Composition and Distribution of Epiphytic Organic Matter in a Neotropical Cloud Forest, Costa Rica[1]

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ABSTRACT

We describe the abundance (dry weight) of angiosperms and other organic matter suspended within the inner crowns of a dominant host tree species, *Ocotea tonduzii* (Lauraceae) in a Neotropical lower montane forest. Epiphytic organic matter (EOM), defined as vegetation and dead organic matter, was randomly sampled from inner canopy branches of ten trees in Monteverde, Costa Rica. Total EOM (grams per square decimeter of branch surface area) showed a strong positive correlation with branch circumference and a strong negative correlation with branch angle. Approximately three times more dry mass occurred on large (86–140 centimeters circumference) branches than on small (15–50 centimeters) branches, and four times more dry mass occurred on less inclined ($\leq 30°$) than on more inclined ($>60°$) branches. The variation of EOM was much greater within trees (between branches) than among different trees. EOM was composed of approximately 60 percent dead organic matter, 20 percent live and dead roots, 10 percent angiosperms, 5 percent ferns, and 5 percent cryptogams. Sixty-five angiosperm species in 18 families, with no strongly dominant species, were found among the 75 percent of plots that supported angiosperms. Araceae, Bromeliaceae, Ericaceae, Melastomataceae, and Orchidaceae contributed about 70 percent of the angiosperm biomass. Orchidaceae and Piperaceae were the most frequently represented families and those with the most species in the study plots. The most species-rich plots (≥ 6 species) occurred on branches >50 centimeters in circumference, but the highest density of epiphytic angiosperm seedlings occurred on smaller, presumably younger branches.

RESUMEN

En forma cuantitativa, se describe la abundancia (peso seco) de especies angiospermas y otra materia orgánica presente en las ramificaciones internas de *Ocotea tonduzii* (Lauraceae), la especie huesped dominante de hábito arboreo, en un bosque húmedo montano bajo. La materia orgánica epifítica (plantas y materia orgánica muerta, o EOM) fue colectada en las ramas internas y próximas a la copa de diez árboles en Monteverde, Costa Rica. El total de EOM (gramos por decimetro cuadrado de superficie de las ramas) mostró una alta correlación positiva con la circunferencia de la rama, y una marcada correlación negativa con el ángulo de la misma. Aproximadamente el triple de abundancia se localizó en las ramas grandes (86–50 cm de circunferencia) en comparación a las ramas pequeñas (15–50 cm); además, la abundancia de EOM encontrada en las ramas de menor inclinación ($\leq 30°$) fue cuatro veces mayor, que en las mas inclinadas ($>60°$). La variación de EOM fue mayor dentro de las árboles (entre sus ramas) que entre los diferentes árboles muestreados. La EOM estaba compuesta de aproximadamente 60 por ciento de materia orgánica muerta, 20 por ciento de raíces, 10 por ciento de angiospermas, 5 por ciento de helechos, y 5 por ciento de briofitas. Sesenta y cinco especies de angiospermas en 18 familias, sin marcada dominancia de especies, fueron encontradas entre el 75 por ciento de los sectores que mostraron angiospermas. Araceae, Bromeliaceae, Ericaceae, Melastomataceae, y Orchidaceae contribuyeron al 70 por ciento aproximadamente del total de biomasa de angiospermas. Orchidaceae y Piperaceae fueron las más frecuentes y las de mayor cantidad de especies en las familias representadas en los sectores estudiados. Los sectores más ricos de especies (≥ 6 especies) ocurrieron en las ramas >50 cm, mientras que la más alta densidad de plántulas angiospermas epifitas se localizó en las pequeñas ramas (15–50 cm), presumiblemente las más jóvenes.

EPIPHYTES ACCOUNT FOR UP TO 35 PERCENT of the vascular flora in some wet Neotropical forests (Gentry & Dodson 1987a), and their biomass may equal 50 percent of tree leaf biomass in some montane rain forests (Edwards & Grubb 1977, Nadkarni 1984). There is increasing awareness that canopy communities are important subsystems in ecosystem-level interactions between atmospheric and terrestrial processes because of their ability to intercept and retain atmospheric nutrients and pollutants, especially in cloud forests (Nadkarni 1984, 1986; Lugo & Scatena 1992).

Few quantitative studies describe the distribu-

tion of epiphytes within and among trees, but some general patterns have been identified. Certain epiphyte species are stratified within individual trees (Valdivia 1977, Kelly 1985, ter Steege & Cornelissen 1989). Successional progressions have been documented in several locations by examining epiphytes on branches of different age/size classes. Generally, younger host trees and branches support different epiphyte associations than older substrates (Yeaton & Gladstone 1982, Catling *et al.* 1986, Catling & Lefkovitch 1989). Epiphytic angiosperms occurring on older, larger branches may require the mantle of dead organic matter ("crown humus," *sensu* Jenik 1973) that accumulates on older bark (Johansson 1974). The relationships among different components of epiphyte communities have not been examined in Neotropical montane regions. Understanding such relationships is necessary to understand patterns and processes of epiphyte distribution.

Although comparing the distribution of epiphytes on two or more host species can be useful to reveal host "preference" of particular epiphytes (*e.g.*, Johnson & Awan 1972, Johansson 1974, Valdivia 1977, Todzia 1986, Bennett 1987, Ackerman *et al.* 1989, ter Steege & Cornelissen 1989, van Leerdam *et al.* 1990), examining the distribution of epiphytes within a single host species is necessary to understand epiphyte distribution and variation at a smaller spatial scale. Epiphyte host preferences are probably less conservative in continuously wet montane forests than in dryer forests (Benzing 1990). We studied epiphytes and their substrata in one tree species to examine epiphyte distributions in relation to structural characteristics of branches without the potential effects of host species-specific factors.

The purpose of this study was to describe the abundance and composition of epiphytic organic matter (EOM) growing within the canopy of a dominant host tree species, *Ocotea tonduzii* Standley (Lauraceae), in a lower montane forest from Costa Rica. We defined EOM as living epiphytes and dead organic matter suspended in the canopy. Hemiepiphytes that germinate in trees and later form root connections with the ground (*e.g.*, some *Clusia* spp.), or ascend trunks and later lose their terrestrial connections (*e.g.*, some Araceae) are included here because much of their life cycle occurs under the same ecological conditions as true epiphytes. Our questions were: how does the variation in EOM compare within and between tree crowns; what is the dry weight and composition of EOM suspended in the inner canopy of mature individuals

of *O. tonduzii*; do associations exist among different epiphytic components and branch substrate characteristics; and how does angiosperm species richness vary with branch size and angle?

