

The Influence of Host Tree Species on the Distribution of Epiphytic Bromeliads in Experimental Monospecific Plantations, La Selva, Costa Rica¹

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ABSTRACT

Epiphytes perform critical functions in primary tropical forests, but their ecological roles have only rarely been studied in secondary forests or in forest plantations. We assessed the composition and distribution of epiphytic bromeliad communities in four- and eight-year-old replicated experimental monospecific tree plantations (3 species) at the La Selva Biological Station, Costa Rica. The bromeliad communities of these stands are dominated by two species, *Guzmania monostachya* (L.) Rusby ex. Mez and *Vriesea gladioliflora* (H. Wendl.) Antoine. We identified bromeliads on over 700 trees and estimated their biomass and leaf area. Mean bromeliad biomass ranged from 2 to 8 g/tree in the four-year-old plots and from 20 to 94 g/tree in the eight-year-old plots. The mean bromeliad leaf area ranged between 104 and 704 cm²/tree and from 1600 to 8500 cm²/tree in the four- and eight-year-old plots, respectively. Although bromeliads accounted for less than 2 percent of the total foliar biomass and leaf area in both four-year-old and eight-year-old plots, the biomass of bromeliads exhibited a 5- to 46-fold increase between the four-year-old and eight-year-old plots, respectively. Bromeliads showed clear patterns of host tree preference, which may be attributed to host tree characteristics that differentially favor recruitment and survivorship. Between four and eight years of growth, differences among host tree species with respect to the amount of available host tree woody biomass, host tree foliar biomass, and host tree leaf surface area were positively correlated with the abundance of epiphytic bromeliads.

RESUMEN

Se ha documentado que las epífitas ejecutan funciones críticas en bosques tropicales primarios. Sin embargo, se sabe muy poco de su ecología en bosques secundarios o en plantaciones forestales. Determinamos la composición, distribución, y la abundancia de comunidades de bromelias epífitas en plantaciones forestales experimentales de 4 y 8 años de edad en la Estación Biológica La Selva, Costa Rica. Dos especies de bromelias, *Guzmania monostachya* (L.) Rusby ex. Mez. y *Vriesea gladioliflora* (H. Wendl.) Ant., dominan las comunidades de epífitas en estas plantaciones. Un análisis de la altura sobre el suelo a la que se encuentran las bromelias y de su distribución de tamaño, realizado en más de 700 árboles, junto con medidas del área foliar y biomasa, demostró que el área foliar de las bromelias es <2% del total en parcelas de 4 y 8 años de edad. La biomasa promedio de bromelias varía entre 2–8 g/árbol en las parcelas de 4 años, y entre 20–94 g/árbol en las parcelas de 8 años. El área foliar promedio de las epífitas estudiadas en las parcelas de 4 años fué de 104–704 cm²/árbol, y entre 1600 y 8500 cm²/árbol en las parcelas de 8 años. La biomasa de bromelias aumentó de 5 a 46 veces más entre los 4 y los 8 años, mientras que el área foliar aumentó de 2 a 40 veces más. Entre los 4 y 8 años de edad, los cambios en la abundancia relativa de epífitas estuvieron relacionados positivamente con la edad del sustrato y con la fenología de las hojas.

Key words: biomass; Bromeliaceae; Costa Rica; epiphytes; *Guzmania*; host tree specificity; leaf area; tropical forests; *Vriesea*.

THE BIOMASS AND DYNAMICS OF EPIPHYTIC COMMUNITIES have been documented in many primary forest habitats (Edwards & Grubb 1977, Tanner 1980, Nadkarni 1984, Ackerman *et al.* 1989, Veneklaas 1990, Hofstede *et al.* 1993). They, however, have rarely been studied in secondary forests

and agricultural settings (Catling *et al.* 1986). This lack of studies in non-primary forests is surprising because of the ease with which they can be examined relative to primary forests. For example, secondary forests tend to have shorter stature than primary forests, which reduces problems with canopy access. Because the history of trees in many secondary forests has been documented and sometimes manipulated, and because tree species diversity is usually much lower than primary forests, the confounding factors of different host tree ages and species encountered in primary forests can be minimized in secondary forests. Investigations that en-

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hance our understanding of epiphyte ecology in secondary forest habitats become more important as disturbed forests dominate increasing areas of tropical landscapes (Brown & Lugo 1990).

Manipulated forests and plantations also allow us to investigate potential host tree–epiphyte interactions, particularly the question of how different host tree species affect epiphyte distribution and abundance. Studies of host tree specificity in natural forests, where the paucity of individuals from a given age or size class for the many coexisting species precludes adequate replication, have often yielded inconclusive results (Frei & Dodson 1972, Cornelissen & ter Steege 1989, Hietz & Hietz-Seifert 1995, Arseneau *et al.* 1997, Baars *et al.* 1998). In contrast, manipulated forests of low diversity (or, even better, monospecific plantations or experimental stands) allow us to carry out inventories of epiphytes with numerous replicates of host trees that have been exposed to the same environmental conditions and grow on the same soil types. The few studies that have approached this in plantations (Catling *et al.* 1986) have pointed out intriguing trends in epiphyte specificity of host trees.

We quantified the abundance of the dominant vascular epiphytes in young monospecific forest plantations in a lowland tropical forest. We took advantage of a long-term experimental project composed of replicated stands of three host tree species of two ages (4 and 8 years old; hereafter, “young” and “old,” respectively). We report estimates of bromeliad density, biomass, and leaf area, and compare these to the biomass and leaf area of host trees. This study is one of the few that has addressed the effects of host tree species on bromeliad distribution with sufficient replication and is a first step to understanding the ecological roles that epiphytes play in early successional forests and plantations.

STUDY AREA AND METHODS

STUDY SITE.—Fieldwork was conducted from June to August 1999 at the La Selva Biological Station (10°26'N, 84°00'W, 30 m elev.) in the Atlantic lowlands of northeastern Costa Rica. The surrounding primary forest is classified as tropical premontane wet forest (Hartshorn 1983). Mean annual rainfall at La Selva is *ca* 3900 mm, with the majority of precipitation occurring between May and December (Clark 1994). For a detailed site description of La Selva, see McDade *et al.* (1994).

