

Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador

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(Accepted 17th March 2000)

ABSTRACT. Epiphyte diversity as well as distribution and composition of epiphytic biomass was investigated in two lowland and two montane rain forests in Ecuador. Species numbers of epiphytes per tree were slightly higher in the montane (22–41 in Los Cedros, 33–54 in Otonga) than in the lowland forests (9–43 in Yasuni, 19–32 in Tiputini), however differences were not significant. In contrast, some epiphyte families did show significant altitudinal differences. The total epiphytic biomass per branch surface decreased from the centre of the crown to the periphery, and was generally higher in the montane (6.0 kg m⁻² on central branches in Los Cedros, 1.8 kg m⁻² in Otonga) than in the lowland forests (1.3 kg m⁻² in Yasuni and 1.8 kg m⁻² in Tiputini). Especially, dry weight of bryophytes and dead organic matter was higher in the mountains. In contrast, the biomass of green parts of vascular epiphytes on central branches was about the same in all four forests (0.4–0.6 kg m⁻²). A comparison with literature data from other study sites of tropical moist forests supports the observation that biomass of vascular epiphytes does not significantly change with altitude. It is discussed, that the high bryophytic biomass in montane compared to lowland forests is a major reason for differences in humus biomass between these forest types.

KEY WORDS: biodiversity, biomass, canopy, Ecuador, epiphytes, epiphyte humus, tropical rain forest

INTRODUCTION

To document and compare vascular epiphyte diversity several types of references have been used in the literature. Numbers of epiphytic species have been reported on single trees (Biedinger & Fischer 1996, Ek 1997; Freiberg 1996a, 1999; Johansson 1974, Valdivia 1977), in forest plots of defined sizes (Bøgh 1992, Ibisch 1996), in larger investigation areas with undefined size (Hietz 1997, Ibisch 1996), and of political units like countries (Aguirre-Leon 1992,

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Ibisch *et al.* 1996) or worldwide (Gentry & Dodson 1987b, Kress 1989). Furthermore, the epiphyte quotient has been used to compare different regions (Ibisch 1996, Ibisch *et al.* 1996, Johansson 1974). Among other factors, possible influences of altitude and precipitation on epiphyte diversity have been studied (Benzing 1983, Gentry & Dodson 1987a, Grubb *et al.* 1963, Ibisch 1996, Sugden & Robins 1979). According to these studies, the highest diversity of vascular epiphytes can be found in wet forests of montane habitats, however the altitude with maximum diversity varies between sites. In contrast to vascular epiphytes, epiphytic bryophytes are most diverse at even higher elevations (Wolf 1993).

Besides the epiphyte diversity the epiphytic biomass also changes with altitude in tropical regions (Wolf 1993), but only very few comparative studies had been made. They focused on montane forests (Coxson 1991, Edwards & Grubb 1977, Hofstede *et al.* 1993, Ingram & Nadkarni 1993, Nadkarni 1984, Pócs 1980, Tanner 1980, Veneklaas *et al.* 1990) or considered only the epiphytic bryophytes on tree trunks in the understorey (Frahm 1990, Frahm & Gradstein 1991). Data on biomass of vascular epiphytes in tropical lowland forests are very rare (Golley *et al.* 1971, Hietz-Seifert *et al.* 1996, Murphy & Lugo 1986).

Vascular epiphytes, bryophytes, lichens, roots and dead organic matter form a more or less compact mat on the branches (Hofstede *et al.* 1993, Klinge 1966, Nadkarni 1984). The dead organic matter can be divided furthermore into litter, partly decomposed dead organic matter and humus (Klinge 1966). These accumulations of living and dead biomass influence the microclimate in the canopy (Bohlman *et al.* 1995; Freiberg 1997, 2000), whereas microclimate influences phenomorphology of certain epiphytes (Freiberg 1996b). Moreover, the epiphytic biomass is able to efficiently collect and retain rain water (Pócs 1980, Veneklaas *et al.* 1990) and therefore plays an important role in the water cycle of the ecosystem.

