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Vertical Distribution of Bromeliads in a Montane Forest in the Eastern Cordillera of the Colombian Andes

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Abstract. During a study of the vertical distribution of bromeliads and their biomass in a montane forest near Bogotá, Colombia, the authors found, at a 0.1 ha site, 4395 bromeliads with a biomass of 0.9 tons. Species making up the community were *Guzmania gloriosa, Racinaea tetrantha, Tillandsia biflora, T. complanata, T. fendleri,* and *T. turneri.* Differences in the morphometric variables used to determine age classes (i.e., dry weight, coverage, height, leaf length, and tank basal perimeter) were significant in all species except for number of leaves. Of the total, 62.3% of the bromeliad individuals belonged to immature age class 1, followed by adults (classes 3 and 4) with 24.3%. Adult biomass accounted for 74.6% of the total. The bromeliad community, populations, and age classes had an aggregated vertical distribution pattern in terms of biomass and number of individuals, mainly in the middle and high strata of the forest. *Tillandsia turneri* had the highest accumulated biomass (47%) and was the most abundant species (62.3%). Mean biomass per individual was highest in *T. fendleri* (87.4 g). Bromeliad individuals show a tendency to be near the main phorophyte axis. A strong correlation was found between abundance and biomass of bromeliads and the phorophyte height, crown coverage, and circumference breast height.

Key words: Andes, Bromeliaceae, Colombia, epiphytes, vertical distribution

Resumen. Estudiamos el patrón de distribución vertical de los individuos y de la biomasa de la comunidad de bromelias en un bosque alto andino de la Sabana de Bogotá, Colombia. En 0.1 ha muestreada se encontraron 4395 individuos de bromelias, con una biomasa de ca. 0.9 toneladas, pertenecientes a los géneros *Guzmania* (*G. gloriosa*), *Racinaea* (*R. tetrantha*) y *Tillandsia* (*T. biflora, T. complanata, T. fendleri* y *T. turneri*). Las diferencias en las variables morfométricas evaluadas (peso seco, cobertura, altura, largo de la lámina y perímetro de la base) para determinar las clases de edad fueron significativas en todas las especies, excepto el número de hojas. El 62.3 % de los individuos de la comunidad pertenecen a la clase de edad 1, seguidos por los adultos (clases 3 y 4) con el 24.3 %. El 74.6 % de la biomasa de la comunidad la acumularon los individuos adultos. La comunidad, las poblaciones y las clases de edad estimadas presentaron un patrón de distribución vertical agregado, tanto para la biomasa como para la abundancia, y con preferencia por las partes medias a altas del bosque. *Tillandsia turneri* fue la especie más abundante (con el 62.3 % de los individuos totales) y con mayor biomasa acumulada (47 % del total). El mayor promedio de biomasa por individuo lo presentó *T. fendleri* con 87.4 g. Los individuos tendieron a ubicarse cerca al eje principal del forofito y, además, se encontró una fuerte correlación entre la abundancia y la biomasa de las bromelias con la altura, la cobertura y la circunferencia a la altura del pecho de los forofitos.

Palabras clave: Andes, Bromeliaceae, Colombia, epífitas, distribución vertical

Introduction

About 10% of vascular plant species are epiphytes and in some tropical montane forests, they represent more than 50% of the species of the local flora and accumulated biomass (Kelly 1985, Kress 1986, Nadkarni 1984). In lowland forests, however, epiphytes are less abundant and also less α-diverse (Bøgh 1992, Churchill et al. 1995). This pattern has been related to the constant presence of mist and the broad variety of microclimates found in montane forests (Betancur & Jaramillo 1998, Gentry & Dodson 1987, Sugden & Robins 1979). The original area

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occupied by montane forests in Colombia has diminished dramatically because of the high rates of deforestation generated by demographic pressure (70% of the population of Colombia lives in the Andes) and the expansion of agriculture and livestock farming (Hernández-Camacho et al. 1992, IGAC 1992).

Bromeliaceae is one of the most diverse and largest families among vascular epiphytes containing about 2500 species (Benzing 1990, Gentry & Dodson 1987, Kress 1986). Its distribution is mostly neotropical. The diversity and high density of bromeliads makes them a distinctive floristic component of neotropical montane forests. Bromeliads also play an important ecological role by capturing and redistributing water and nutrients, as well as contributing to the total biomass enclosed in these forests. Bromeliads provide a habitat for a large number of fresh water organisms associated with the water impounded between their leaves (Nadkarni 1984, Lugo & Scatena 1992). Tank-type bromeliads keep reserves of water during the whole year, holding complex trophic chains involving different organisms such as bacteria, fungi, protozoa, bryophytes, invertebrates, some vertebrates, and vascular plants (Laessle 1961, Reitz 1983). From this biotic association, bromeliads benefit by capturing nutrients from vegetal and animal material shed in the tank; meanwhile, organisms that use the tanks for shelter and a source of food also benefit (Laessle 1961, Benzing 1990).

The distribution of epiphytes varies along the vertical axis of the host tree (phorophyte), from the forest floor to the canopy (Ter Steege & Cornelissen 1989). This vertical distribution pattern is presumably the consequence of microhabitat diversity. Considering that protected forests contain more environmental gradients and microhabitats than disturbed ones, we might expect higher abundance and epiphyte diversity in protected areas compared to those where human intervention has occurred (Bennet 1986, Catling & Lefkovitch 1989, Wolf 1995).