Our study site was located in a series of experimental plots established in June 1991 as part of a

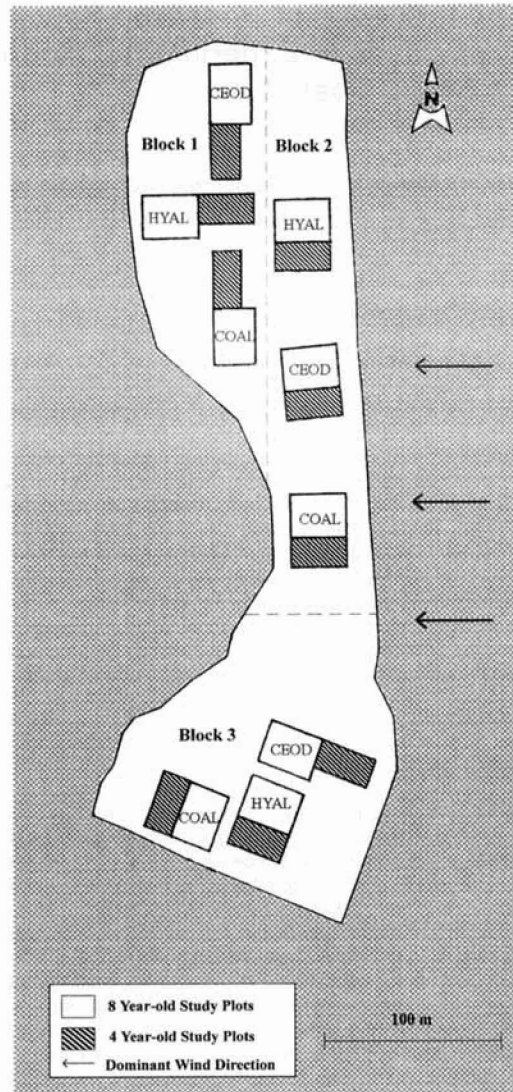


FIGURE 1. A map of the study site showing plots of the three tree species (HYAL = *Hyeronima*; CEOD = *Cedrela*; COAL = *Cordia*) surrounded by primary forest (gray shaded area).

long-term study (“Proyecto Huertos”) designed to assess the impact of plant longevity on sustainability in model tropical ecosystems (Haggar & Ewel 1994). The 8 ha study site is situated on alluvial (dystropept) soil and is immediately surrounded by regrowing cacao plantation (*ca* 60 yr old) that supports a forest 10–20 m in stature with occasional emergent trees and abundant epiphytes. The common species in the experimental plots are also common in the surrounding forest.

TABLE 1. Mean biomass (g/ind) and leaf area (cm²/ind) values for individual bromeliads by size class. Standard deviations are in parentheses.

Size Class	<i>Guzmania monostachya</i>		<i>Vriesea gladioliflora</i>		Other Bromeliads	
	Biomass	Leaf Area	Biomass	Leaf Area	Biomass	Leaf Area
Small	0.2 (±0.03)	35.9 (±6.1)	0.6 (±0.4)	67.4 (±37.1)	0.4 (±0.)	39.6 (±29.1)
Medium	2.3 (±1.1)	268.6 (±92.6)	2.4 (±1.0)	240.5 (±127.3)	1.7 (±0.5)	146.0 (±26.6)
Large	10.1 (±3.8)	931.2 (±303.8)	28.0 (±11.6)	2427.6 (±1134.8)	4.2 (±4.3)	278.3 (±262.2)

The study area consisted of three replicated blocks, each composed of monoculture plots of three tree species: *Hyeronima alchorneoides* Allemão (Euphorbiaceae), *Cedrela odorata* L. (Meliaceae), and *Cordia alliodora* (Ruíz & Pavon) Oken (Boraginaceae). Within each block, monospecific plots were subdivided into a 20 × 40 m plot that was harvested and replanted at four-year intervals, and a 30 × 40 m plot that has not been harvested since the time of planting, yielding a total of six plots per block (18 plots total) (Fig. 1). Trees were planted in evenly spaced rows, so that each tree was equidistant (2 m) from its six nearest neighbors. The mean number of trees per plot was 106 ± 23 (SD) in the young plots and 75 ± 9 in the old plots. The mean diameter (std) of trees was 9.1 cm (0.19) in the young stands and 15.4 cm (0.22) in the old stands.

In the young stands, nonvascular epiphytes (bryophytes and lichens) accounted for 93 to 99 percent of the epiphyte biomass; bromeliads made up less than 1 percent of the epiphyte biomass (M. Merwin & S. Rentmeester, pers. obs.). In the old stands, bromeliads were the dominant epiphytes, accounting for 70 to 75 percent of the epiphyte biomass in *Cordia* and *Cedrela* plots and ca 90 to 95 percent in the *Hyeronima* plots (A. Reich, pers. comm.).

BROMELIAD DISTRIBUTION.—Using binoculars and a spotting scope, we identified all individual bromeliads on each tree to species. Given that juveniles of many bromeliads are very small, quite similar,

and were observed from the ground, there was some uncertainty for this size class. Our analyses, however, are based on biomass, and so this may not be as critical as the larger individuals for which identification was more straightforward. For clonal plants (e.g., *Guzmania monostachya*), we counted each tank as an "individual." The 25 individual bromeliads that could not be identified to species accounted for less than 1 percent of the total; we excluded these from the analyses. Vouchers are housed at The Evergreen State College Herbarium.

BROMELIAD BIOMASS AND LEAF AREA.—We assigned each individual bromeliad to a size class (small, 5–<15 cm tall; medium, 15–<25 cm; large, ≥25 cm). Because two species (*G. monostachya* and *Vriesea gladioliflora*) made up the clear majority of the epiphytic bromeliads, we quantified biomass and leaf area of these separately and combined biomass and leaf area measurements of all the other bromeliad species (pooled and labeled "other bromeliads"). Ten individuals from each of the three size classes of *G. monostachya* and of *V. gladioliflora* were destructively sampled. Recently fallen bromeliads (by assessing the freshness of their appearance and by observing newly fallen plants during our frequent visits to the site) were also collected opportunistically and measured. For the other bromeliad species, 17 plants were measured for the small and large size classes, and 4 individuals were sampled for the medium size class.