The aim of the study was to compare montane and lowland tropical rain forests regarding the diversity of vascular epiphytes and the amount and composition of epiphytic biomass. It was tested whether the hypothesis that epiphyte diversity and biomass increase with altitude above sea level in tropical forests also applies to the four study sites that were chosen in Ecuador. All four forests, two in the western Andes and two in the Amazon basin, had relatively low seasonality and mean annual precipitation between 2500 and 3300 mm. The analysis of the amount and composition of epiphytic biomass on different branches, trees, and altitudes above sea level helps to explain and evaluate the factors that influence the establishment and maintenance of biomass accumulations in the canopy of tropical forests.

STUDY SITES

The investigations were carried out between March and August 1996 in four 2-ha forest plots of different altitudes in Ecuador. Major climatic data and

Table 1. Climate and geographical data for the four forests studied in Ecuador. The responsible organizations are Pontificia Universidad Católica del Ecuador, Quito, for Otonga and Yasuni, Universidad San Francisco de Quito for Tiputini, and Centro de Investigación de Bosques Tropicales, Quito, for Los Cedros.

	Otonga	Los Cedros	Yasuni	Tiputini
Province	Cotopaxi	Imbabura	Napo	Napo
Location	0° 25' S 79° 0' W	0° 19' N 78° 47' W	0° 40' S 76° 25' W	0° 45' S 75° 45' W
Height of forest (m)	30–35	30–35	35–40	30–35
Altitude of study plots (m asl)	1800	1400	250–300	250–300
Annual temperature (°C)	18	19–21	25–30	25–30
Annual precipitation (mm)	2600–2900	2800–3300	2500–3000	2500–3000

geographical positions of the areas are presented in Table 1. Climate data for Los Cedros were provided by CIBT, Quito, and are based on 7 y of recording (August 1991–June 1998). On average, there was 1 arid mo, 1 humid mo and 10 perhumid mo y^{-1} (definition from Walter 1973). Climate data of only 1.5 y were available from Otonga. In this period, there were 1–2 arid, 3–4 humid and 7 perhumid mo y^{-1} . For Yasuni and Tiputini, the data of the two meteorological stations, Limoncocha and Tiputini, were taken (Ministerio de Agricultura y Ganadería, Ecuador; Cruz & Rovere 1978), revealing 12 perhumid mo y^{-1} .

METHODS

Selection of phorophytes and canopy access

Within each investigation area, five emerging or canopy trees were chosen as phorophytes upon accessibility of crown and maturity of tree. Canopies were reached by using single-rope climbing techniques (Perry 1978). For each phorophyte the altitude above sea level, the diameter of the trunk, the diameter of the crown, the height of the tree, and the base of the crown were measured and recorded. Specimens of phorophytes were sampled and deposited at the Herbarium of Pontificia Universidad Católica del Ecuador (QCA) and at the National Herbarium of Ecuador (QCNE), both in Quito. Most specimens were vegetative and therefore could only be identified to the family level (Gentry 1993). The trees were three Leguminosae and two *Ficus* (Moraceae) in Los Cedros, one *Croton* (Euphorbiaceae), one *Ficus*, and two unknown trees in Otonga, one Leguminosae, one Lecythidaceae, one *Ficus*, and two unknown trees in Yasuni, and one *Ceiba* (Bombacaceae), one Euphorbiaceae, two *Ficus*, and one unknown tree in Tiputini. The tree heights were 30–39 m in Los Cedros, 25–38 m in Otonga, 19–44 m in Yasuni and 30–38 m in Tiputini.

Detection of diversity of vascular epiphytes and epiphyte cover

From several positions in the canopy the number of epiphytic vascular species and the respective plant family were recorded. Where sampling of specimens was not possible or in the case of a vegetative specimen, the species reflect morphospecies. Otherwise, determination was made by specimen comparisons

in the Herbarium of the Universidad Católica (QCA) and National Herbarium (QCNE). Specimens were deposited at these herbaria.

