Turpinia insignis* (Kunth) Tul. (3), *Xylosma flexuosum* (Kunth) Hemsl. (1), *Zanthoxylum riedelianum* Engl. (2).

restricted further comparisons to the five most abundant angiosperm species and the two tree fern species (Table 1). Epiphyte diversity and abundance on these seven hosts were compared with a Kruskal–Wallis test.

Epiphyte frequencies for species which occurred on at least five trees, were compared between host groups with 2 × 2 contingency tables, applying Fisher's exact test, as recommended by Zar (1999). Table categories were determined by the presence–absence of each epiphyte on tree ferns and angiosperms (Appendix 1). We did not apply the alternative analysis method by Sabatier *et al.* (1997), which uses the number of epiphyte individuals per host species as table categories and requires more than 20 observed individuals per species, a condition only met by nine species of our data set. Moreover, it would not have allowed the comparison of our data with results of Moran *et al.* (2003). We took five bark samples of *c.* 2 × 5 cm per species at 0.75 m height of the trunk. Mean thickness of the root mantle of tree ferns and the bark of angiosperm trees was measured with a calliper as the average on four sides of each sample. Samples were weighed after immersion for 48 h in water and draining for 5 min on paper tissue (saturated weight = SW), after 48 h at room temperature (25 °C) (intermediate weight = IW), and after 72 h at 60 °C (dry weight = DW). The maximum water content was calculated as $WC = (SW - DW)/SW \times 100$. Water retention capacity was determined as $100 - ((SW - IW)/WC \times 100)$. We measured the pH of the solutions of the immersed samples and standardized the values to 1 g of dry weight and 100 ml solution. All bark characteristics of hosts were compared with a one-way ANOVA. Analyses were performed with STATISTICA 5.0 (Statsoft Inc., Tulsa, Oklahoma, USA).

RESULTS

Of the 100 sampled trees, 28 belonged to two tree fern species and 72 were angiosperms (25 species). The seven most abundant species were *Alsophila firma*, *Cyathea divergens* (both tree ferns, Cyatheaceae), *Arachnothryx capitellata* (Rubiaceae), *Clethra mexicana* (Cyrillaceae), *Bernardia interrupta* (Euphorbiaceae), *Liquidambar styraciflua* (Hamamelidaceae) and *Styrax glabrescens* (Styracaceae), and comprised 65.4% of all hosts (Table 1).

Both host groups were uniformly distributed along the transects (tree ferns, Kolmogorov–Smirnov, $D_{max} = 0.19$, $P > 0.05$, $n = 28$, and angiosperm trees $D_{max} = 0.09$, $P > 0.05$, $n = 72$, respectively) and their dbh was not correlated with the distance from the creek ($r_s = -0.24$, $P = 0.21$ and $r_s = -0.18$, $P = 0.88$, respectively). Consequently, we concluded that observed differences of epiphyte diversity and abundance between host groups can be attributed to physical host characteristics and neither to the spatial distribution of the hosts nor to microclimatic differences.

We found 910 epiphyte individuals from 55 species (38 species and 17 morphospecies) on all hosts together, 38 species on tree ferns and 35 species on angiosperms (Appendix 1). Ferns (24 spp.) and orchids (9 spp.) were the most diverse groups. Most abundant species were *Trichomanes reptans* (168 individuals), *T. capillaceum* (142), *Peperomia quadrifolia* (75), *Peltapteris peltata* (37) and the hemiepiphyte *Syngonium sagittatum* (34).

The non-parametric estimator of species richness, Jackknife 1, predicted for this forest site a total diversity of 78 epiphyte species, 53 for the lower trunk of tree ferns, and 47 for the lower trunk of angiosperm hosts (Table 2).

Table 2. Observed versus estimated epiphyte species richness for the two studied host groups and all host trees together. The number of uniques (species found on only one tree) is needed to calculate Jackknife 1 ± SD (non-parametric species richness estimator, Burnham & Overton 1978, Chazdon *et al.* 1998, Gimaret-Carpentier *et al.* 1998).