Further research on the distribution of vascular epiphytes may provide a better understanding of tropical forest dynamics and processes. Some studies have addressed the distribution of bromeliads in lowland forests (Bennet 1986, Catling & Lefkovitch 1989, Cleef et al. 1984, de la Sota 1972, Nieder et al. 2000, Pittendrigh 1948, Sugden & Robins 1979, Ter Steege & Cornelissen 1989). Only a few, however, have been carried out in montane forests where the abundance and diversity of epiphytes reaches its maximum (Gilmartin 1973, Serna-Isaza 1994, VanDunné 2001, Wilde 1988). In the following results of our study of the vertical distribution of bromeliads in a montane forest in the Eastern Cordillera of the Colombian Andes, emphasis is placed on the distribution of individuals and biomass.

Study Site

The study site was located in a high Andean forest fragment of ca. 20 ha, known as "El Santuario" (5°01′N and 73°42′W), at 2900 m, in the municipality of Chocontá, on the Sabana de Bogotá, department of Cundinamarca, Colombia. Mean annual temperature is 11.9°C and annual rainfall is 924.7 mm/yr. The rainy season occurs between May and August and the dry season between September and April (Estévez-Varón & Viña 1999). According to the Holdridge life zone classification system, the area corresponds to a montane humid forest (bh-M) (Holdridge 1967, IGAC 1977).

The forest canopy has an average height of 15 m, with some emergent trees to 25 m. The average canopy aperture is 5.67%. Dominant tree species at the study site are *Drimys granadensis, Myrsine* cf. *ferruginea,* and *Weinmannia tomentosa* (Estévez-Varón & Viña 1999).

Methods

Data Collection

Fieldwork was carried out from August to December 2001. Ten transects of 50 × 2 m were chosen randomly within the forest amounting to a 0.1 ha sampling area, avoiding overlap with edge effects. In each transect, all phorophytes with bromeliads were recorded. In each case, the height, circumference at breast height (CBH), and crown cover was measured. Single rope techniques were used to access the canopy (Perry 1978).

Morphometry and Age Classes

During the initial stage of the study, each bromeliad species present in the forest and its developmental stages were visually identified. The visual estimation of age classes for each species was based on its size and developmental stage. Age classes were assigned from 1 (smaller) to 4 (larger). Measurements were performed to characterize age classes and to determine if visual estimation had clear ranges. Collecting 14–20 individuals for each age class per species, we measured the following: 1) the tank basal perimeter (measured from the point where the sheath ends and the lamina leaves begin), 2) the coverage (estimated as the product of the superior perpendicular diameters), 3) height, 4) number of leaves, 5) mean leaf length of five peripheral leaves, and 6) biomass, defined as the dry weight of living matter (Nadkarni 1984). The category "undetermined" was used for juveniles that could not be assigned to a particular species.

Vertical Stratification

Samples were taken of all bromeliads hosted by trees with trunk inside transects, from the forest floor to the canopy. Bromeliads with exclusive epiphytic habits found fallen to the forest floor were not recorded. For each individual, we registered: 1) the transect and phorophyte number, 2) species, 3) age class, 4) height from ground, and 5) distance from the epiphyte to the main axis of the phorophyte. Height of facultative or terrestrial bromeliads found on the ground was considered as 0 m.

Data Analysis

Data on vertical distribution and bromeliad distance to the main axis of the phorophyte were put into 1 m ranges for statistical treatment and assembly of figures. Statistical tests were carried out using Statistix and Padis software for Windows V 1.01 (Lopez-Collado & Osada-Velásquez 1997). The Kruskal-Wallis test (Zar 1999) was performed to establish which of the morphometric variables were determinant in characterizing the different age classes, visually estimated, in each species. The dispersion coefficient and Morisita index were used to determine vertical distribution patterns for individuals in terms of biomass (Morisita 1962, Pielou 1977). These indices were calculated at community, population, and age-class levels. Multiple regression (Zar 1999) was carried out to establish the relationship between host structural variables (height, crown coverage, and CBH) and the number of associated epiphytes and biomass.

For community abundance and biomass analysis (per age class and total) in species with two age classes, age 1 was considered a juvenile plant, and age 2 was an adult. In species with three and four age classes, ages 1 and 2 were considered juveniles, and 3 and 4 were adults. For these analyses, individuals classified as "undetermined" were included within age class 1 because of their incipient development.

RESULTS

Morphometry and Age

Six bromeliad species were recorded in the study plots: *Guzmania gloriosa* (André) André ex Mez, *Racinaea tetrantha* (Ruíz & Pav.) M.A. Spencer & L.B. Sm., *Tillandsia biflora* Ruíz & Pav., *T. complanata* Benth., *T. fendleri* Griseb., and *T. turneri* Baker. Observed in the forest but not present in the study plots were *G. squarrosa* (Mez & Sodiro) L.B. Sm. & Pittendr., *R. subalata* (André) M.A. Spencer & L.B. Sm., and *T. compacta* Griseb.

Age classes differed among species because of their size and developmental characteristics. We determined two age classes for the smallest recorded bromeliad species in the forest, *Tillandsia biflora*, three for *Guzmania gloriosa, Racinaea tetrantha,* and *T. turneri,* and four for *T. complanata* and *T. fendleri,* which were larger species. TABLE 1 summarizes the morphometric measurements obtained for each age class and species. For each species, significant differences occurred between age class and morphometric variables (Kruskal-Wallis test, $P < 0.05$, see APPENDIX 1), except for leaf number in *T. turneri, R. tetrantha,* and the "undetermined" category. Basal perimeter, leaf length, and height had the greatest variation ($P = 0.000$).