STUDY SITE

Our study took place in the Monteverde Cloud Forest Reserve (MVCFR) in northcentral Costa Rica (10°18'N, 84°48'W), situated along the crest of the continental divide in the Cordillera de Tilarán. The area is subject to persistent cloud-bearing trade winds that move across the Cordillera from the northeast. The trade winds occur throughout the year, but most frequently deliver mist between November and May. Total annual rainfall is 2000–2500 mm, most of which falls during the May to October period of thunderstorm activity, although fog and mist contribute an additional 500–2000 mm of annual precipitation (Clark & Nadkarni, pers. obs.).

The vegetation structure and floristic composition of the forest change markedly with distance from the continental divide. The 20 ha research area of MVCFR, in which the 2 ha study site is located, is part of the leeward cloud forest, a wet atmospheric association in the transition between tropical lower montane wet and lower montane rain forest (Lawton & Dryer 1980). The study site (1480 to 1530 m elevation) is located 1 km southwest of the MVCFR Headquarters, and 1 km from the divide. This primary forest is 20–30 m high with a few emergents to 35 m tall. *Ocotea tonduzii* is a dominant species in the study site, and comprises 31 percent of the basal area of trees with diameter at breast height (DBH) ≥ 2 cm. Among large (DBH ≥ 50 cm) trees, this species makes up 29 percent of the basal area and 22 percent of the individuals (Nadkarni *et al.*, pers. obs.). Epiphytic vegetation occurs on virtually all trees taller than 2 m.

METHODS

TREE SELECTION.—Fieldwork was carried out during April–May and September–November, 1988. We characterized all large (DBH $\geq$ 50 cm) individuals of *O. tonduzii* in the 2 ha study site by DBH, height of the bole, total tree height, and total length of inner canopy branches. We could safely gain access to the canopies of a subset of mature trees, *i.e.*, those of suitable architecture and size. Structural characteristics of canopy-accessible (sampled) and canopy-inaccessible (nonsampled) trees were com-

TABLE 1.   *Characteristics and sample size for ten O. tonduzii trees used for sampling EOM and 23 nonsampled trees. Four to five plots were sampled per branch in sampled trees. There were no significant differences in structural characteristics between sampled and nonsampled trees.*

	DBH (cm)		Bole height (m)		Total height (m)		No. branches sampled per tree		No. plots
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Total
Sampled trees	89.3	67–132	15.6	12–22	24.0	21–32	5.4	3–8	231
Nonsampled trees	99.6	55–149	13.1	9–18	21.3	9–27	—	—	—

pared to determine whether the sampled trees were representative of all large *O. tonduzii* trees in this forest. To characterize the canopy branches of non-sampled trees, we estimated the total length of branches within three size classes and three angle classes using binoculars at ground level. Small (15–50 cm circumference), medium (51–85 cm), and large (≥ 86 cm) branch size classes were subdivided into three angle classes (angle from horizontal): 0–30° (1); 31–60° (2); and, 61–90° (3).

SAMPLING EPIPHYTIC ORGANIC MATTER.—We used single-rope techniques to climb a subgroup of accessible tree canopies following Nadkarni (1988) and Tucker and Powell (1991). EOM was sampled from all branches with a circumference of 15–140 cm that could be reached from the inner canopy (1–3 m of central trunk), and that had at least 60 cm of their length accessible. We confined our sampling to the inner canopy where epiphytic biomass and diversity are greatest (ter Steege & Cornelissen 1989, van Leerdam *et al.* 1990), and where access is less difficult than in the outer canopy. Plots were randomly located within the accessible branch portion and encircled the branch in a 15 cm wide band; plots thus varied in surface area from 225 cm² to 2100 cm². All EOM was collected from within each plot. The number of plots varied from tree to tree because of differences in accessibility (Table 1). Circumference, cardinal direction, branch angle from horizontal, and height above ground were recorded for each plot.

Epiphytic materials were separated into five categories: dead organic matter (DOM, dead and decaying epiphytes, partially decomposed tree bark, insect frass, and intercepted litter); roots (live and dead fern and angiosperm roots); live angiosperm shoots; live fern stems and fronds; and, live cryptogams (lichens and bryophytes). The components from each plot were dried to constant weight (12–48 hr) at *ca* 55°C. Angiosperm seedlings (juvenile plants weighing less than 0.5 g fresh weight) were

counted. Angiosperms were pressed and dried for later identification. Voucher specimens are deposited at the Herbarium of the University of California, Santa Barbara (UCSB).

STATISTICAL ANALYSES.—Differences between sampled and nonsampled trees with respect to height, DBH, and inner canopy branch lengths, were tested using a *t*-test. Total EOM dry weight for each plot was converted to g dm⁻² of branch surface area and log-transformed to provide a normal distribution (Sokal & Rohlf 1969). Analyses of variance and *a posteriori* comparisons of mean dry weight values were calculated for an unbalanced design using the General Linear Models Procedure of SAS (1987). The log-transformed EOM dry weight values were used in a three-way ANOVA with tree, branch angle, plot circumference class, and their two-way interactions as class variables, and in a nested two-way ANOVA to compare within-tree and between-tree variation. Correlations among physical habitat factors (with plot circumference as a continuous variable) and epiphytic components were investigated with the Spearman rank correlation test.

Because of the predominant north to north-easterly direction of wind and mist, the aspect data were transformed three times to identify relationships (if any) between EOM and aspect axes. With south set to −1, southeast and southwest equal to −0.5, east and west equal to 0, north equal to +1, and so on, associations along the north–south axis could be found. Similarly, aspects were transformed with northeast set equal to +1, and with east set equal to +1.

Frequencies of each angiosperm taxon (species, genera, and families) among all plots, branches, and trees were calculated. The chi-squared statistic was used to test whether the species richness per plot was independent of plot angle and plot circumference. A Kruskal-Wallis ANOVA, followed by Student-Newman-Keuls multiple range tests (Zar 1984), was used to test for differences in the number

TABLE 2.   *Nested ANOVA table with variance estimates. The dependent variable is log total EOM dry weight.*

Source of variation	df	SS	F value	MS	Variance estimate
Trees	9	10.522	10.89**	1.169	−0.067 (0%)
Branches within trees	44	119.398	25.28**	2.714	0.609 (85%)
Plots within branches (error)	177	18.996		0.107	0.107 (15%)
Corrected total	230	148.916			
R-square = 0.872					

**$P \leq 0.001$.

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RESULTS

ANALYSIS OF SAMPLED AND NONSAMPLED HOST TREES.—There were 33 large (DBH ≥ 50 cm) *Ocotea tonduzii* trees found within the study site, of which ten were canopy-accessible. All ten were climbed and their epiphytes sampled. There were no significant differences between the sampled and nonsampled groups with respect to trunk and total heights, DBH (Table 1; $P \leq 0.001$), and lengths of canopy branches (Ingram 1989; $P \leq 0.001$), so we are confident that the sampled trees were representative of the population of *O. tonduzii* trees in the study site.