Host group	Observed	Uniques	Estimated (Jackknife 1)
All hosts (n = 100)	55	23	78 ± 6.7
Tree ferns (n = 28)	38	16	53 ± 5.5
Angiosperms (n = 72)	35	12	47 ± 4.8

Host size

The first hypothesis that epiphyte diversity and abundance are positively correlated with host size can be confirmed for angiosperms (species $r_s = 0.39$, $P < 0.001$, and individuals $r_s = 0.42$, $P < 0.001$), while tree ferns showed no correlation, perhaps because 20 out of 28 individuals fell in the same dbh class of 10–20 cm (Table 3). In contrast, the angiosperms had more individuals in smaller and in larger dbh classes. The two largest trees, one *Carpinus caroliniana* and one *Liquidambar styraciflua* had a dbh of 56 cm. However, the few large trees might indicate some degree of disturbance, perhaps as consequence of the steep slope and the small size of the forest fragment.

Tree fern trunks had a slightly, although not significantly lower mean dbh (12.9 ± 0.9 cm) than angiosperms (15.9 ± 1.5 cm), but the former taper stronger upwards than trunks of angiosperms ($U = 706$, $P < 0.05$). However, these differences between dtb and dbh were small (8.7 ± 1.8 cm for tree ferns and 5.9 ± 0.7 cm for angiosperms), so that the mean dtb of angiosperms was still larger (21.8 ± 2.0 cm) than in tree ferns (21.6 ± 2.5 cm). If we use the above means for dbh and dtb in the following formula for the calculation of the surface of a truncated circular cone

$$A = \pi \frac{(\mathrm{dtb} + \mathrm{dbh})}{2} \sqrt{130^2 + \left(\frac{\mathrm{dtb} - \mathrm{dbh}}{2}\right)^2}$$

(Stöcker 1995), an angiosperm tree has on average 8.5% more trunk area (A) than a tree fern.

Tree ferns versus angiosperms

Our results partially support the second hypothesis that tree ferns are better hosts than angiosperms, depending on host size. On the study site, tree ferns were not so frequent as angiosperm trees (Table 1), but the number of epiphyte species for both host groups was nearly the same, 38 and 35, respectively (Table 2). Tree ferns had a higher mean number of epiphyte individuals ($U = 1926$, $P < 0.001$) and higher mean of epiphyte species ($U = 1733$, $P < 0.05$) (Table 1), but these differences varied with host size. On smaller hosts that fell within the dbh range of 5–10 cm, the number of epiphyte individuals ($U = 201$, $P < 0.01$) and species ($U = 182$, $P < 0.05$) was significantly higher on tree ferns. However, on intermediate host sizes with a dbh range of 10–20 cm, there were no differences between host groups, because the numbers of epiphytes increased in angiosperms, but not in tree ferns (Table 3). Largest host sizes cannot be compared, because no tree ferns fell in this host size group. Hosts with more epiphyte individuals are generally more diverse, and vice versa (tree ferns, $r_s = 0.87$, angiosperm trees $r_s = 0.85$, both $P < 0.001$).

Bark characteristics

The third hypothesis that epiphytes are more diverse and more abundant on host species with supposedly favourable bark characteristics, such as high water content and high water retention capacity, was partially supported. Bark thickness and water retention capacity were strongly correlated between each other ($r = 0.90$, $P < 0.001$). The root mantle of tree ferns was thicker and retained significantly more water than the bark of angiosperms (ANOVA, multiple comparisons, $P < 0.05$), with the exception of *L. styraciflua*, but the pH and the water content of the root mantle of tree ferns did not differ significantly from angiosperm bark (Table 4). However, at host species level the only significant correlation among the four bark characteristics and the number of epiphytes was found between water content and epiphyte abundance ($r_s = 0.82$, $P < 0.05$).

Table 3. Number of epiphyte individuals and species in four dbh classes of the two host groups. Mean ± SE (n in parentheses). Different superscripts indicate significant differences between host groups of same dbh classes, Mann–Whitney ($P < 0.05$).