We measured fresh leaf area with a leaf area meter (Li-Cor 3100, Lincoln, Nebraska). Plants

TABLE 2. Mean total bromeliad biomass (g/tree) and leaf area (cm²/tree) in the 4- and 8-year-old plots. Standard deviations are in parentheses. Letters denote significant difference (P < 0.01) within an age class.

Host tree species	Bromeliad Biomass		Bromeliad Leaf Area	
	4-year-old plots	8-year-old plots	4-year-old plots	8-year-old plots
<i>Hyeronima alchorneoides</i>	1.0 (±1.2) ^a	94.4 (±19.7) ^a	108.4 (±114.4) ^a	8645.9 (±833.9) ^a
<i>Cedrela odorata</i>	1.9 (±2.1) ^a	21.8 (±3.5) ^b	179.4 (±201.1) ^a	1746.6 (±426.7) ^b
<i>Cordia alliodora</i>	7.5 (±5.0) ^b	46.2 (±27.3) ^b	721.3 (±483.3) ^b	2576.0 (±968.2) ^c

were then oven-dried to constant mass at 70°C for 24 hours and biomass was recorded. We calculated the mean whole-plant biomass and the mean leaf area of whole plants for each size class separately for *Guzmania monostachya*, *Vriesea gladioliflora*, and other bromeliads. We multiplied these values by the density of bromeliads in each size class to estimate the total bromeliad biomass and bromeliad leaf area on a per plot basis. We also calculated bromeliad biomass and leaf area on a per tree basis by summing measurements of all of the bromeliads on each stem.

The equation used to calculate the relative increase (i) in bromeliad biomass and leaf area in the old plots relative to the young plots on a per tree basis was $o - y/y = i$, where o and y are biomass or leaf area values in the old and young plots, respectively.

TREE BIOMASS AND LEAF AREA.—To assess the proportion of bromeliad biomass relative to the other vegetative components of the ecosystem, we used data from previous sampling in the plots (J. Ewel, pers. comm.). In 1995, six or seven trees per plot were harvested in the young plots, and in 1999, one tree per plot was harvested in the old stands. Trees had been felled and components were sorted into the categories of “wood” and “foliage.” The former group included stems, branches, and rachises or petioles. Foliage was measured with a leaf area meter using fresh leaves. All plant material was oven-dried to constant mass. Allometric data from these measurements were used to calculate 1999 biomass and leaf-area values on a per tree basis (T. Cole, pers. comm.).

STATISTICAL ANALYSES.—Four- and eight-year-old plots were treated as separate populations for analysis. We tested for differences in mean biomass and mean leaf area in the young and old plots following the ANOVA procedures for a randomized block design (Sokal & Rohlf 1981). This nested test was based on mean response per plot with sample size of three. Host species was treated as a fixed effect and block as a random effect. The hypothesis of equal response on all host species was tested as mean squares treatment over mean squares residu-

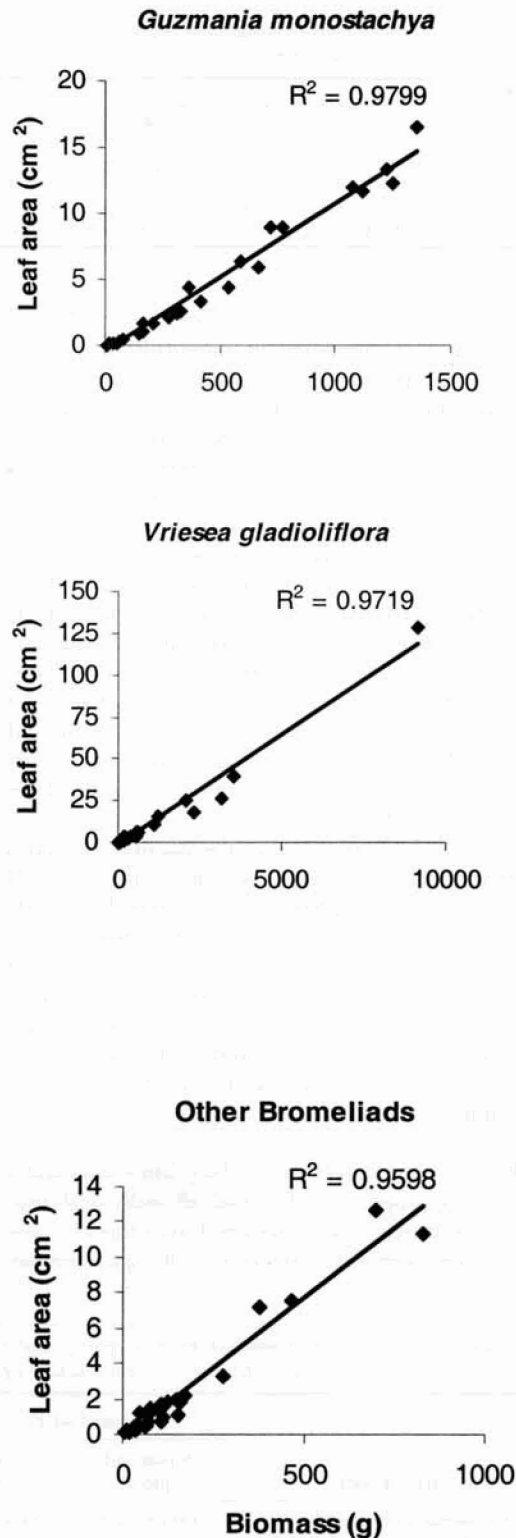


FIGURE 2. Total leaf area as a function of whole plant biomass in *Guzmania monostachya*, *Vriesea gladioliflora*, and other bromeliad species in experimental plantations at La Selva.