VARIATION IN EOM MASS.—A two-level nested ANOVA showed that 85 percent of the variance in total EOM occurred at the branch (within-tree) level, and the balance of the variance (15%) occurred at the plot level (within branches) (Table 2). Tree effect contributed a negligible amount to the overall variability in EOM.

A high degree of variability for all components was evident because the standard deviations exceeded the mean values in nearly every case among

the nine size/angle classes. The average coefficients of variation for the vascular epiphytes (ferns and angiosperms) were 212 and 177 respectively, 1.3 to 2.5 times higher than the average values for the other epiphytic components.

TOTAL EOM IN RELATION TO BRANCH SIZE AND ANGLE.—Of the structural characteristics we measured, total EOM was most closely associated with circumference (positively) and with angle class (negatively) (Table 3). Among aspect transformations, total EOM was significantly correlated with the north–south axis only; slightly more epiphytic matter was found on southward pointing plots (*i.e.*, the lee side of trees). Mean total EOM showed significant differences among all three circumference classes (Table 4). The largest branch size class held roughly three times more EOM than the smallest size class. Approximately four times more EOM occurred on angle class 1 branches (≤30°) than the angle class 3 branches (>60°). The three-way ANOVA indicated significant interactions between tree and branch angle ($F = 6.87$, $P \leq 0.001$), and between tree and branch circumference ($F = 13.39$, $P \leq 0.001$), but not between angle and circumference ($F = 0.96$, $P = 0.43$). These significant interactions illustrate that individual trees differed with respect to size and angle of their accessible branch portions.

TABLE 3.   *Spearman rank correlation (rho) for total EOM dry weight (g dm⁻²) and all measured physical variables: circumference (Circum), angle class (Angle), diameter at breast height (DBH), height, and north-south aspect (Aspect N-S).*

Spearman rank correlation (rho) (df = 229)

	EOM	Circum	Angle	DBH	Height
EOM					
Circum	0.371**				
Angle	−0.464**	0.149*			
DBH	0.175*	0.359**	0.030		
Height	0.075	0.065	0.164*	0.050	
Aspect N-S	−0.141*	−0.126	0.021	−0.027	0.029

*$P \leq 0.05$; **$P \leq 0.01$.

TABLE 4.   *Sample size and mean total EOM for 3 circumference classes, 3 angle classes, and for all plots. ANOVA on log-transformed data with a posteriori comparison of means (R-square = 0.771; Tukey's HSD, df = 187, P ≤ 0.05) showed significant differences (within like classes) between means with different letters.*

Size class	Circumference (cm)	N	Mean EOM (g dm^{-2})
Small	15–50	94	4.7[a]
Medium	51–85	88	8.6[b]
Large	86–140	49	14.2[c]
Angle class	Inclination	N	Mean EOM (g dm^{-2})
1	0–30°	130	10.9[a]
2	31–60°	34	9.2[a]
3	61–90°	67	2.5[b]
Total	—	231	9.9

DISTRIBUTION AND COMPOSITION OF EOM.—EOM was composed overall of *ca* 60 percent DOM, 20 percent roots, 10 percent angiosperms, 5 percent ferns, and 5 percent cryptogams. Cryptogam biomass was almost entirely bryophytes; lichen biomass was negligible. Among the smallest size class of branches, dry mass of all components decreased as angle class increased. Among the largest branches, all components were less abundant on the more inclined (angle class 3) branches. However, the greatest mean biomass of angiosperms was on the angle class 2 branches, not the least inclined branch-

es, due to the presence of a few large epiphytes (*Clusia* sp. 1 and *Blakea* sp. 1) among three of the nine plots in this category. Root and angiosperm dry mass was approximately two times greater on large than on small size class branches; DOM was nearly five times greater (Fig. 1). All components except the cryptogams were least abundant on the smallest, and presumably youngest, branches.

RELATIVE ABUNDANCE OF COMPONENTS.—The composition of EOM differed among the three branch size classes (Fig. 2a). The proportion of DOM in-
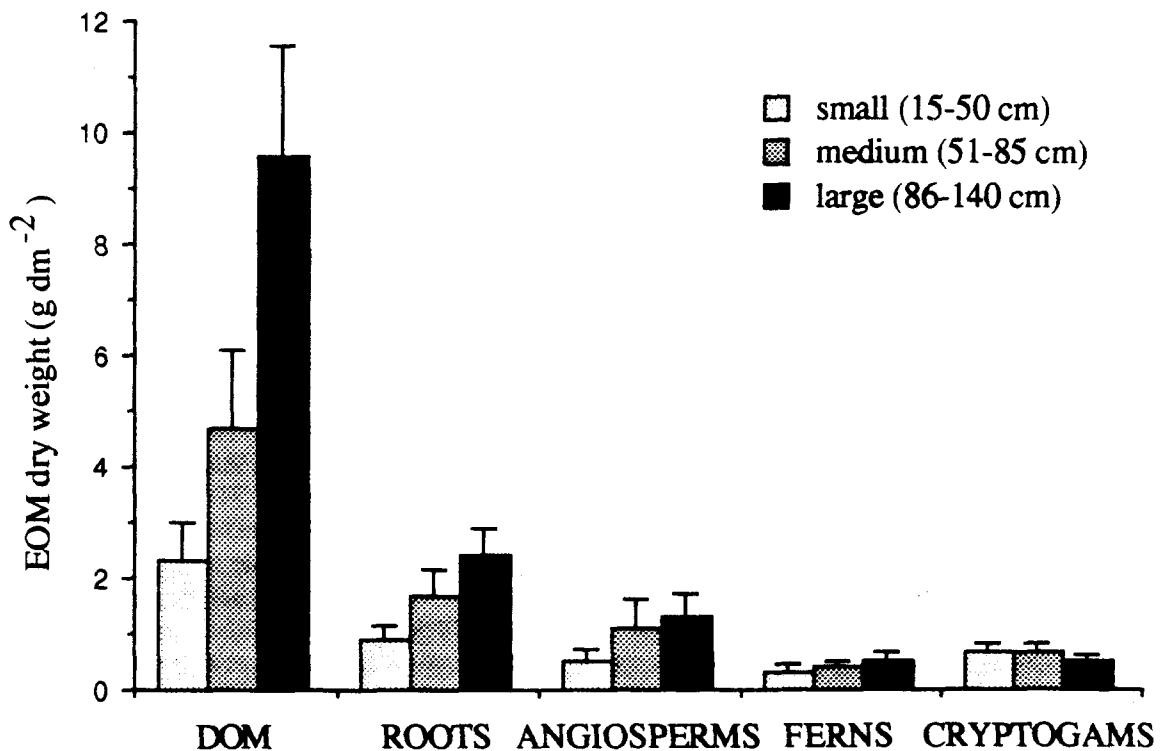