Abundance and Vertical Distribution

A total of 4395 individuals were recorded in the 0.1 ha study site. Of these plants, 75.8% belonged to juveniles followed by adults with 24.3% (TABLE 2). The highest numbers of individuals in total and per age class were found between 4 m and 11 m in height, decreasing progressively above 11 m (FIGURE 1).

The "undetermined" category presented the highest abundance (2181 individuals), comprising almost half of the individuals in the community (TABLE 3). Apart from the "undetermined" category, *Tillandsia turneri* was the most common species (62.3%), followed by *T. fendleri* (17.8%). *Guzmania gloriosa* and *T. biflora* had the lowest number of individuals with less than 1% of the total sample (TABLE 3). *Racinaea tetrantha, T. fendleri,* and *T. turneri* had a similar vertical distribution pattern within the community, with most of the individuals concentrated between 4 m and 11 m in height (FIGURES 2–4). On the contrary, the species *G. gloriosa* and *T. complanata* (FIGURE 5) were more abundant below 6 m. The distribution pattern of *T. biflora* was erratic and unpredictable.

The community, total species, and species per age class showed an aggregate distribution pattern along the vertical gradient. In general, adult Morisita index values were higher than were juvenile ones (APPENDIX 2).

Tillandsia turneri had twice as many adults (class 3) as juveniles (classes 1 and 2). Adults of *T. fendleri* (classes 3 and 4) were less numerous than juveniles. With regard to *Racinaea tetratha,* fewer differences were found between the number of adult and juvenile individuals. The other species (*Guzmania gloriosa, T. biflora,* and *T. complanata*) did not present differences between age classes by numbers of individuals (TABLE 3).

The species vertical distribution among age classes did show differences. The different age classes of *Tillandsia turneri* showed a similar distribution pattern (FIGURE 4). Adults of *T. fendleri* showed a preference for the upper forest stratum (ca. 11–16 m) while younger individuals preferred the middle stratum (ca. 5–12 m) (FIGURE 3). Age classes 1 and 2 of *Racinaea tetrantha* were concentrated in the middle strata (ca. 5–10 m), but no particular trend was observed for adults (FIGURE 2). Age classes of *Guzmania gloriosa* and *T. complanata* tend to be in the lower strata (ca. 0–1 and 0–6 m, respectively). *Tillandsia biflora* did not show marked preferences as regards the vertical distribution.

Biomass and Vertical Distribution

Estimated biomass for the bromeliad community was 91.06 kg/0.1 ha. The highest biomass (74.6% of the total) was estimated for adults of classes 3 and 4 (TABLE 2). The greatest biomass values were recorded in the upper and middle forest strata (ca. 5–12 m) (FIGURE 1).

Although the "undetermined" species category had the highest number of individuals, it had the lowest biomass value (TABLE 4). *Tillandsia turneri* and *T. fendleri* presented the highest biomass (47% and 39% of the total, respectively), followed by *Racinaea tetrantha* (10%). The other species contributed less than 3.4% each. The average individual dry weight of *T. fendleri* was 87.3 g, the highest among all species, followed by *G. gloriosa* with 51.9 g. *Tillandsia biflora* had the lowest value with 5.6 g (TABLE 4).

Vertical distribution of the biomass with respect to the community, total species, and age classes was clumped (APPENDIX 3). Spatial distribution pattern indices for adults were higher than for juveniles. The total biomass of all species was concentrated in the same height ranges as for the adult biomass (class 2 in *Tillandsia biflora,* other species: classes 3 and 4) (FIGURES 2–5). In contrast, biomass distribution for individual species differed with regard to the community. For example, the distribution of biomass of juveniles of *T. fendleri* was similar to that of the community, concentrated between 4 m and 12 m in height, while adult biomass was clumped from 9 m to 15 m (FIGURE 3). The biomass of different age classes in *Racinaea tetrantha* was not concentrated in any particular stratum (FIGURE 2); and the biomass of *T. complanata* was slightly greater at locations below 1 m (FIGURE 5).

Phorophyte Structure and Bromeliad Density and Biomass

The total number of recorded phorophytes (321) averaged 13.68 bromeliads each. Phorophyte average height was 8.53 m, the mean crown cover was 9.32 m^2, and the average CBH was 33.45 cm.

Bromeliad individuals, biomass of the community, and age classes were conspicuously grouped near the phorophyte main axis. Most of the individuals sampled (in total and per age class) were grouped within a horizontal range of 0–0.5 m from the main axis (FIGURE 6).

Structural variables of the phorophytes were proportional to abundance and biomass of bromeliads (multiple regression analysis r^2 = 0.3751, P = 0.0000 and r^2 = 0.3303, P = 0.0000, respectively). For example, the phorophyte with the greatest height, CBH, and crown cover was host to 426 bromeliads (9.7% of the total), equaling 14.4 kg in dry weight (15.8% of the total community biomass).

DISCUSSION

Morphometry and Age

The morphometric variables of bromeliads recorded in this study, particularly leaf length, height, and tank basal perimeter, were found to be a useful tool for estimating age class in future studies, as these variables differed significantly. Such differences reflect plant growth and elongation as found in bromeliad variables measured in other neotropical forests (Dunn 2000, Van-Dunné 2001).