TABLE 3. Mean biomass (g/tree) and leaf area (cm²/tree) of epiphytic bromeliads in 4- and 8-year-old plots. The percent total of each species is in parentheses. Letters denote significant differences ($P < 0.01$) among bromeliad taxa within host species of a single age.

Host tree species	Biomass					
	4-year-old plots			8-year-old plots		
	<i>Guzmania</i>	<i>Vriesea</i>	Other	<i>Guzmania</i>	<i>Vriesea</i>	Other
<i>Hieronima alchorneoides</i>	0.7 (71) ^a	0.3 (25) ^a	<0.1 (4) ^a	27 (28) ^a	66 (70) ^b	2 (2) ^c
<i>Cedrela odorata</i>	2 (97) ^a	<0.1 (2) ^b	<0.1 (2) ^b	13 (66) ^a	4 (21) ^b	1 (5) ^c
<i>Cordia alliodora</i>	7 (95) ^a	0.2 (2) ^b	0.2 (3) ^b	41 (88) ^a	5 (10) ^b	1 (2) ^c

Host tree species	Leaf Area					
	4-year-old plots			8-year-old plots		
	<i>Guzmania</i>	<i>Vriesea</i>	Other	<i>Guzmania</i>	<i>Vriesea</i>	Other
<i>Hieronima alchorneoides</i>	77 (71) ^a	28 (25) ^a	4 (4) ^a	3287 (38) ^a	5234 (61) ^b	124 (1) ^c
<i>Cedrela odorata</i>	175 (97) ^a	3 (2) ^b	2 (1) ^b	1336 (76) ^a	326 (19) ^b	85 (5) ^c
<i>Cordia alliodora</i>	687 (95) ^a	16 (2) ^b	18 (2) ^b	2116 (82) ^a	414 (16) ^b	45 (2) ^c

als. Tukey's multiple-range pairwise comparisons were used to identify differences among means. Statistical analyses of measured and derived values were performed with SAS (SAS 1989) and SPSS (Green *et al.* 2000).

RESULTS

BROMELIAD COMMUNITY COMPOSITION AND STRUCTURE.—We counted and identified 6759 individual epiphytic bromeliads on 716 trees (mean density = 9.4/tree). The two most abundant vascular epiphyte species, *G. monostachya* and *V. gladioliflora*, accounted for 6649 individuals (98% of all bromeliads). The eight other species were *Aechmea nu-*

dicaulis (L.) Griseb., *Catopsis juncifolia* Mez & Wercklé, *C. sessiliflora* (Ruíz ex Pav.) Mez, *Guzmania lingulata* (L.) Mez, *Tillandsia anceps* Lodd., *T. bulbosa* Hook., *T. festucoides* Brongn., and *T. pruinosa* SW.

BROMELIAD BIOMASS AND LEAF AREA.—For the large and small size classes, *V. gladioliflora* was consistently larger than *G. monostachya*, but there was little difference for the medium size class. Plants in the "other bromeliads" category were consistently smaller than both species (Table 1). The biomass and leaf area of all bromeliad size classes showed a strong linear relationship (*G. monostachya*, $R^2 = 0.980$, $P < 0.001$; *V. gladioliflora*, $R^2 = 0.972$, P

TABLE 4. Mean biomass (g/tree) and leaf area (cm²/tree) of epiphytes, and phorophyte foliage and wood in 4- and 8-year-old plots. The epiphyte foliage of the percent mean total plot-level foliage is in parentheses. Phorophyte biomass and leaf area data are from J. Ewel (pers. comm.).

Host tree species	Biomass					
	4-year-old plots			8-year-old plots		
	Epiphyte Foliage	Phorophyte		Epiphyte Foliage	Phorophyte	
		Foliage	Wood		Foliage	Wood
<i>Hieronima alchorneoides</i>	2 (0.1)	977	15,148	94 (1.3)	7330	87,368
<i>Cedrela odorata</i>	3 (0.2)	803	10,514	20 (0.8)	2320	48,613
<i>Cordia alliodora</i>	8 (0.4)	1889	21,044	47 (1.6)	2812	48,177

Host tree species	Leaf Area			
	4-year-old plots		8-year-old plots	
	Epiphytes	Phorophytes	Epiphytes	Phorophytes
<i>Hieronima alchorneoides</i>	104 (<0.1)	130,604	8521 (1)	878,219
<i>Cedrela odorata</i>	413 (0.3)	145,134	1661 (0.4)	379,557
<i>Cordia alliodora</i>	704 (0.2)	287,960	2531 (0.8)	313,216