FIGURE 1.   Mean EOM dry weight (±2 standard errors) of each component for three branch circumference classes.
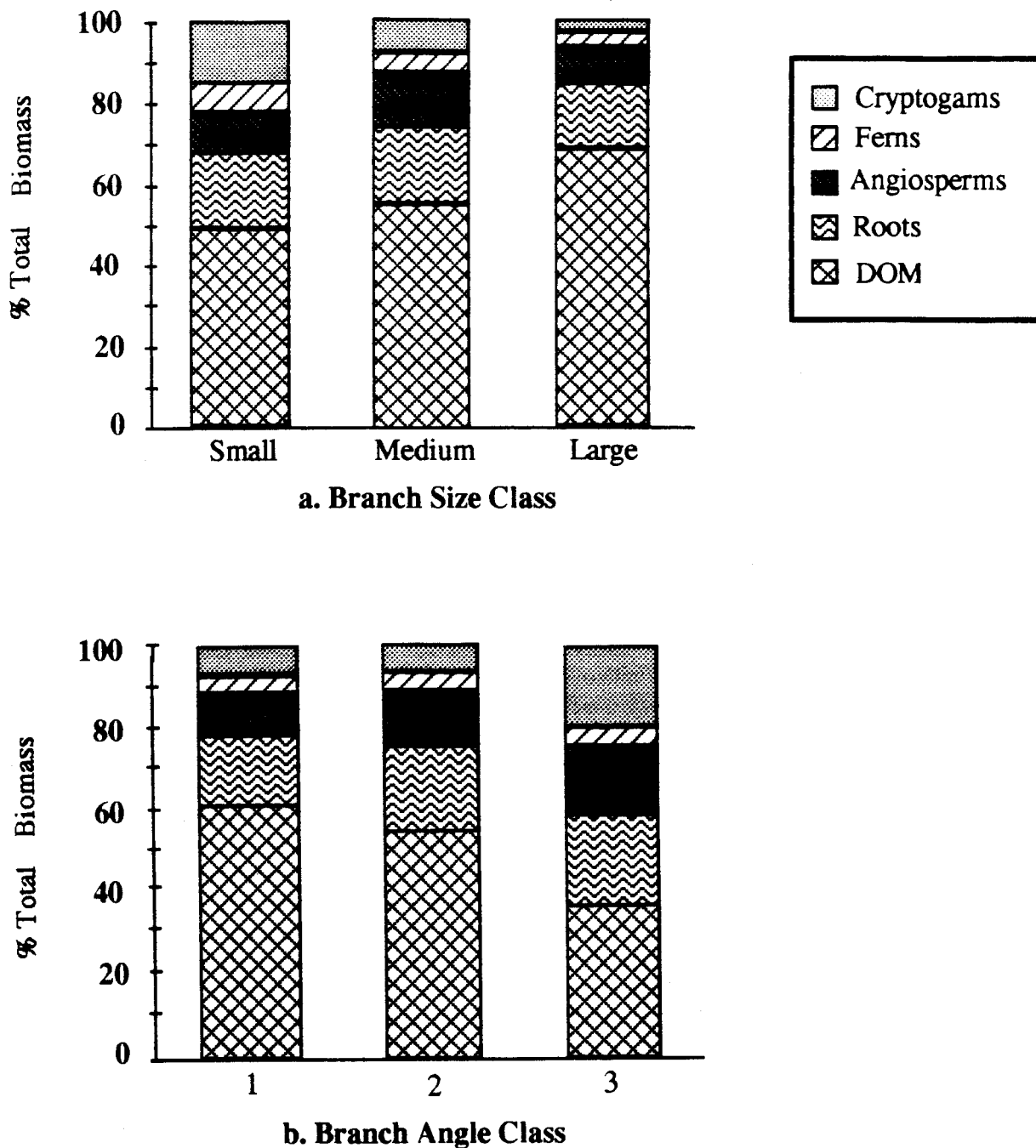
FIGURE 2.   Composition of EOM for (a) branch size classes, and (b) branch angle classes.

creased and the proportion of cryptogams decreased with increasing branch size. Among the small size class plots, DOM made up slightly less than half of the EOM mass; DOM made up about two-thirds of the EOM among the larger, and presumably older, branches. In contrast, cryptogams contributed 15 percent of the EOM on small branches and less than five percent on the larger branches. Relative abundance of angiosperms and cryptogams

increased as the branches deviated from horizontal, while the relative amount of DOM decreased (Fig. 2b).

Associations.—Spearman rank correlations indicated that DOM, roots, angiosperms, and ferns were all positively correlated with each other significantly and with circumference on branches inclined ≤30° (Table 5a). In contrast, the cryptogams showed a

TABLE 5. *Spearman rank correlations (rho) for total EOM (g dm⁻²) of each component (dead organic matter, roots, angiosperms, ferns, and cryptogams) and circumference (Circum).*

Spearman rank correlation (rho)	Circum	DOM	Roots	Angio	Ferns
a. Angle class 1 (≤30°, df = 128)					
DOM	0.628**				
Roots	0.553**	0.803**			
Angiosperms	0.336**	0.569**	0.554**		
Ferns	0.488**	0.627**	0.647**	0.434**	
Cryptogams	−0.282**	−0.081	−0.098	0.075	0.081
b. Angle class 3 (>60°, df = 65)					
DOM	0.235*				
Roots	0.299**	0.862**			
Angiosperms	0.161	0.707**	0.706**		
Ferns	0.183	0.619**	0.722**	0.549**	
Cryptogams	0.027	0.493**	0.320**	0.333**	0.360**

$*P \leq 0.05$; $**P \leq 0.01$.

significant negative correlation with circumference on the least inclined branches. All of the associations between epiphytic components and branch circumference were much weaker on the most inclined branches (Table 5b). The abundance of cryptogams and the abundance of all other epiphytic components were significantly positively correlated among the branches with angles > 60°, but no such associations existed on the less inclined branches.