Abundance and Vertical Distribution

Bromeliad density at the study site is high (4.4 bromeliads/m^2) when compared to other tropical forests. For example, in the Central Cordillera of Colombian Andes (3150 m), Van-Dunné (2001) found 0.41 bromeliads/m^2, while Dunn (2000) recorded 3.5 bromeliads/m^2 in an Ecuadorian forest (1800 m).

The high abundance of *Tillandsia turneri,* particularly in the upper and middle strata, may be the result of morphological adaptations, such as high trichome density, crassulacean acid metabolism (CAM), and the basal rosette (Serna 1994). Such adaptations enable this species to survive conditions of high hydrical stress and extreme fluctuations of daily temperatures that occur in these strata of the forest (Benzing

TABLE 1. Morphometric measurements for bromeliad species by age class, including the "undetermined" category; n = number of individuals; $\bar{x}$ = mean or average value; σ = standard deviation.

Species	Age class	(n)	Dry weight (g)		Cover (cm^2)		Height (cm)	
			$\bar{x}$	σ	$\bar{x}$	σ	$\bar{x}$	σ
Tillandsia turneri	1	15	7.88	0.72	776.58	100	25.57	1.16
	2	15	18.76	1.712	1231.66	157.95	33.8	1.41
	3	16	44.41	3.236	2042.26	167.11	43.32	1.69
Tillandsia fendleri	1	19	14.86	1.45	916.97	97	28.45	1.35
	2	15	54.96	8.10	2241.23	307.32	42.4	2.24
	3	15	159.19	14.23	4576.46	240.42	60.23	1.76
	4	15	277.43	33.01	6452.67	451.8	73.68	2.61
Racinaeae tetrantha	1	16	5.31	0.86	470.45	59	19.34	0.77
	2	17	19.44	2.57	1020.69	132.89	29.41	1.55
	3	16	47.44	8.04	1757.13	243.67	42.5	2.76
Tillandsia complanata	1	15	4.99	0.58	642.07	42	19.97	0.86
	2	16	13.48	1.02	1442.29	127.56	29.97	1.13
	3	15	39.12	4.78	2315.9	166.45	40.25	1.71
	4	16	71.45	5.48	3501.77	178.09	44.34	1.19
Tillandsia bilfora	1	15	2.92	0.58	51.17	55	16.36	0.89
	2	17	7.85	1.06	820.14	80	21.76	1.46
Guzmania gloriosa	1	15	5.82	0.84	988.37	83	28.73	2.28
	2	15	20.89	4.44	2708.6	263.23	48.27	3.57
	3	14	76.29	10.44	5112.57	415.91	65.71	2.42
"Undetermined"	1	17	0.34	0.04	135.38	16	10.76	0.39
	2	19	1.16	0.11	288.5	36	16.13	0.81
	3	20	2.29	0.21	471	50.18	19.24	0.94

1976). In addition, the high number of *T. turneri* adults in relation to the other bromeliad species increases the proportion of potential propagules, and therefore, potential colonists (Yeaton & Gladstone 1982). Such abundance is supported by the higher number of juveniles (classes 1 and 2) of *T. turneri* than of other species.

The clumped vertical distribution pattern of bromeliads corresponds to the distribution pattern of epiphytes in general at different forests sites (García-Franco & Peters 1987, Kelly 1985, Serna 1994, Sugden & Robins 1979, VanDunné 2001). Bennet (1987) and Nieder et al. (2000) found that more than 50% of bromeliads were located in the middle and upper forest strata both in Florida and in Venezuelan Guayana forests.

In this study, the aggregated distribution of epiphytes in the middle and upper strata suggests several explanations. First, at these strata, branching parts of the phorophyte tend to be more inclined and better illuminated than the main trunk. Bromeliad establishment, therefore, is enhanced by better microclimatic conditions (Rudolph et al. 1998). Light intensity is the most important condition for bromeliad establishment, along with humidity. High humidity, however, does not constitute a constraint, as it is a characteristic of this cloud montane forest. Second, the tillandsioid species found have equal ecophysiological requirements; therefore they are placed at similar microhabitats (Bennet 1986, Hietz & Hietz-Seifert 1995). Third, mechanical (foliar trichomes) and physiological (CAM) aspects, as well as anemocoric dispersal adaptations, allow tillandsioid specialists to inhabit the higher and middle forest strata (Kelly 1985, Nieder et al. 1999). In addition, the caespitose habit of these plants enhances the aggregation of individuals.

Tillandsia complanata showed a different distribution, being more abundant in the lower strata. This particular pattern can be explained by considering the morphological characteristics of the species. *Tillandsia complanata* has a small tank and wide, long, thin, pendant leaves that allow a major sun capture, low trichome density in the shoot, and a deep green tank color (Benzing 1976) These adaptations make *T. complanata* shade tolerant according to Pittendrigh's classification (1948). Species grouped in shade-tolerant classes are more suitable for shaded environments, where humidity is not a constraint.

The rare *Guzmania gloriosa* and *Tillandsia biflora* were the species with the most erratic and unpredictable distribution patterns. This finding is reflected in other studies, where spatial distribution patterns of less abundant species differ from those of the community, but the pattern of abundant species does not (Yeaton & Gladstone 1982, VanDunné 2001). This is because larger populations produce higher number of seeds, and therefore the anemocoric dispersion

TABLE 1. Extended.