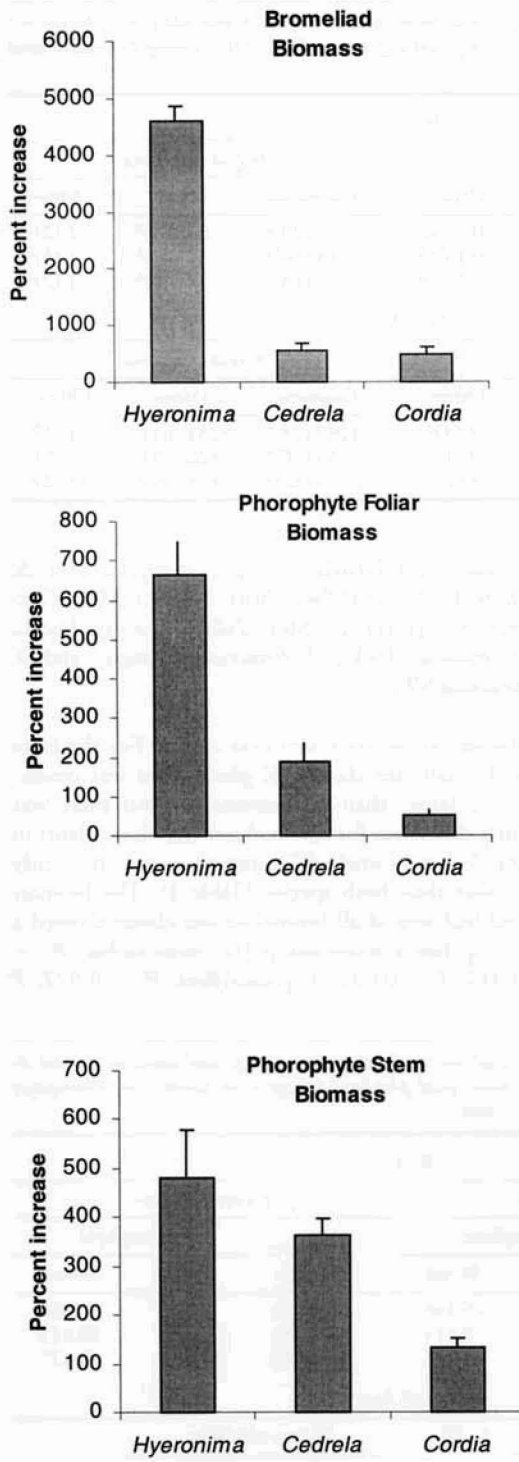


FIGURE 3. The mean difference in bromeliad biomass, and host tree foliar and stem biomass between 4 and 8 years of growth relative to the 4-year-old plot value. Note that graphs have different scales.

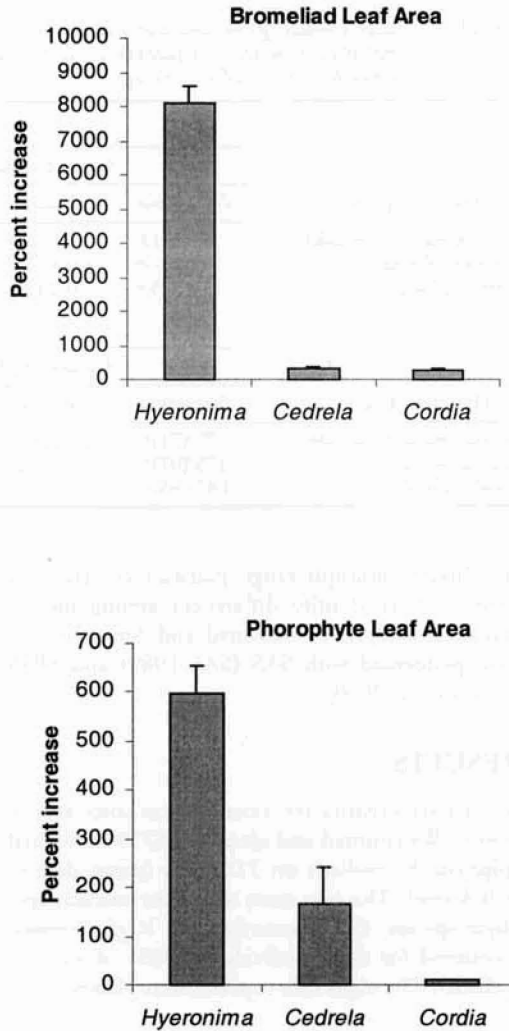


FIGURE 4. The mean difference in bromeliad and host tree leaf area between 4 and 8 years of growth relative to the 4-year-old plot value. Note that graphs have different scales.

< 0.0001; “other bromeliads,” $R^2 = 0.960$, $P < 0.0001$; Fig. 2).

HOST TREE EFFECTS ON BROMELIAD BIOMASS AND LEAF AREA.—There was a pronounced host tree species effect on total bromeliad biomass and leaf area in both the young ($P = 0.034$) and old plots ($P = 0.006$). The order of “host tree preference” differed between the young and the old stands, a phenomenon that has not been previously documented. In the young plots, bromeliads on *Cordia* trees ($P = 0.0001$) had significantly greater biomass and leaf area than did the bromeliads in the *Cedrela* and *Hye-*

TABLE 5. Average dry weight (t/ha) of epiphytes in tropical forest habitats (modified from Hofstede et al. 1993; Coxson & Nadkarni 1995). NR = not reported.

Location	Forest Type	Elevation (m)	Biomass	Source
Colombia	Upper Montane	3700	44	Hofstede et al. 1993
Colombia	Upper Montane	3370	12	Veneklaas 1990
New Guinea	Upper Montane	2500	5.2	Edwards & Grubb 1977
Tanzania	Upper Montane	2120	13.7	Pócs 1980
Costa Rica	Upper Montane	1700	4.7	Nadkarni 1984
Costa Rica	Lower Montane	1550	33.0	Nadkarni et al. 2000
Tanzania	Lower Montane	1415	2.1	Pócs 190
Puerto Rico	Lower Montane	725	0.5	Weaver & Murphy 1990
Panama	Premontane	400–600	1.4	Golley et al. 1971
Panama	Lowland	250–600	1.6	Golley et al. 1971
Panama	Riverine	150	0.08	Golley et al. 1971
Costa Rica	Lowland 8-year-old <i>Hyeronima</i> Plantation	30	0.08	A. Reich, pers. comm.
Brazil	Moist Forest	NR	0.5	Klinge et al. 1975
Costa Rica	Lowland 8-year-old <i>Cordia</i> Plantation	30	0.04	A. Reich, pers. comm.
Costa Rica	Lowland 8-year-old <i>Cedrela</i> Plantation	30	0.02	A. Reich, pers. comm.

ronima plots (Table 2). Within the young *Cedrela* and *Hyeronima* plots, biomass and leaf area were not significantly different ($P = 0.671$). In the old plots, the mean biomass and leaf area were greatest on *Hyeronima*, followed by *Cordia* and then *Cedrela*. The bromeliads in the *Hyeronima* plots had a sig-

nificantly greater biomass and leaf area than the bromeliads in the *Cordia* plots ($P = 0.0001$), which had significantly greater biomass and leaf area than *Cedrela* plots ($P = 0.0001$; Table 2).

There were significant differences ($P > 0.01$) in size and distribution between *G. monostachya*

TABLE 6. Epiphyte abundance (% trees with epiphytes) in tropical forest habitats (modified from Grubb et al. 1963). NR = not reported.