FLORISTIC COMPOSITION OF ANGIOSPERMS.—Of the 231 plots from which EOM was sampled, 174 (75%) contained angiosperms. In all, 65 angiosperm taxa representing 41 genera and 18 families were identified (Appendix). Of the 65 taxa, 11 "morphospecies" could not be identified beyond the genus. Sterile, immature, and damaged plants undetermined at the family level were found in 64 plots. However, these were dicotyledonous plants from families other than Begoniaceae, Melastomataceae, and Piperaceae. Undetermined epiphytes accounted for seven percent of the angiosperm biomass and less than one percent of the total EOM mass.

The Araceae composed almost 30 percent of the total angiosperm biomass, three times more biomass than any other flowering plant family (Fig. 3). Bromeliaceae, Ericaceae, Melastomataceae, and Orchidaceae each accounted for approximately ten percent of the angiosperm biomass. The total biomass of any one mature species ranged from less than 0.5 g (*Anthurium pittieri* var. *pittieri*) to nearly 250 g (*A. protensum*). The most common epiphyte was *A. scandens* ssp. *pusilum,* which was found in 30 plots and in nine of the ten trees

sampled. Twenty of the angiosperm taxa occurred in only one of the ten trees, and seven of these were orchids.

The relative biomass among angiosperms and the relative frequency among plots with angiosperms were calculated for all taxa identified to at least the family level. Importance values (I.V. = relative biomass + relative frequency) for the 65 species were ranked in descending order of importance (Appendix), and were plotted as a dominance–diversity curve (Fig. 4). The magnitude of the slope is not great, indicating that these taxa are fairly similar in terms of their relative abundance, and that there are many relatively uncommon (low I.V.) species. The curve is similar in shape to other curves of high diversity plant communities described by Whittaker (1965, 1975), and for epiphytic bryophytes in the Olympic Peninsula (Hoffman 1971). The unidentified plants would increase total diversity without appreciably altering the general shape of the curve.

SPECIES RICHNESS.—The most species-rich plots (6–11 species) of the 174 plots that had angiosperms had low frequencies and were lumped (for a total of six categories) to increase the validity of the chi-square tests. A significant chi-square value (40.52, $P \leq 0.001$) indicated that species richness per plot is not independent of the plot angle class. Species richness was not independent of the plot circumference class (22.81, $P \leq 0.05$); higher species richness was associated with wider branches. However, plots representing the largest circumference class had the greatest surface area, hence the high species richness found there was not unexpected.
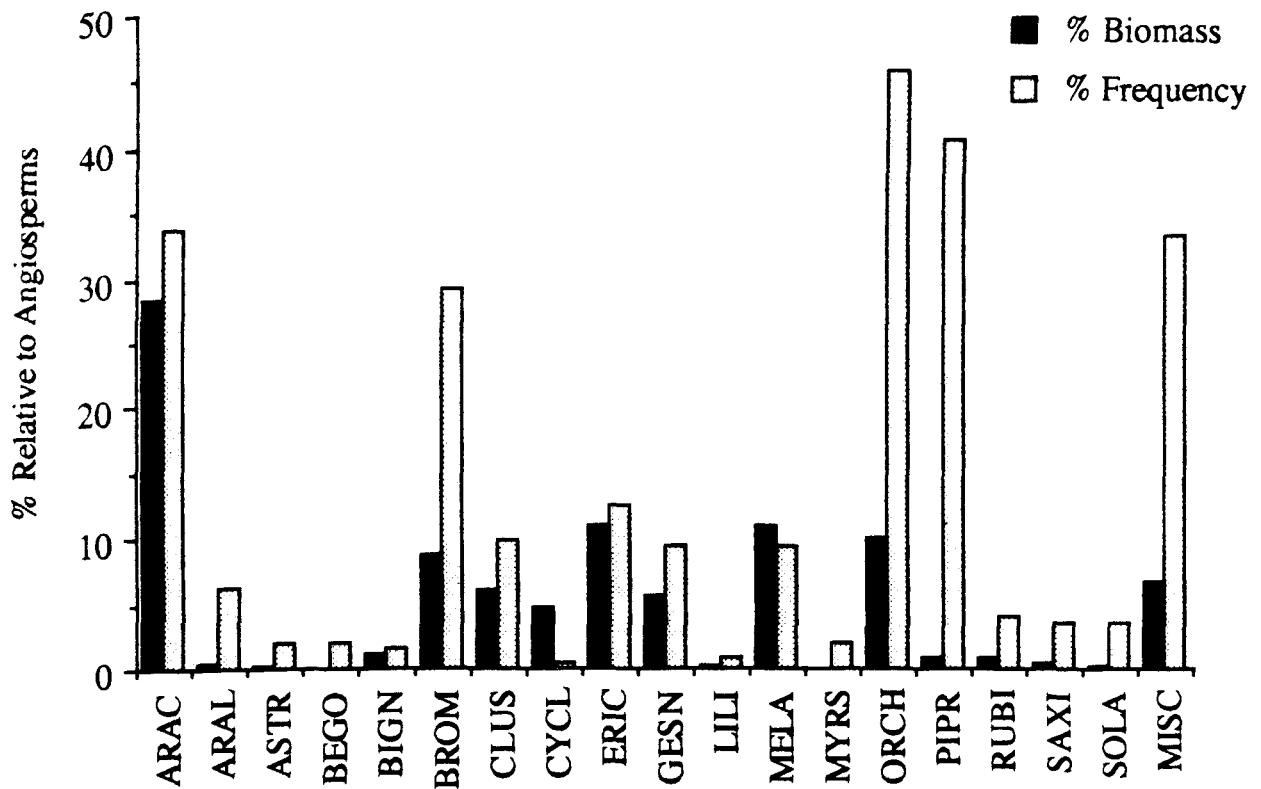
FIGURE 3. Percent biomass and frequency of angiosperm families for all epiphytes identified to family level. Percent values are relative to angiosperms. Family names are given in order of their abbreviations from left to right as follows: Araceae, Araliaceae, Asteraceae, Begoniaceae, Bromeliaceae, Clusiaceae, Convallariaceae, Cyclanthaceae, Ericaceae, Gesneriaceae, Grossulariaceae, Melastomataceae, Myrsinaceae, Orchidaceae, Piperaceae, Rubiaceae, Solanaceae, and plants unidentified at family level.