Leaf length (cm)		Leaf number		Perimeter (cm)	
x̄	σ	x̄	σ	x̄	σ
19.33	0.91	22.2	11.1	17.83	0.67
26.51	1.59	24.27	1.37	24.87	0.87
29.97	0.93	32.19	1.86	35.97	0.95
19.9	1.29	19.16	1.11	23.82	1.3
27.95	1.39	27.6	1.77	36.12	1.91
36.26	1.2	39.53	2.04	58.82	1.41
45.33	1.27	47.27	3.39	70.21	3.05
15.14	1.15	22.38	1.11	19.84	0.98
21.22	1.23	19.82	1.12	24.51	1.21
30.25	1.78	24	1.71	32.08	1.51
14.41	0.46	21.73	0.89	17.43	0.75
21.08	0.96	24.75	0.94	25.44	0.96
28.05	1.31	31.27	1.31	36.14	2.08
29.18	1.13	36.19	1.67	46.45	1.18
11.28	0.67	25.13	1.38	16.63	0.71
14.15	0.77	33.18	2.06	24.62	1.29
17.01	0.85	19.33	0.99	17.47	0.99
31.31	2.48	23.27	1.72	28.45	3.57
43.97	1.36	29.43	1.41	47.5	2.19
8.59	0.32	24.24	3.63	5.88	0.26
13.21	0.61	21.42	2.14	10.31	0.41
15.37	0.82	18.95	0.66	12.91	0.53

guarantees a wider colonization of available sites (Hietz & Hietz-Seifert 1995, VanDunné 2001).

Concentration of juvenile and adult bromeliads at the same vertical forest strata suggests that initial environmental conditions act as a selection filter determining successful bromeliad establishment. Similar bromeliad aggregation patterns among age classes were found in the Central Colombian Andes (VanDunné 2001).

Concentration of individuals near the phorophyte main axis is not surprising, as branches become thinner further away from the main axis and therefore less resistant to the weight of adult bromeliads. Similar clumping was observed in the Venezuelan Amazonia, French Guiana, and Florida (Bennet 1987, Freiberg 1996, Nieder et al. 2000).

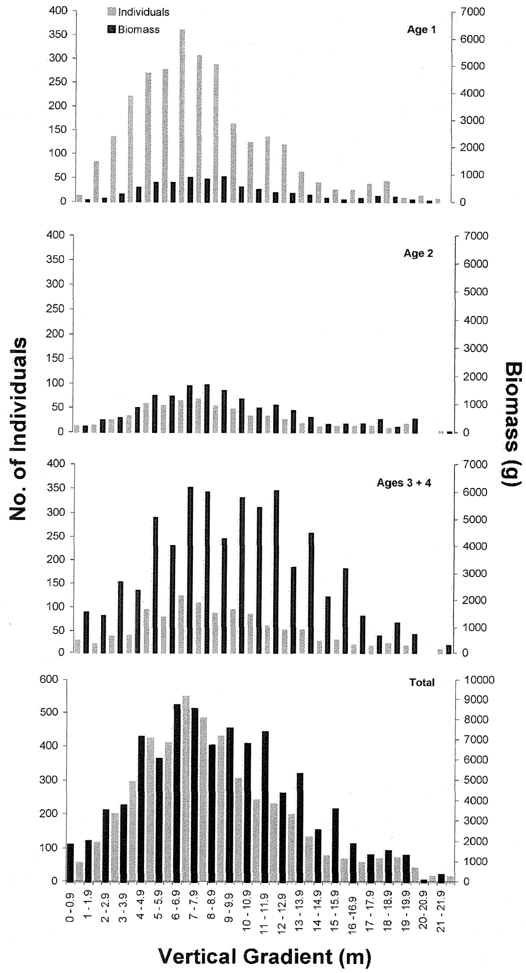

FIGURE 1. Vertical distribution of the bromeliad community, El Santuario, Chocontá, Colombia, 2001.

Biomass and Vertical Distribution

Biomass of the bromeliad community was high (91.06 kg/0.1 ha). Unfortunately direct comparisons are difficult, as most studies do not isolate bromeliad biomass. Several authors,

TABLE 2. Correlative abundance and biomass of the bromeliad community by age class. Class 1 also includes individuals from the "undetermined" category. Adults include age class 2 of *Tillandsia biflora* and classes 3 and 4 of the other species.

Age class	Abundance (n)	Relative abundance (%)	Biomass (g)	Relative biomass (%)
1	2737	62.3	7590.06	8.3
2	592	13.5	15,577.09	17.1
Adults (classes 3 and 4)	1066	24.3	67,892.12	74.6
Total	4395	100	91,059.27	100

TABLE 3. Absolute and relative abundance of the species in total and per age class. Because relative abundance was calculated excluding the "undetermined" category, n = 2214 individuals.

Age class	*Tillandsia turneri*	*Tillandsia fendleri*	*Racinaea tetrantha*	*Tillandsia complanata*	*Tillandsia biflora*	*Guzmania gloriosa*	"Undetermined"
1	275	151	85	38	6	1	2181
2	361	126	73	28	7	4	
3	743	61	144	31		7	
4		56		17			
Total	1379	394	302	114	13	12	2181
Relative abundance (%)	62.3	17.8	13.6	5.1	0.6	0.5	