	Number of epiphyte individuals		Number of epiphyte species	
dbh range (cm)	Tree ferns	Angiosperms	Tree ferns	Angiosperms
5–10	12.5 ± 2.2^a (6)	3.9 ± 0.6^b (33)	4.3 ± 0.9^a (6)	1.9 ± 0.2^b (33)
10–20	12.9 ± 1.7 (20)	11.7 ± 2.5 (21)	4.2 ± 0.7 (20)	3.8 ± 0.5 (21)
20–30	24.0 ± 10.0 (2)	7.6 ± 1.2 (7)	5.0 ± 1.0 (2)	3.7 ± 0.6 (7)
> 30	–	9.2 ± 1.8 (11)	–	3.5 ± 0.7 (11)

Table 4. Characteristics of the root mantle of two tree fern species (marked *) and the bark of five angiosperm tree species: bark thickness at 0.75 m trunk height, pH of the solution, per cent water content after immersion for 48 h, per cent water retention (% of retained water content) after 48 h at room temperature. Means ± SE, n = 5. Different superscripts indicate significant differences among species ($P < 0.05$).

Species	Thickness (mm)	pH	Water content (%)	Water retention (%)
*Alsophila firma**	14.2 ± 2.28^{a}	5.20 ± 0.05^{cd}	69.4 ± 3.19^{abc}	15.2 ± 4.04^{a}
*Cyathea divergens**	17.7 ± 2.89^{a}	5.56 ± 0.29^{abc}	66.6 ± 3.06^{abc}	20.2 ± 8.12^{a}
Arachnothryx capitellata	1.76 ± 0.06^{c}	6.11 ± 0.07^{a}	59.2 ± 0.46^{c}	2.45 ± 0.86^{b}
Bernardia interrupta	3.12 ± 0.92^{bc}	4.69 ± 0.13^{d}	68.5 ± 0.84^{ab}	0.38 ± 0.16^{b}
Clethra mexicana	5.25 ± 1.04^{bc}	5.93 ± 0.20^{ab}	60.6 ± 2.28^{bc}	5.00 ± 1.84^{b}
Liquidambar styraciflua	8.31 ± 0.81^{b}	5.36 ± 0.16^{bc}	45.7 ± 2.07^{d}	12.4 ± 1.11^{a}
Styrax glabrescens	2.43 ± 0.17^{c}	5.87 ± 0.11^{ab}	60.9 ± 1.93^{abc}	0 ± 0^{b}

Host preferences

Our fourth hypothesis that some epiphytes show host preferences could be tested for the 19 epiphyte species, which appeared at least five times. Three of these species were significantly more frequent on one host group (Fisher's exact test, $P < 0.05$): *Trichomanes reptans* on angiosperms, *Elaphoglossum petiolatum* and sp. 1 (juveniles of an unidentified species) on tree ferns, and three other species were found on only one host group. While all individuals of *Trichomanes capillaceum* and *Conostegia* sp. 1 grew exclusively on both tree fern species, *Peltapteris peltata* occurred exclusively on angiosperm trees (Appendix 1, Figure 1). The latter species showed no preferences among the angiosperm hosts, growing on nine different tree species.

Additionally, some epiphyte species showed preferences for one of the tree fern species. *Elaphoglossum petiolatum* was significantly more frequent on *A. firma* than on *C. divergens* (Fisher's exact test, $P = 0.037$).

DISCUSSION

Epiphyte diversity on the lower trunk

The lower tree trunk has been reported to contain the lowest epiphyte diversity (ter Steege & Cornelissen 1989).