Comparisons per unit area among branch size classes indicated that angiosperm species densities did not differ significantly (Table 6). Mean species richness per unit area was significantly different among angle classes ($H = 25.91$, $P \leq 0.001$), and pairwise comparisons showed there were significantly more species per dm² on the least inclined branches than on the most inclined class of branches ($Q = 5.05$, $P \leq 0.001$). Counts of seedlings (irrespective of taxa) indicated significant differences among circumference classes (Table 6), and angle classes ($H = 14.80$, $P < 0.001$). Pairwise comparisons indicated significant differences in seedling density between angle classes 1 and 3 only ($Q = 3.70$, $P < 0.001$). The largest branches had significantly fewer seedlings per dm² than either the medium size branches or the small branches (Table 6).

DISCUSSION

VARIATION AND DISTRIBUTION OF EOM.—Crowns of *Ocotea tonduzii* support a diverse epiphytic community with a live plant composition and DOM

abundance that varies with branch size and anₚ. The high variation of total EOM between brancḥ is due mostly to angle and size, among the variabḷ measured. Microclimate and history (particulaṛ, disturbance) also undoubtedly influence the distribution of epiphytic material. In other tropical forests, microclimate has been shown to vary through the forest and within individual tree crowns according to gradients in light, temperature, humidity, and air movement (Allee 1926, Geiger 1965, Allen *et al.* 1972). Generally, epiphytes are exposed to higher insolation (Yoda 1974), greater extremes of temperature and relative humidity, and more rapid and frequent wetting and drying than forest understory vegetation. The relatively low variation of total EOM within branches may be partly due to similar microclimatic conditions within a branch of the inner canopy. Plots from within one braᵤ.ḥ probably also share a similar history of colonizaṭion and/or disturbance.

The distribution and abundance of EOM are determined partly by branch inclination and size, and partly by the distribution and abundance of
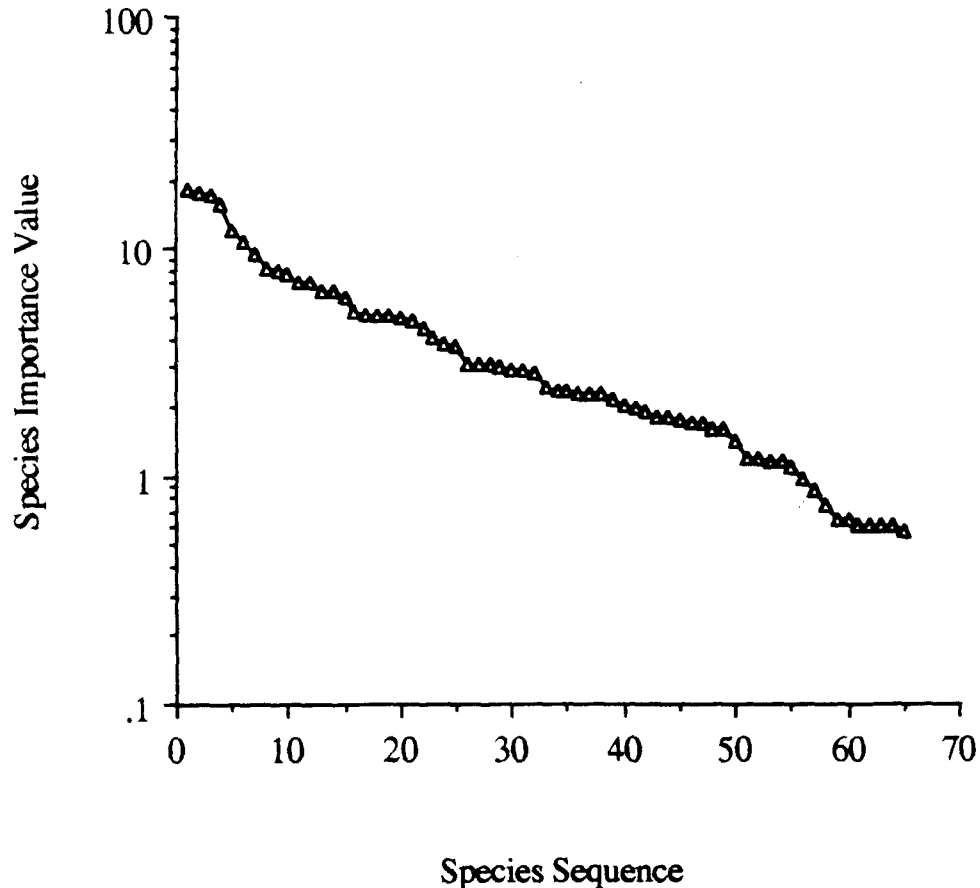
FIGURE 4.   Species importance value curve for 65 epiphytic angiosperms. Relative importance values are plotted on a logarithmic scale.

other epiphytic components. The amount of epiphytic roots is obviously associated closely with the amount of fern and angiosperm shoots. The abundance of angiosperms was more strongly correlated with the abundance of DOM than with any other epiphytic component except roots (Table 5). Angiosperms intercept significantly more airborne organic material than bare branches (Nadkarni 1986), and their roots help bind it together. For all branch angle classes, virtually all of the angiosperms were associated with humus; DOM is undoubtedly important to the survival of many angiosperms as its water-retention capacity provides a more continuous moisture supply for epiphytes than the atmosphere or bare bark (Benzing 1984, 1987, 1990). In addition to nitrate from the atmosphere, the mineralized DOM is a source of N for epiphytes (Vance & Nadkarni 1990), and is probably a more reliable source than the atmosphere (Clark & Nadkarni 1990).

Although more DOM was found on the least inclined branches, the association between angiosperms and DOM abundance is stronger on the more inclined, angle class 3 branches (Table 5). A more inclined branch should receive less wet season (*i.e.*, vertical) rainfall and experience more rapid runoff than a less inclined branch. Gravity may operate directly or indirectly to promote lower abundance of vascular epiphytes on more inclined branches. Propagules and canopy litter are less likely to settle on inclined bark and the rapid runoff of moisture could accelerate leaching compared to conditions on horizontal surfaces.