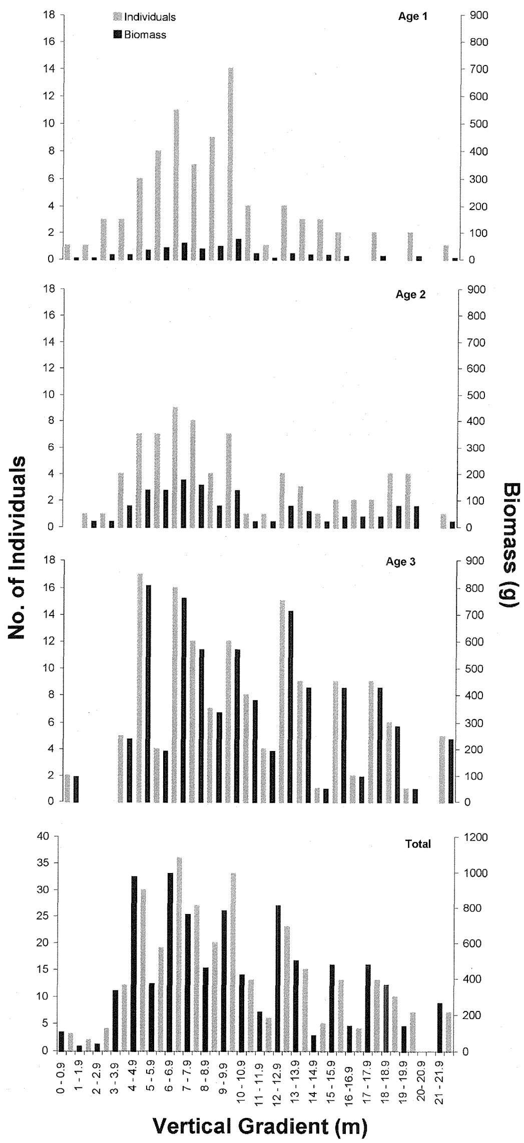

FIGURE 2. Vertical distribution of individuals and biomass of *Racinaea tetrantha.*

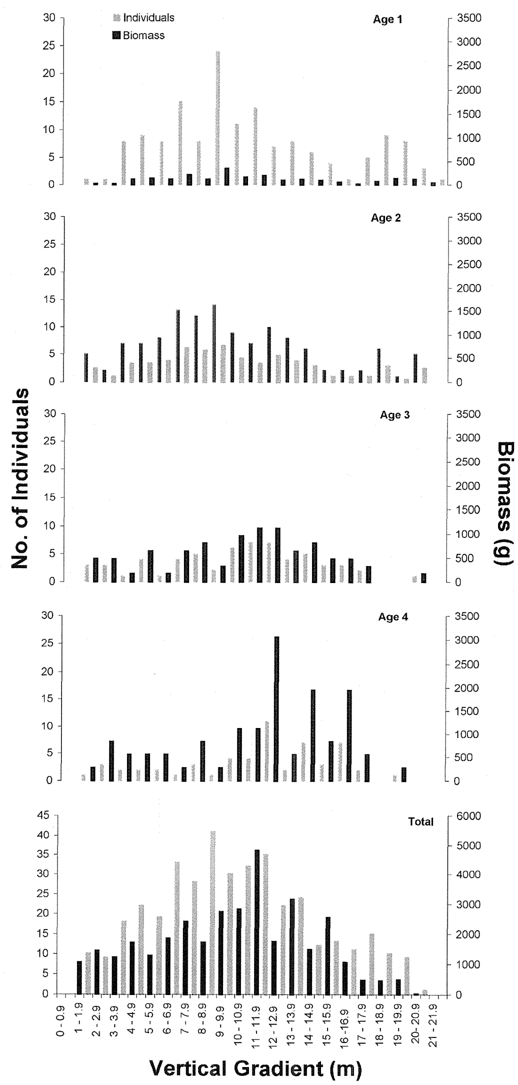

FIGURE 3. Vertical distribution of individuals and biomass of *Tillandsia fendleri.*

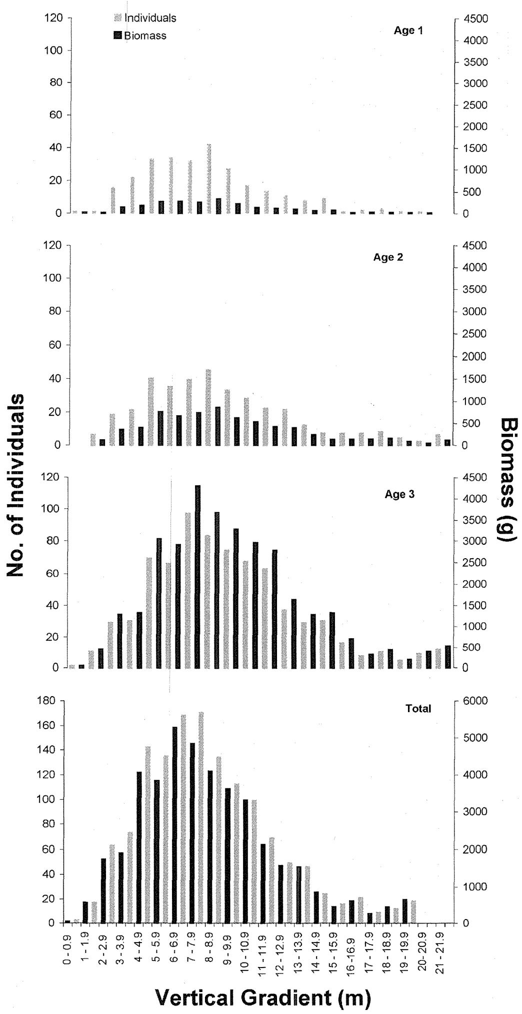

FIGURE 4. Vertical distribution of individuals and biomass of *Tillandsia turneri.*