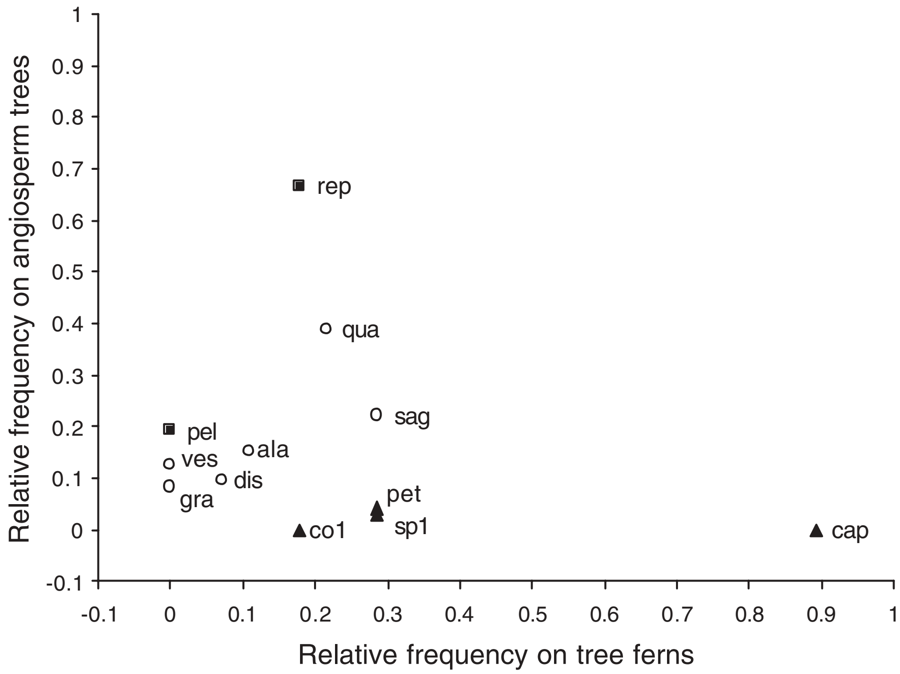

Figure 1. Host preferences as revealed by the relative frequencies of epiphyte species on two phorophyte groups: tree ferns and angiosperms. Species with significant preferences for one host groups: tree ferns (filled triangles) or angiosperms (filled squares) (Fisher's exact test, $P < 0.05$), and species without preferences (open circles). Acronyms mean: ala, *Peperomia alata*; cap, *Trichomanes capillaceum*; co1, *Conostegia* sp. 1; dis, *Polypodium dissimile*; gra, *Dichaea graminoides*; pel, *Peltapteris peltata*; pet, *Elaphoglossum petiolatum*; qua, *Peperomia quadrifolia*; rep, *T. reptans*; sag, *Syngonium sagittatum*; sp1, Sp. 1 (juveniles of an unidentified species); ves, *E. vestitum*.

However, some epiphytes, for instance Hymenophyllaceae, prefer this stem zone (Zotz & Büche 2000), and most epiphyte studies do not specify the species richness for this zone (Hietz & Hietz-Seifert 1995a, b; Rudolph *et al.* 1998, Zapfack *et al.* 1996). Our data suggest that low-trunk epiphytes represent a high percentage of the total epiphyte diversity in a cloud forest, since we found 55 species of which 22 species were new and need to be added to the 81 species recorded by Flores-Palacios & García-Franco (2001) at this forest site. However, the contribution of low-trunk epiphytes to the whole epiphyte diversity varies among different forest types (Gentry & Dodson 1987), and is typically lower in lowland rain forests (Nieder *et al.* 2000).

Epiphyte abundance and host size

Tree ferns have no secondary stem growth, but their root mantle grows and covers the trunk gradually upwards. However most individuals fell in the same dbh class, supposedly because of the slow growth of the root mantle, and consequently did not result in a correlation between dbh and epiphyte richness. For angiosperm trees, dbh was positively correlated with the number of epiphyte species and individuals. Most epiphyte studies confirm this correlation between host size and epiphyte richness (Hietz & Hietz-Seifert 1995a,b; Zotz & Vollrath 2003). This is not surprising because large trees offer more surface than small trees and older hosts have been available for a longer time than younger hosts for epiphyte colonization.