One-third to one-half of the epiphytic biomass of a montane forest in New Guinea was composed of canopy humus (Edwards & Grubb 1977). Similarly, DOM accounted for 45 percent of the total biomass in an elfin forest adjacent to our study site (Nadkarni 1984), and 60 percent within the leeward cloud forest (this study). Among "inner branches" of elfin forest trees, DOM constituted 57 percent of the epiphytic dry mass, very similar to the proportion found among the sampled "inner canopy" of leeward cloud forest trees. EOM made up *ca* 35 percent of epiphytic dry mass among larger, inner canopy branch portions and only zero

TABLE 6.   *Mean number of angiosperm species dm⁻² and angiosperm seedlings dm⁻² (with standard deviation) for three branch size classes. There was no significant difference in mean number of angiosperm species dm⁻² (Kruskal-Wallis test statistic, H = 3.09, P = 0.122). Mean number of angiosperm seedlings dm⁻² differed significantly (H = 7.63, P = 0.022) among branch size classes. Pairwise comparisons showed that seedling density was significantly less on large branches than on both the medium size branches (O = 2.46, P < 0.05), and the small branches (O = 2.88, P < 0.02). (Means with different superscripts are significantly different at P < 0.05).*

	Mean number of angiosperm species dm⁻²	Mean number of angiosperm seedlings dm⁻²
Small	0.40 (0.40)	0.47 (0.64)[a]
Medium	0.28 (0.24)	0.41 (0.55)[a]
Large	0.24 (0.18)	0.17 (0.23)[b]

to five percent among smaller, outer canopy portions in a Colombian cloud forest (van Leerdam *et al.* 1990). Overall, bryophytes comprised 40 percent of the epiphytic biomass in the elfin forest (Nadkarni 1984) compared to 6 percent in the leeward cloud forest, but bryophytes were most abundant in both forests among the smallest branches. The gnarled, windblown trees and the frequent mist in the elfin forest provide extremely favorable conditions for bryophytic growth (see Lawton & Dryer 1980).

SUCCESSION.—Epiphyte communities can be useful for studying succession because of the proximity of young and old substrata and the relatively rapid growth of substrata. Epiphyte succession in a Liberian forest was documented by examining the remains of older vegetation under living epiphytes (Johansson 1974). Successive stages of epiphytic vegetation were described by Dudgeon (1923) for a Himalayan oak forest, beginning with lichens covering bare bark, leading to colonization by bryophytes, and culminating, after more than 20 years, in the "climatic climax" dominated by angiosperms and ferns. Although local changes in epiphytic vegetation may not always be marked by the clearness of successive stages that Dudgeon observed, the observation that cryptogams are typically the first to colonize small branches, gradually giving way to larger, vascular epiphytes, is consistent with our study. Bryophytes may favor their own displacement by providing vascular epiphytes with retained water (Barkman

1958, Pócs 1980), by forming humus, by accelerating bark decay (Barkman 1958), and/or by improving physical anchorage of seeds and propagules. In addition, a greater density of angiosperm seedlings among smaller branches may indicate that the epiphytes that persist as branches grow are better able to utilize the resources available in the accumulating humus than more recent colonizers.

FLORISTIC COMPOSITION.—The floristic composition of epiphytic flowering plants we encountered in Monteverde was typical for a Central American lower montane rain forest. The six angiosperm families with the most epiphytic species (Araceae, Bromeliaceae, Ericaceae, Melastomataceae, Orchidacea and Piperaceae) (Kress 1986), were the six most common families at our study site (Appendix). Based on the numbers of epiphytic families from Central and South American locations according to their annual precipitation (Gentry & Dodson 1987b), the number of families represented (18) was slightly greater than expected. The highest epiphyte species diversity recorded occurs between 1000 m and 2000 m in the Andes and slightly lower in Costa Rica (Gentry & Dodson 1987b), and Monteverde lies within this elevational range. Ongoing floristic studies indicate that epiphytic angiosperms from 26 families occur within the study area, and that many of the undetermined epiphytes must have been conspecific with those identified and listed in the Appendix (Ingram *et al.*, pers. obs.).

Pleurothallis and *Peperomia*, the largest monocot and dicot genera of Neotropical epiphytes, respectively (Kress 1986, Gentry & Dodson 1987b), were the two best represented and most frequently encountered genera at our study site (Appendix). Four or five species of *Anthurium, Peperomia*, or *Pleurothallis* often occurred on the same branch. The only records of the biomass of epiphytic angiosperm species were collected in a lowland, semideciduous forest in Veracruz, Mexico, where *Anthurium* spp. contributed less biomass than either orchids, bromeliads or cacti, and the arborescent *Clusia* spp. added more to total epiphytic biomass than any other genus (Valdivia 1977).

The dominance–diversity curve (Fig. 4) indicated co-occurrence of many species with no clear dominants, many of which seemed to have patchy distribution. The orchids, *Dichaea* aff. *cryptarrhena, Encyclia pseudopygmaea, Maxillaria linearifolia*, and *Pleurothallis ruscifolia* were relatively frequent but were found in only one or a few trees (Appendix), suggesting that relatively recent colonization and local dispersal may explain some epiphyte distri-

butions. It is likely that a windblown seed or propagule became established on one site and its progeny colonized suitable sites within that tree, eventually spreading to more distant host trees. The presence of patchily distributed epiphytes may reflect chance recruitment more than competition (Benzing 1981). Alternatively, the high species richness of angiosperms and the relative similarity of species importance values may indicate diverse microhabitats promoted in part by relatively intense small-scale disturbances that create an ecological mosaic. Spatial heterogeneity of the epiphytic habitat, represented by variable branch sizes, angles, and orientations, may contribute substantially to the overall high species richness of epiphytic angiosperms observed in neotropical montane forests.

More extensive sampling of host trees is necessary to fully characterize species distributions in diverse epiphyte communities and to identify the underlying patterns and mechanisms. Detailed investigations of the climatic gradients and patterns of small-scale disturbances within the canopy will provide insights on the importance of these abiotic factors.