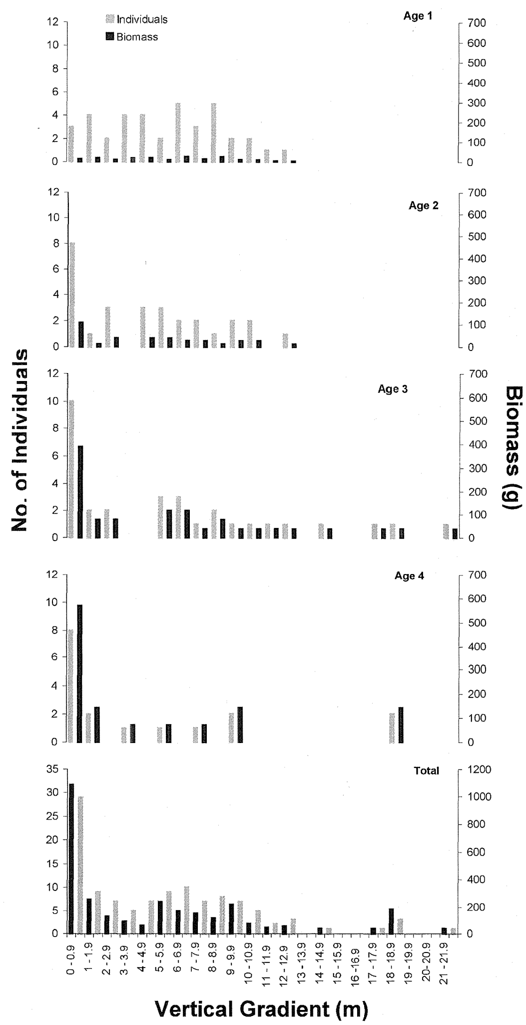

FIGURE 5. Vertical distribution of individuals and biomass of *Tillandsia complanata.*

TABLE 4. Absolute and relative biomass (g) of the species in total and per age class. Because relative biomass was calculated excluding the "undetermined" category, total biomass = 88,543.19 g.

Age class	*Tillandsia turneri*	*Tillandsia fendleri*	*Racinaea tetrantha*	*Tillandsia complanata*	*Tillandsia biflora*	*Guzmania gloriosa*	"Undetermined"
1	2167.00	2243.41	450.5	189.73	17.52	5.82	2516.08
2	6772.36	6924.96	1418.76	377.47	54.96	83.54	
3	32,798.25	9710.35	6830.93	1212.72		534.04	
4		15,536.25		1214.62			
Total	41,737.61	34,414.97	8700.19	2994.54	72.48	623.4	2516.08
Relative biomass (%)	47.1	38.9	9.8	3.4	0.1	0.7	
Biomass/individual	30.27	87.35	28.81	26.27	5.58	51.95	1.15

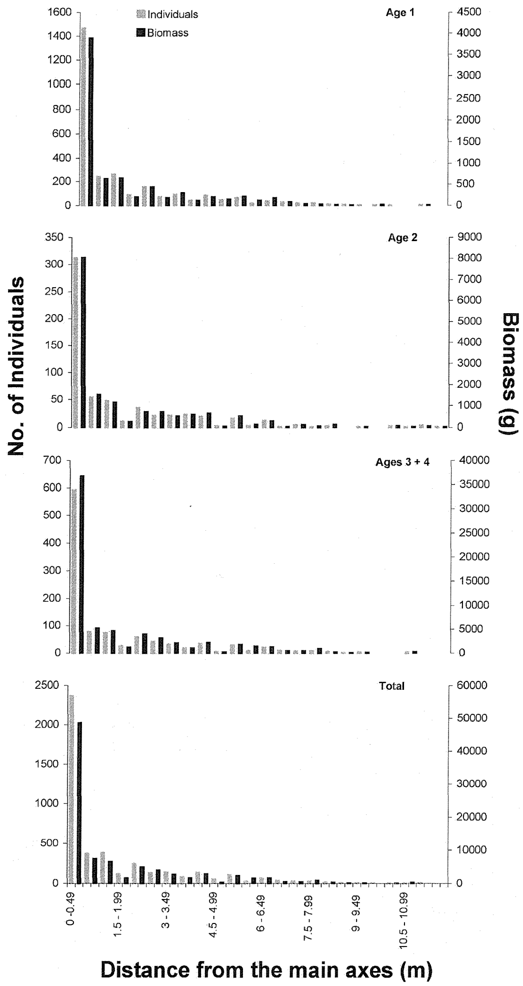

FIGURE 6. Bromeliad individuals and biomass distribution in relation to the distance from the main phorophyte.

however, have recorded the high biomass contribution made by epiphytes in montane forest (Golley et al. 1971, Nadkarni 1984, Hofstede et al. 1993). Because bromeliads reserve valuable biomass capital in their tissues and rosettes (as fallen organic matter and organisms inhabit the tanks), the plants play an important role in resilience and nutrient efficiency of these ecosystems. Bromeliad biomass measures, which remain scattered, have the potential to advance understanding of epiphyte, nutrient, and forest structure dynamics.

Studies performed in Ecuadorian forests with successional stages suggest that mature forests contain more and heavier bromeliads (Dunn 2000). We observed this pattern in secondary disturbed forest patches near the study site. In these patches, species numbers were similar to the primary forest studied, but the size and number of individuals were markedly smaller (J. Betancur pers. obs.). The causes may be a shorter period for bromeliad growth and establishment along with a simplified forest structure. These observations have important implications for conserving the ecology of upper montane forest; biomass may be more meaningful than diversity in measuring productivity and forest recovery, because some disturbed forests act as islands, where arrival of new species may be a hazardous event.