Tree ferns versus angiosperms

The results support our second hypothesis that tree ferns are better substrates for epiphytes than angiosperms, but only for the smallest dbh class. Tree ferns were a conspicuous element of the cloud-forest vegetation, but they were not as frequent as angiosperm trees (Table 1), and they offered on average 8.5% less trunk area per host. This suggests that epiphytes should have a greater opportunity to establish on angiosperm trees than on tree ferns. However, the species total, the predicted species richness (Jackknife 1), and the epiphyte abundance and diversity on the larger dbh class (10–20 cm) were similar for tree ferns and for angiosperms (Table 2), but tree ferns of the smallest dbh range (5–10 cm) had more epiphyte species and individuals per host than angiosperm trees of the same dbh (Table 3). We suppose that tree fern trunks of the smallest dbh class may be older than angiosperm trunks of the same dbh. Tree fern trunks thicken first and need at least 3 y to start their longitudinal growth, 10–15 y to build a trunk of 1.50 m height, and even longer to form the root mantle (K. Mehltreter, *pers. obs.*). On larger dbh classes angiosperm trunks may be of similar age than tree fern trunks, because the former primarily grow longitudinally (e.g. *Quercus* spp. 1–5 m y^{-1}, Benítez *et al.* 2004) and then they thicken. Moran *et al.* (2003) found significant epiphyte preferences for tree fern trunks of all dbh classes at four sites in Costa Rica. However, that study was restricted to fern epiphytes, which may have stronger host preferences than angiosperm epiphytes. Moreover, they investigated different tree fern species, which may grow faster than that of the present study.

At host species level we did not find any significant differences, perhaps as a consequence of the relative low number of host trees per species, and the restriction of this study to the lower trunk zone.

Bark characteristics

Epiphytes were present on 92% of host trees (fern epiphytes grew on 86%), in comparison to 12.5% of host trees with fern epiphytes in lowland rain forests in Sumatra (Gardette 1996). Thus, the macroclimatic conditions at our cloud-forest site may favour epiphyte establishment on all our host tree species. Comparing the seven most frequent host species, water content was the only bark characteristic significantly correlated with epiphyte abundance ($r_s = 0.82$, $P < 0.05$), but not with epiphyte diversity. However, neither the maximum water content nor the pH of the root mantle of tree ferns differed significantly from angiosperm bark (hypothesis 3). On the other hand, the water retention capacity and the thickness of the bark (or root mantle) were significantly different between host groups and may explain the observed host preferences of epiphytes for tree ferns. Humidity retention in the bark is the single most important factor in experimental and observational epiphyte surveys, and explains the abundance and survivorship of some vascular epiphytes (Callaway *et al.* 2002, Castro Hernández *et al.* 1999). For example, *Ceiba pentandra* is considered to be a good host tree, because of abundant stemflow keeping the bark humid and enabling the establishment of many epiphytes (Andrade & Nobel 1997, Valdivia 1977). The irregular surface structure of the root mantle of tree fern trunks is an excellent substrate for the adherence of seeds and spores, and they enhance water retention and epiphyte root aeration (Beever 1984, Palacios-Rios & Mehltreter 1999, Pócs 1982). This might be the reason why we found most of the accidental epiphytes (i.e. young epiphytic individuals of terrestrial species, which do not reach maturity in this life form) on tree fern trunks. In Africa, Johansson (1974) observed that *Cyathea camerooniana*, without adventitious roots, had no epiphyte flora, while *C. manniana*, with adventitious roots, was highly covered with epiphytes, especially ferns. However, even without the formation of a root mantle, the surface structure of the remaining petiole bases, which break irregularly and rot still attached to the tree fern trunk is suited for epiphyte establishment (K. Mehltreter, *pers. obs.*).