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APPENDIX.   *Epiphytic angiosperm taxa, frequency (number of plots and trees in which species was encountered), biomass, importance values (relative biomass + relative frequency), and (for 65 individual species) importance value ranks. Nomenclature follows Dahlgren et al. (1985) and Cronquist (1988).*

Family Species	Frequency (no. plots/ no. trees)	Biomass (g)	I.V.	(Rank)
Araceae				
Anthurium friedrichsthalii Schott	11/4	201.2	15.6	(4)
A. obtusilobum Schott	5/3	47.5	5.1	(19)
A. pittieri Engl. var. *pittieri*	1/1	1.0	0.6	(62)
A. protensum Schott	13/7	245.0	18.8	(1)
A. scandens (Aubl.) Engl. ssp.				
pusilum Sheffer	30/9	13.9	17.9	(2)
Anthurium spp.	8/6	17.1	5.4	
Philodendron cf. *wilburi*				
Croat & Grayum (ined.)	1/1	3.9	0.8	(58)
Stenospermation sessile Engl.	5/2	142.8	9.5	(7)
Araceae spp.	11/6	2.6	6.4	
Araliaceae				
Oreopanax sp. 1	8/5	4.2	4.8	(21)
Schefflera cf. *robusta*				
A. C. Smith (A. C. Smith)	3/2	4.9	2.0	(42)
Araliaceae sp. 1	1/1	0.2	0.6	
Asteraceae				
Liabum polyanthum Klatt	1/1	0.3	0.6	(65)
Neomirandea parasitica (Klatt) K&R	3/3	5.5	2.0	(41)
Begoniaceae				
Begonia heydei C.DC.	4/2	0.7	2.3	(37)
Bromeliaceae				
Catopsis nitida (Hook.) Griseb.	1/1	1.8	0.7	(60)
Guzmania angustifolia (Bak.) Wittm.	15/6	75.2	12.1	(5)
G. nicaraguensis Mez & C. F. Baker ex Mez	6/3	37.2	5.2	(18)
Tillandsia insignis (Mez) L. B. Sm. & Pittd.	3/1	7.2	2.1	(40)
Vriesea cf. *viridiflora* (Regal) Wittm. ex Mez	3/3	31.1	3.2	(26)
Bromeliaceae spp.	31/8	38.4	19.6	
Bignoniaceae				
Schlegelia sp. 1	3/3	26.6	3.0	(30)
Clusiaceae				
Clusia sp. 1	2/2	55.5	3.7	(25)
Clusia spp.	17/5	74.5	13.2	
Convallariaceae				
Maianthemum monteverdense LaFr.	2/2	6.4	1.5	(50)
Cyclanthaceae				
Sphaeradenia cf. *irazuensis* (Cuf.) Harl.	1/1	102.2	5.3	(16)
Ericaceae				
Cavendishia capitulata Donn. Sm.	2/2	106.1	6.1	(15)
C. melastomoides (Kl.) Hemsl.	5/3	50.1	5.2	(17)
Disterigma humboldtii (Kl.) Ndzu.	8/3	7.8	5.0	(20)
Psammisia ramiflora Kl.	2/2	1.1	1.2	(51)
Sphyrospermum cordifolium Benth.	4/2	11.6	2.8	(32)
Ericaceae spp.	4/2	60.8	5.1	
Gesneriaceae				
Columnea lepidocaula Hanst.	2/2	22.9	2.2	(39)
C. microcalyx Hanst.	10/5	16.8	6.5	(14)
Drymonia conchocalyx Hanst.	6/2	80.0	7.2	(11)

APPENDIX. *Continued.*

Family Species	Frequency (no. plots/ no. trees)	Biomass (g)	I.V.	(Rank)
Grossulariaceae				
Phyllonoma cf. *tenuidens* Pittier	7/4	8.5	4.4	(22)
Melastomataceae				
Blakea anomala J. D. Smith	6/2	67.7	6.6	(13)
B. tuberculata J. D. Smith	3/1	45.7	3.8	(24)
Blakea sp. 1	5/3	109.9	8.0	(9)
Topobea brenesii Standl.	2/1	10.1	1.6	(49)
Melastomataceae spp.	2/2	2.2	1.3	
Myrsinaceae				
Cybianthus costaricanus Hemsl.	4/2	2.5	2.4	(34)
Orchidaceae				
Ada chlorops (Endres & Rchb. f.) N. H. Wms.	1/1	6.5	0.9	(57)
Dichaea aff. *cryptarrhena* Rchb. f. ex Kränzl.	12/3	5.4	7.2	(12)
Dracula cf. *erythrochaete* (Rchb. f.) Luer	1/1	9.1	1.0	(56)
Elleanthus cf. *aurantiacus* (Lindl.) Rchb. f.	2/1	10.2	1.6	(48)
Encyclia pseudopygmaea (A. Finet)				
Dressl. & Poll.	11/1	32.2	7.8	(10)
Lepanthes spp.	5/3	0.8	2.9	
Maxillaria dendrobioides (Schltr.) L. O. Wms.	1/1	1.0	0.6	(61)
M. linearifolia Ames & Schweinf.	9/2	63.9	8.1	(8)
M. reichenheimiana Endres & Rchb. f.	1/1	0.7	0.6	(64)
Pleurothallis amparoana Schltr.	2/2	1.2	1.2	(52)
P. eumecocaulon Schltr.	1/1	1.9	0.7	(59)
P. homalantha Schltr.	5/3	4.9	3.1	(28)
P. rowleei Ames	6/2	13.3	4.1	(23)
P. ruscifolia (Jacq.) R. Br.	26/4	48.6	17.2	(3)
Pleurothallis aff. spp.	31/7	6.5	18.1	
Restrepia cf. *subserrata* Schltr.	4/2	2.3	2.4	(35)
Scaphyglottis cf. *cuneata* Schltr.	3/2	0.5	1.8	(46)
Stelis pardipes Rchb. f.	3/2	2.7	1.9	(43)
Stelis spp.	2/2	0.4	1.2	
Orchidaceae spp.	21/7	5.6	12.3	
Piperaceae				
Peperomia angularis C.DC.	3/2	0.5	1.8	(47)
P. costaricensis C.DC.	5/3	3.6	3.0	(29)
P. dotana Trel.	1/1	0.9	0.6	(63)
P. hylophila C.DC.	5/2	1.7	3.0	(31)
P. peltilimba C.DC. ex Trel.	3/2	1.3	1.8	(45)
P. pseudo-alpina Trel.	2/1	0.2	1.1	(55)
P. reptabunda Trel.	4/2	0.7	2.3	(38)
P. serpens (Sw.) Loud.	4/1	1.1	2.4	(36)
P. tenella (Sw.) A. Dietrich	18/5	5.1	10.6	(6)
Peperomia spp.	42/10	6.1	24.4	
Rubiaceae				
Hillea triflora (Oerst.) C. Taylor	3/2	2.0	1.8	(44)
Psychotria pithecobia Standl.	3/1	15.8	2.5	(33)
Psychotria sp. 1	2/2	0.5	1.2	(53)
Solanaceae				
Lycianthes synanthera (Sendt.) Bitt.	5/4	6.3	3.2	(27)
Solanaceae spp.	3/2	0.4	1.7	
Unidentified plants	64/10			