Following Johansson (1974), the crowns of each tree were subdivided into three sections. Within each section, only the branches with the largest diameters were chosen, with the consequence that distance to the crown centre and branch diameter correspond to each other. Branch sections in the crown centres had diameters of 18–40 cm, in the middle of 9–17.9 cm and in the periphery 1–8.9 cm. Furthermore, branches were subdivided into three classes of inclination: horizontal (0–30°), inclined (31–60°), and vertical (61–90°) branches. For each inclination class in each crown section, the average cover of vascular epiphytes and of bryophytes was estimated by eye in 20% classes, based on experiences of Freiberg (1996a), and the thickness of the humus-bryophyte layer was measured.

Biomass of epiphytes and of dead organic matter in the canopy

Within each investigation area, between 10 and 22 branch positions on four to five trees were chosen for the analysis of biomass. Criteria for selection of branches were accessibility and typical representation of biomass for the respective crown section. At each position, height above forest floor, distance to the periphery, distance to crown centre, diameter of branch, inclination of branch, and thickness of humus-bryophyte layer were measured using a measuring tape. Then, a complete sample of the epiphyte and dead organic matter load of branch sections of about 30–50 cm length were carefully cut and put into large plastic bags. In the laboratory of the respective biological station, the samples were subsequently separated into the following fractions: living plants (monocotyledons, dicotyledons, ferns, roots, bryophytes and lichens) and dead organic matter ('litter', including dead leaves, fruits and twigs; 'semi-humus', which is partly decomposed dead organic matter with small pieces of twigs, roots, leaves or fruits of up to 1 cm as well as dead bryophytes; 'humus', which is highly decomposed dead organic matter without recognizable parts). Living and dead roots were separated from each other on the base of their turgor and colour. The biomass of fauna that did not escape during collection and separation was added to the respective fraction where it was found. Of each fraction, the fresh weight was measured; 10–20 g of fresh weight were then stored in paper bags and dried at 60 °C for 3 d to constant weight for subsequent determination of dry weight. Finally, the epiphytic biomass per branch length as well as per branch surface were determined. The branch surface was calculated as the length of a branch section multiplied by its circumference.

Statistical analysis

Statistical analyses were performed using STATISTICA (StatSoft, 1993). Values of $P < 0.05$ were accepted as significant. In all cases the data were not normally distributed and thus non-parametric tests were applied. The Mann–

Whitney U-test was performed to test for differences in epiphyte species number, cover and biomass. Spearman's rank correlation coefficient was calculated to test the relationships between epiphyte diversity and biomass.

RESULTS

Epiphyte diversity

The number of epiphytes per tree varied between 33–54 species in Otonga, 22–41 in Los Cedros, 9–43 in Yasuni, and 19–32 in Tiputini (Table 2). At all sites, the taxonomic groups with most species were Orchidaceae, Araceae, Bromeliaceae and Pteridophyta. In Otonga, 10–20 spp. of orchids per tree contributed to 30–50% of epiphyte diversity; in Los Cedros 4–16 to 20–40%, in Yasuni 0–16 to 0–75%, and in Tiputini 3–11 to 10–40%. The diversity of other families was relatively constant and small with less than 10%: 1–3 Peperomiaceae, 1–3 Gesneriaceae, and 1–2 Clusiaceae occurred on almost every tree. Members of the families Cactaceae, Melastomataceae, Ericaceae, Cyclanthaceae, Bignoniaceae, Marcgraviaceae and Moraceae occurred irregularly.

The differences in species number between the four sites were not very pronounced. Before combining the values of Los Cedros and Otonga, as well as those of Yasuni and Tiputini, to compare montane and lowland forests a Mann–Whitney U-test was carried out to ensure that the differences in species number (total and groups) between the two sites were not significant (lowland sites Yasuni and Tiputini: in all cases $P > 0.1$; montane sites Otonga and Los Cedros: in almost all cases $P > 0.05$, the only exceptions being pteridophytes with $P = 0.02$ and Ericaceae with $P = 0.03$). Differences between the montane

Table 2. Number of species of vascular epiphytes per tree at four study sites in Ecuador. Values are medians, (minimum–maximum are in parentheses).