Host preferences

Six of 19 epiphyte species showed preferences for one host group, supporting our fourth hypothesis. No epiphyte species was strictly host specific. Our results coincide with data from Benzing (1995), Migenis & Ackerman (1993), ter Steege & Cornelissen (1989), Zimmerman & Olmsted (1992), and indicate that cases of host specificity, as reported by Tremblay *et al.* (1998) for the orchid *Lepanthes caritensis* on *Micropholis guyanensis* (Sapotaceae) in Puerto Rico, are rare. However, three epiphyte species grew on only one host group: *Trichomanes capillaceum* and *Conostegia* sp. 1 exclusively on tree ferns, and *Peltapteris peltata* exclusively on angiosperm trees. In a similar study, Moran *et al.* (2003) found no epiphyte species with angiosperm host preferences. Why did *Peltapteris peltata* not grow on tree fern trunks, if these offer a supposedly favourable substrate for most epiphytes? Axeny, i.e. the epiphyte expulsion by host trees (Benzing 1995) as consequence of a biochemical antagonism (Frei & Dodson 1972, Medeiros *et al.* 1993), for example a low pH (Pócs 1982), should exclude several epiphyte species from tree ferns. However, *Peltapteris peltata* was the only excluded species, in spite of its presence on all frequent angiosperm hosts except *Bernhardia interrupta*, the one with the lowest pH and latex. The alternative explanation, that *Trichomanes capillaceum* as the dominant species on tree fern trunks might exclude *Peltapteris peltata* through competition seems unlikely (Benzing 1981, Catling & Lefkovitch 1989), because large areas of the tree fern trunks were still unoccupied.

We conclude that epiphytes of the lower trunk contribute considerably to the species richness in a cloud forest of central Veracruz, Mexico. The higher epiphyte diversity and abundance of tree fern trunks of the smallest dbh class (5–10 cm) in comparison to angiosperm trunks of the same size is attributed to their thicker root mantle and higher water retention capacity in comparison to the bark of angiosperms and their assumed older age. Four of six 'specialized' epiphyte species preferred tree ferns as a host group. The relative frequency of tree ferns in a cloud forest should be considered for conservation of host group-specific or endangered epiphytes.

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Appendix 1. Frequency and life form of low-trunk epiphytes (38 species and 17 morphospecies) in a Mexican cloud forest (28 tree ferns and 72 angiosperms); P-values of the two-sided Fisher's exact test are shown for taxa with significant host preferences ($P < 0.05$); NS, not significant; NA, Not applicable, for presence data of less than five. Life forms: E, epiphyte; H, hemiepiphyte; A, accidental epiphyte (young individuals of species, which sometimes grow as epiphytes, but which were not observed as adult plants in this life form).