Location	Forest Type	Elevation (m)	% Trees with epiphytes	No. Trees Studied	Minimum Tree Height (m)	Source
Costa Rica	Lowland (8-yr-old <i>Hyeronima</i>)	30	100	40	7	This study
Costa Rica	Lowland 8-yr-old <i>Cedrela</i>)	30	95–98	40	7	This study
Costa Rica	Lowland (4-yr-old <i>Cordia</i>)	30	60–90	40	7	This study
Costa Rica	Lowland (8-yr-old <i>Cordia</i>)	30	55–83	40	7	This study
Costa Rica	Lowland (4-yr-old <i>Hyeronima</i>)	30	40–70	40	7	This study
Costa Rica	Lowland (4-yr-old <i>Cedrela</i>)	30	5–65	40	7	This study
Ecuador	Montane	1710	96	52	6.5	Grubb et al. 1963
Ecuador	Lowland	380	60	42	6.5	Grubb et al. 1963
British Guyana	Lowland	NR	38	55	14	Davis & Richards 1933–1934
Nigeria	Lowland	NR	24	75	5	Richards 1939
British Guyana	Lowland	NR	16	193	5	Davis & Richards 1933–1934
Nigeria	Lowland	NR	15	67	5	Richards 1939
Sarawak	Lowland	NR	13	91	8	Richards 1936
Sarawak	Lowland	NR	11	44	8	Richards 1936

and *V. gladioliflora* on host trees of the same species (Table 3). On *Cordia* and *Cedrela* plots of both ages, *G. monostachya* was the most abundant species, with a significantly higher biomass and leaf area. *Vriesea gladioliflora* was the dominant species on old *Hyeronima* plots; but in the young plots, there were no significant differences between any bromeliad species.

AGE EFFECTS ON TREE AND EPIPHYTE BIOMASS AND LEAF AREA.—Wood accounted for over 90 percent of the total aboveground tree biomass in all plots. The total tree biomass (“wood” plus “foliage”) and leaf area in the young plots were greatest in *Cordia*, followed by *Hyeronima* and *Cedrela*. The mean total tree biomass, foliar biomass, and leaf area per plot increased with age, but the relative magnitude of these parameters shifted between species. In the old plots, mean total tree biomass was greatest in the *Hyeronima* plots, followed by the *Cedrela* and *Cordia* plots (Table 4). The changes in host tree foliage biomass represented increases of 0.5- to 7-fold (Fig. 3). For leaf area, the changes between four- and eight-year plots represented increases of 0.1- to 6-fold (Fig. 4).

Between four and eight years of tree growth, the mean bromeliad biomass and leaf area per plot increased dramatically with age of the stand. Changes in mean bromeliad biomass per plot between four and eight years of growth represented increases of 5- to 46-fold and changes in mean bromeliad leaf area represented increases of 2- to 40-fold (Figs. 3 and 4). In the young plots, *Cordia* trees supported the greatest biomass and leaf area of bromeliads. In the old plots, however, *Hyeronima* supported the greatest biomass and leaf area of bromeliads.

There were positive correlations between woody biomass and bromeliad biomass in young plots ($R^2 = 0.4135$, $P = 0.0618$) and old plots ($R^2 = 0.7408$, $P = 0.0029$). In the young plots, the *Cordia* trees had the greatest woody biomass and supported the greatest biomass of epiphytes. In the old plots, however, the *Hyeronima* trees had the greatest woody biomass and supported the greatest bromeliad biomass. The *Hyeronima* trees exhibited tremendous growth relative to the other two host tree species; their foliar biomass increased 7-fold, compared to biomass increases of 0.5- and 2-fold in the *Cordia* and *Cedrela* trees, respectively.

DISCUSSION

Epiphytes play important ecological roles in primary tropical forests. They acquire nutrients di-

rectly from atmospheric sources (wet and dry deposition, N-fixation), and indirectly from soil-rooted sources (litterfall interception, leachate, bark decomposition, suspended humus/carton; Benzing 1990). Epiphytes have physiological and morphological attributes that buffer atmospheric inputs (Benzing 1995, Clark *et al.* 1998). These enhance nutrient and water capture and retention at the ecosystem level (Pócs 1980, 1982; Nadkarni 1981; Coxson & Nadkarni 1995). They can contribute a substantial proportion of the total foliar biomass, which can exceed that of their host trees by as much as four times (Coxson & Nadkarni 1995). Epiphytes also provide animals with substantial resources for food and shelter (Nadkarni & Matelson 1989).

COMPARISONS WITH OTHER SITES.—The few studies of epiphytes in secondary forests have mainly concerned composition (Madison 1979, Yeaton & Gladstone 1982). This is the first report of epiphyte leaf area for a tropical secondary forest; thus, we cannot compare our estimates of community-level epiphyte leaf area to other studies. Weaver and Murphy (1990), however, reported the LAI of the entire epiphyte community of a montane forest in Puerto Rico as 0.30 m²/m².

The epiphyte biomass values reported in this study are considerably lower than those reported for total epiphyte load from primary forests (Table 5). Epiphyte abundance (measured here as biomass) varies tremendously along environmental gradients in the tropics. In comparison to tropical montane forests, lowland forests generally support a small epiphyte biomass (Coxson & Nadkarni 1995). The age of the host tree substrate appears to affect the number of epiphytes occupying the host tree. Our study was conducted in a very young stand composed of relatively short trees; thus, it is not surprising that the biomass values are lower than primary forests. Epiphytes are more heterogeneously dispersed throughout our plots than has been documented in other studies. The percentage of the total number of surveyed trees that support epiphytes in this study was within the range of other sites (including montane forests where epiphytes reach their greatest diversity and abundance; Table 6).