In this study, *Tillandsia turneri* had the highest biomass and number of individuals. Similarly Serna (1994) found that this species presented the highest biomass and also was the second most abundant species within the community in other high Andean forests near the study site. *Tillandsia turneri* is one of the most characteristic bromeliad species of the forests on the Sabana de Bogotá (Betancur 2001).

Bromeliad biomass also affects spatial distributional patterns. For example, the high biomass of adults of *Tillandsia fendleri* clarify its proximity to the phorophyte main axis and its preference for thick tree trunks, which can support higher density and bromeliad mass. This biomass effect also was found for *T. fasiculata,* which reaches maturity only when hosted on an axis strong enough to carry the bromeliad's weight (Benzing 2000).

The positive correlation between phorophyte structural variables and the biomass and number of bromeliads agrees with observations made in different tropical forests (Bennet 1986, Rudolph et al. 1998, Yeaton & Gladstone 1982, Zimmerman & Olmsted 1992). The similar correlation may be because bigger and/or older trees provide a larger area and more time for bromeliad colonization.

Bromeliad diversity is not at its highest in upper montane forests, and the importance of these plants resides in their abundance and biomass. These two features contribute to make a richer vegetation layer especially at canopy level and enhance microhabitat availability and nutrient traps. Measures of abundance and biomass, overlooked in many epiphyte studies, are essential in understanding nutrient cycling, organism symbiosis, and forest recovery.

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APPENDIX 1. Kruskal-Wallis test for morphometric variables to determine age classes in each species. Bars indicate differences among age-class groups.

Species	Upper cover F	Upper cover *P*	Height F	Height *P*	Leaf length F	Leaf length *P*	No. leaves F	No. leaves *P*	Basal perimeter F	Basal perimeter *P*
Tillandsia turneri	26.52	0.000	48.88	0.000	24.98	0.000	0.38	0.688	116.92	0.000
Age 1										
2										
3										
Tillandsia fendleri	90.94	0.000	118.98	0.000	73.82	0.000	43.27	0.000	117.22	0.000
Age 1										
2										
3										
4										
Racinaea tetrantha	25.76	0.000	45.28	0.000	33.31	0.000	1.82	0.172	24.13	0.000
Age 1										
2										
3										
Tillandsia complanata	106.04	0.000	84.57	0.000	45.59	0.000	31.11	0.000	95.16	0.000
Age 1										
2										
3										
4										
Tillandsia biflora	9.24	0.005	9.02	0.000	19.02	0.008	8.74	0.005	35.53	0.000
Age 1										
2										
Guzmania gloriosa	73.68	0.000	49.02	0.000	50.98	0.000	17.47	0.000	59.38	0.000
Age 1										
2										
3										
"Undetermined"	25.13	0.000	41.76	0.000	33.59	0.000	0.30	0.744	80.53	0.000
Age 1										
2										
3										

Note: F = critical value. *P* = probability.

APPENDIX 2. Indices of spatial distribution of bromeliad individuals for the community and per age class. The pattern is aggregated for all species.

Species	Age class	Dispersion index	*P*-value	Morisita index
Tillandsia turneri	All	1.63	0.000	1.07
	1	1.53	0.000	1.07
	2	2.05	0.000	1.14
	3	1.82	0.000	1.10
Tillandsia fendleri	All	1.92	0.000	1.09
	1	2.16	0.000	1.12
	2	2.31	0.000	1.15
	3	1.95	0.000	1.10
	4	1.74	0.000	1.07
Racinaea tetrantha	All	2.55	0.000	1.17
	1	2.13	0.000	1.14
	2	2.93	0.000	1.21
	3	2.48	0.000	1.15
Tillandsia complanata	All	4.54	0.000	1.72
	1	2.09	0.000	1.21
	2	3.33	0.000	1.55
	3	6.47	0.000	1.97
	4	8.95	0.000	2.90
Tillandsia biflora	All	2.71	0.000	1.22
Community	All	2.29	0.000	1.19
	1	2.10	0.000	1.15
	2	2.44	0.000	1.18
	3	2.26	0.000	1.17

APPENDIX 3. Indices of spatial distribution of bromeliad biomass for the community and per age class. The pattern is aggregated for all species.

Species	Age class	Dispersion index	*P*-value	Morisita index
Tillandsia turneri	All	1.84	0.000	1.10
	1	1.53	0.000	1.07
	2	2.04	0.000	1.13
	3	1.72	0.000	1.09
Tillandsia fendleri	All	1.93	0.000	1.09
	1	2.14	0.000	1.11
	2	2.28	0.000	1.14
	3	1.93	0.000	1.10
	4	1.74	0.000	1.07
Racinaea tetrantha	All	2.53	0.000	1.15
	1	2.11	0.000	1.13
	2	2.89	0.000	1.20
	3	2.46	0.000	1.14
Tillandsia complanata	All	6.51	0.000	2.13
	1	2.05	0.000	1.20
	2	3.22	0.000	1.52
	3	6.27	0.000	1.93
	4	8.44	0.000	2.78
Tillandsia biflora	All	2.01	0.000	1.12
"Undetermined"	All	2.06	0.000	1.14
Community	All	2.27	0.000	1.15
	1	2.24	0.000	1.15
	2	2.41	0.000	1.17
	3	2.19	0.000	1.14