Species	Family	Life form	Present on tree ferns	Absent on tree ferns	Present on angiosperms	Absent on angiosperms	P
Anthurium scandens (Aubl.) Engl.	Araceae	H	0	28	1	71	NA
Antrophyum ensiforme Hook.	Vittariaceae	E	0	28	1	71	NA
Asplenium auriculatum Sw.	Aspleniaceae	E	2	26	5	67	NS
Asplenium harpeodes Kunze	Aspleniaceae	E	3	25	0	72	NA
Blechnum fragile (Liebm.) C. V. Morton & Lellinger	Blechnaceae	H	1	27	0	72	NA
Campyloneurum angustifolium (Sw.) Fée	Polypodiaceae	E	0	28	1	71	NA
Chamaedorea schiedeana Mart.	Arecaceae	A	3	25	0	72	NA
Conostegia sp. 1	Melastomataceae	A	5	23	0	72	< 0.001
Conostegia sp. 2	Melastomataceae	A	3	25	0	72	NA
Dichaea graminoides Lindl.	Orchidaceae	E	1	27	6	66	NS
Elaphoglossum petiolatum (Sw.) Urb.	Lomariopsidaceae	E	8	20	3	69	0.001
Elaphoglossum vestitum (Schltdl. & Cham.) T. Moore	Lomariopsidaceae	E	0	28	9	63	NS
Epidendrum repens Cogn.	Orchidaceae	E	1	27	1	71	NA
Epidendrum sp. 2	Orchidaceae	E	0	28	1	71	NA
Erythrodes lunifera (Schltr.) Ames	Orchidaceae	A	1	27	0	72	NA
Gibasis sp. 1	Orchidaceae	A	1	27	0	72	NA
Gongora galeata (Lindl.) Rchb.f.	Orchidaceae	E	0	28	2	70	NA
Malaxis excavata (Lindl.) O. Kuntze	Orchidaceae	A	2	26	0	72	NA
Melpomene sp. 1	Grammitidaceae	E	3	25	2	70	NS
Oreopanax capitatus (Jacq.) Decne. & Planch.	Araliaceae	H	1	27	0	72	NA
Pecluma alfredii (Rosenst.) M. G. Price	Polypodiaceae	E	1	27	5	67	NS
Peltapteris peltata (Sw.) C. V. Morton	Lomariopsidaceae	E	0	28	14	58	0.009
Peperomia alata Ruiz & Pav.	Peperomiaceae	E	3	25	11	61	NS
Peperomia pseudoalpina Trel.	Peperomiaceae	E	0	28	1	71	NA
Peperomia quadrifolia (L.) Kunth	Peperomiaceae	E	6	22	28	44	NS
Philodendron advena Schott	Aracaeae	H	4	24	7	65	NA
Phlebodium areolatum (Humb. & Bonpl. ex Willd.) J. Sm.	Polypodiaceae	E	0	28	1	71	NA
Piper sp. 1	Piperaceae	A	1	27	0	72	NA
Pleopeltis angusta Humb. & Bonpl. ex Willd.	Polypodiaceae	E	0	28	2	70	NA
Pleurothallis pachyglossa Lindl.	Orchidaceae	E	0	28	1	71	NA
Pleurothallis platystylis Schltr.	Orchidaceae	E	0	28	1	71	NA
Polypodium dissimile L.	Polypodiaceae	E	2	26	7	65	NS
Polypodium loriceum L.	Polypodiaceae	E	1	27	0	72	NA

Appendix 1. Continued.

Species	Family	Life-form	Present on tree ferns	Absent on tree ferns	Present on angio-sperms	Absent on angio-sperms	P
Polypodium plebeium Schltdl. & Cham.	Polypodiaceae	E	0	28	1	71	NA
Polypodium sp. 1	Polypodiaceae	E	6	22	10	62	NS
Polypodium sp. 2	Polypodiaceae	E	3	25	5	67	NS
Polypodium sp. 3	Polypodiaceae	E	3	25	1	71	NA
Prescottia stachyodes (Sw.) Lindl.	Orchidaceae	E	0	28	2	70	NA
Psilotum complanatum Sw.	Psilotaceae	E	1	27	0	72	NA
Saurauia sp. 1	Saurauiaceae	A	3	25	0	72	NA
Saurauia sp. 2	Saurauiaceae	A	1	27	0	72	NA
Selaginella sp. 1	Selaginellaceae	A	3	25	1	71	NA
Sp. 1		A	8	20	2	70	< 0.001
Sp. 2		A	1	27	0	72	NA
Sp. 3		A	1	27	0	72	NA
Sp. 4	Melastomataceae	A	1	27	0	72	NA
Sp. 5	Melastomataceae	A	1	27	0	72	NA
Syngonium sagittatum G. S. Bunting	Araceae	H	8	20	16	56	NS
Terpsichore asplenifolia (L.) A. R. Sm.	Grammitidaceae	E	1	27	0	72	NA
Tillandsia viridiflora (Beer) Baker	Bromeliaceae	E	0	28	4	68	NA
Trichomanes bucinatum Mickel & Beitel	Hymenophyllaceae	E	2	26	5	67	NS
Trichomanes capillaceum L.	Hymenophyllaceae	E	25	3	0	72	< 0.001
Trichomanes pyxidiferum L.	Hymenophyllaceae	E	0	28	3	69	NA
Trichomanes reptans Sw.	Hymenophyllaceae	E	5	23	48	24	< 0.001
Vittaria graminifolia Kaulf.	Vittariaceae	E	0	28	6	66	NS