We documented a tremendous increase in epiphyte biomass between four and eight years of growth; thus, epiphytic biomass in our plots may reach levels similar to other lowland primary forest sites over time. The only published estimate of epiphyte biomass in a tropical lowland forest in Pan-

ama documented 1.6 t/ha of epiphytes (Golley *et al.* 1971); however, the steep increases in epiphytic bromeliad biomass may not continue at the same rate we documented between four and eight years of growth. It is possible we "captured" the crucial seedling growth-vegetative growth phase of the epiphytic plant population following initial seedling establishment, and therefore, rates of increase are likely to decline when the population becomes saturated. Further work at intermediate and later stages of succession in these plantations is needed to ascertain the amount of time it takes to achieve an equilibrium in epiphyte biomass.

HOST TREE EFFECTS ON BROMELIAD BIOMASS AND LEAF AREA.—In contrast to most terrestrial plants, which are rooted on static growth media, mechanically dependent epiphytes live on the relatively ephemeral and generally expanding substrates of growing trees. Trees present a dynamic medium because their surface area is in constant flux due to stem growth, bark shedding, and frequent branchfall. At the community level, especially in late-successional forests, host tree surface area availability may ultimately determine the total epiphyte biomass a stand can support. Changes in host stem surface area during forest development may directly influence bromeliad biomass and leaf area. Light availability may also be important, as tank bromeliads require a combination of high light intensity with high humidity. The possibility that these bromeliads may become shaded out as the canopy closes should be considered.

The *Hyeronima* monocultures exhibited a relatively large increase in woody biomass compared to the *Cedrela* and *Cordia* plots between four and eight years of growth. These increases were positively correlated with epiphyte abundance; however, the dramatic increase in epiphyte biomass and leaf area that we documented cannot be explained by increased growing area alone. Indirect effects of changes in the light regime due to structural changes in tree canopies may also influence bromeliad distribution because heliophilic bromeliads react strongly to changes in light (Benzing 1990). As the canopy develops, changes in leaf morphology and total leaf surface area of the host tree may affect the distribution of epiphytes. For example, after four years of growth, reproductively mature *Cordia* trees are fully deciduous in the wet season (July) and partially deciduous in the dry season at La Selva (February–April). Similarly, leaves of *Hyeronima* change morphologically. They range from very large, broad leaves averaging 280 cm² at four years

of age to smaller leaves averaging 60 cm² when fully mature (Hiremath 2000), which create a different light and moisture regime that could potentially affect the distribution of epiphytes. The absence of leaves on the *Cordia* trees undoubtedly creates a drier, higher light microclimate, which could affect the establishment and growth of epiphytes. Although the *Cordia* plots had the highest bromeliad density in the young stands, the light intensity may become too high after eight years. Conversely, the large leaves of the young *Hyeronima* trees create a darker understory than the older plots. As the trees mature, the leaves become smaller, which allows more light to penetrate the canopy. Note that all of the trees supported bromeliads.

This hypothesis is supported by the interspecific changes in bromeliad distribution in the young and old plots. In the young plots of *Hyeronima*, *G. monostachya* had the highest relative abundance, but within the old *Hyeronima* plots, *V. gladiifolia* dominated the bromeliad community. Such a dramatic change in the relative abundance of *V. gladiifolia* in the old *Hyeronima* plots over only four years suggests that changes in microenvironment created by changes in leaf morphology could substantially influence the distribution and abundance of different species of epiphytic bromeliads. Future studies are needed to determine how factors of tree morphology, phenology, and tree demography (following Zotz 1998 and Castro Hernández *et al.* in press) influence epiphyte establishment and growth.

ECOLOGICAL IMPORTANCE OF EPIPHYTES.—Estimating epiphyte biomass is one approach to assessing the magnitude to which the epiphyte community affects ecosystem-level processes. Epiphytic bromeliads did not contribute a substantial proportion of the total stand biomass and leaf area in the experimental plots (<0.1–1.6%); however, the dramatic increase in epiphyte biomass and leaf area between four and eight years of growth suggests that in four years, epiphytes rapidly increase in abundance following initial colonization and therefore may play increasingly greater roles in ecosystem function as plantations develop. Further research is needed to assess epiphyte biomass and leaf area and their functional relevance at later successional stages.

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LITERATURE CITED

- ACKERMAN, J. D., A. M. MONTALVO, AND A. M. VERA. 1989. Epiphyte host specificity of *Encyclia krugii*, a Puerto Rican endemic orchid. *Lindleyana* 4: 74-77.
- ARSENEAU, M.-J., L. SIROIS, AND J.-P. OUELLET. 1997. Effects of altitude and tree height on the distribution and biomass of fruticose arboreal lichens in an old growth balsam fir forest. *Ecoscience* 4: 206-213.
- BAARS, R., D. KELLY, AND A. D. SPARROW. 1998. Liana distribution within native forest remnants in two regions of the South Island, New Zealand. *N.Z. J. Ecol.* 22: 71-85.
- BENZING, D. H. 1990. Vascular epiphytes. Cambridge University Press, Cambridge, England.
- . 1995. Vascular epiphytes. In M. D. Lowman and N. M. Nadkarni (Eds.). *Forest canopies*, pp. 225-254. Academic Press, San Diego, California.
- BROWN, S., AND A. E. LUGO. 1990. Tropical secondary forests. *J. Trop. Ecol.* 6: 1-32.
- CASTRO HERNÁNDEZ, J. C., J. H. D. WOLF, J. G. GARCÍA-FRANCO, AND M. GONZÁLEZ-ESPINOSA. The influence of humidity, nutrients and light on the establishment of the epiphytic bromeliad *Tillandsia guatemalensis* in the highlands of Chiapas, Mexico. *Rev. Biol. Trop.* 47. In press.
- CATLING, P. M., V. R. BROWNWELL, AND L. P. LEFKOVICH. 1986. Epiphytic orchids in a Belizean grapefruit orchard: distribution, colonization, and association. *Lindleyana* 1: 194-202.
- CLARK, D. A. 1994. Plant demography. In L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn (Eds.). *La Selva: Ecology and natural history of a Neotropical rain forest*, pp. 90-105. University of Chicago Press, Chicago, Illinois.
- CLARK, K. L., N. M. NADKARNI, AND H. L. GHOLZ. 1998. Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. *Biotropica* 30: 12-23.
- CORNELISSEN, J. H. C., AND H. L. TER STEEGE. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. *J. Trop. Ecol.* 5: 131-150.
- COXSON, D. S., AND N. M. NADKARNI. 1995. Ecological roles of epiphytes in nutrient cycles of forest ecosystems. In M. D. Lowman and N. M. Nadkarni (Eds.). *Forest canopies*, pp. 495-543. Academic Press, San Diego, California.
- DAVIS, T. A. W., AND P. W. RICHARDS. 1933-1934. The vegetation of Moraballi Creek, British Guiana: An ecological study of a limited area of tropical rain forest. Parts I and II. *J. Ecol.* 21: 106-155; 22:350-384.
- EDWARDS, P., AND P. J. GRUBB. 1977. Studies of mineral cycling in a montane rain forest in New Guinea. *J. Ecol.* 65: 943-969.
- FREI, S. J. K., AND C. H. DODSON. 1972. The chemical effect of certain bark substrates on the germination and early growth of epiphytic orchids. *Bull. Torrey Bot. Club* 99: 301-307.
- GOLLEY, F., K. MCGINNIS, Y R. CLEMENTS. 1971. La biomasa y la estructura de algunos bosques de Darien, Panama. *Turrialba* 21: 189-196.
- GREEN, S. B., N. J. SALKIND, AND T. M. AKEY. 2000. *Using SPSS for Windows*. Prentice Hall, Upper Saddle River, New Jersey.
- GRUBB, P. J., J. R. LLOYD, T. D. PENNINGTON, AND T. C. WHITMORE. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The floristic structure, physiognomy, and floristics. *J. Ecol.* 51: 567-601.
- HAGGAR, J. P., AND J. J. EWEL. 1994. Experiments on the ecological basis of sustainability: early findings on nitrogen, phosphorous, and root systems. *Interciencia* 19: 347-351.
- HARTSHORN, G. 1983. Plants: Introduction. In D. H. Janzen (Ed.). *Costa Rican natural history*, pp. 118-183. University of Chicago Press, Chicago, Illinois.
- HIETZ, P., AND U. HIETZ-SEIFERT. 1995. Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. *J. Veg. Sci.* 6: 487-498.
- HIREMATH, A. J. 2000. Nutrient use efficiency in simplified tropical ecosystems. Ph.D. dissertation, University of Florida, Gainesville, Florida.
- HOEFSTEDE, R. G. M., J. D. H. WOLF, AND D. H. BENZING. 1993. Epiphytic biomass and nutrient status of a Colombian upper montane rain forest. *Selbyana* 14: 37-45.
- KLINGE, H., W. A. RODRIGUEZ, E. BURNING, AND G. FITTKAU. 1975. Biomass and structure in a Central American rainforest. In F. B. Golley and E. Medina (Eds.). *Tropical ecological systems*, pp. 115-122. Springer-Verlag, New York, New York.
- MADISON, M. 1979. Distribution of epiphytes in a rubber plantation in Sarawak. *Selbyana* 5: 207-213.
- MCDADE, L. A., K. S. BAWA, H. A. HESPENHEIDE, AND G. S. HARTSHORN (Eds.). 1994. *La Selva: Ecology and natural history of a Neotropical rain forest*. University of Chicago Press, Chicago, Illinois.
- MURPHY, P. G., AND A. E. LUGO. 1986. Structure and nutrient capital of a subtropical dry forest in Puerto Rico. *Biotropica* 18: 89-96.

- NADKARNI, N. M. 1981. Canopy roots: convergent evolution in rainforest nutrient cycles. *Science* 213: 1024–1025.
- . 1984. Epiphyte biomass and nutrient capital of a Neotropical elfin forest. *Biotropica* 16: 249–256.
- , R. O. LAWTON, K. L. CLARK, T. J. MATELSON, AND D. A. SCHAEFER. 2000. Ecosystem ecology and forest dynamics. In N. M. Nadkarni and N. T. Wheelwright (Eds.), *Monteverde: ecology and conservation of a tropical cloud forest*, pp. 303–350. Oxford University Press, New York, New York.
- , AND T. J. MATELSON. 1989. Bird use of epiphyte resources in Neotropical trees. *Condor* 91: 891–907.
- PÓCS, T. 1980. The epiphytic biomass and its effect on the water balance of two rainforest types in the Uluguru Mountains (Tanzania, East Africa). *Acta Bot. Hung.* 26: 143–167.
- . 1982. Tropical forest bryophytes. In A. J. E. Smith (Ed.), *Bryophyte ecology*, pp. 59–104. Chapman and Hall, London, England.
- RICHARDS, P. W. 1936. Ecological observations on the rain forest of Mount Dulit, Sarawak. I, II. *J. Ecol.* 24: 1–37, 340–360.
- . 1939. Ecological studies on the rain forest of southern Nigeria. I. The structure and floristic composition of the primary forest. *J. Ecol.* 27: 1–61.
- SAS INSTITUTE. 1989. SAS user's guide. Version 6, 4th edition. SAS Institute, Cary, North Carolina.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry: the principles and practice of statistics in biological research*. 2nd Edition. W. H. Freeman, New York, New York.
- TANNER, E. V. 1980. Studies on the biomass and productivity in a series of montane rain forests in Jamaica. *J. Ecol.* 68: 573–588.
- VENEKLAAS, E. J. 1990. Nutrient fluxes in bulk precipitation and throughfall in two montane tropical forests, Colombia. *J. Ecol.* 78: 974–992.
- WEAVER, P. L., AND P. G. MURPHY. 1990. Forest structure and productivity in Puerto Rico's Luquillo Mountains. *Biotropica* 22: 69–82.
- YEATON, R. L., AND D. E. GLADSTONE. 1982. The pattern of colonization of epiphytes on calabash trees (*Crescentia alata* HBK) in Guanacaste Province, Costa Rica. *Biotropica* 14: 137–140.
- ZOTZ, G. 1998. Demography of the epiphytic orchid, *Dimerandra emarginata*. *J. Trop. Ecol.* 14: 725–741.