Number of trees	Otongapa 4	Los Cedros 5	Yasuni 5	Tiputini 5
Pteridophyta	8 (6–9)	5 (4–6)	4 (2–8)	5 (3–6)
Monocotyledonae	24 (13–28)	14 (8–23)	16 (3–26)	13 (9–20)
Araceae	5 (1–5)	3 (2–5)	5 (0–8)	5 (0–7)
Bromeliaceae	2 (2–3)	2 (1–2)	2 (0–5)	2 (1–4)
Cyclanthaceae	1 (0–1)	0 (0–1)	0 (0–2)	1 (0–1)
Orchidaceae	16 (10–20)	9 (4–16)	8 (0–16)	7 (3–11)
Other families	0 (0)	0 (0–1)	0 (0)	0 (0)
Dicotyledonae	12 (6–20)	10 (9–14)	6 (1–10)	9 (7–12)
Bignoniaceae	1 (0–1)	1 (0–1)	1 (0–1)	0 (0–1)
Cactaceae	0 (0)	0 (0)	1 (0–1)	0 (0–1)
Clusiaceae	2 (1–2)	1 (1–3)	1 (0–1)	1 (1)
Ericaceae	4 (3–5)	3 (3)	0 (0)	0 (0)
Gesneriaceae	2 (1–3)	2 (1–3)	1 (0–2)	2 (0–3)
Marcgraviaceae	1 (0–1)	0 (0–1)	0 (0–1)	0 (0–1)
Melastomataceae	0 (0–1)	1 (0–1)	0 (0)	0 (0)
Moraceae	0 (0–1)	0 (0–1)	1 (0–1)	1 (0–2)
Peperomiaceae	2 (0–4)	1 (1–2)	1 (0–3)	2 (1–3)
Other families	2 (0–4)	1 (0–2)	0 (0–2)	2 (2–4)
Total	42 (33–54)	31 (22–41)	21 (9–43)	30 (19–32)

and the lowland forests were significant in the case of Orchidaceae (Mann–Whitney U-test: $P = 0.03$), Cactaceae ($P = 0.02$), Clusiaceae ($P = 0.02$), Ericaceae ($P = 0.0001$), Melastomataceae ($P = 0.02$) and Moraceae ($P = 0.01$). Among these groups, Orchidaceae and Clusiaceae were more abundant and Ericaceae and Melastomataceae were exclusive to the montane sites, where the Ericaceae contributed up to 13% to the vascular epiphytic species. In contrast, Cactaceae were restricted to the lowland forest sites, where about one species was found on each tree. Altitudinal differences in species number of all other groups (total species number, pteridophytes, Araceae, Bromeliaceae, etc.) were not significant ($P > 0.05$).

Epiphyte cover and thickness of humus-bryophyte layer

The relative cover of vascular epiphytes and bryophytes as well as the thickness of the humus-bryophyte layer depended on the branch diameter (distance from the trunk) and on the inclination of the branch (Figure 1). Generally, thick and more or less horizontal branches in the centre of the crowns had the highest epiphyte cover and the thickest humus-bryophyte layer.

Before comparing epiphyte cover and thickness of the humus-bryophyte layer in the two montane sites Otonga and Los Cedros with the two lowland sites Yasuni and Tiputini, differences between the two respective sites were tested for each inclination and branch diameter (crown position) class. In all cases, differences were not significant (Mann–Whitney U-test: $P > 0.1$), regarding cover of vascular epiphytes, bryophytes and thickness of humus-bryophyte layer. This result allowed merging values of Los Cedros and Otonga, as well as those of Yasuni and Tiputini, to analyse differences between the montane and the lowland forests.

The relative cover of vascular epiphytes on more or less horizontal branches in the centre and the middle of the crowns was slightly higher in the mountains (70%) than in the lowlands (50%) but differences were not significant (Mann–Whitney U-test: $P > 0.05$; top of Figure 1). However, the cover of bryophytes differed distinctly between montane and lowland sites at all crown positions (Mann–Whitney U-test: $P < 0.03$; middle of Figure 1). While in the mountains almost all central and middle branches with inclinations up to 60° (horizontal and inclined) had a bryophyte cover of 100%, in the lowland forests even on branches in the centre of the crowns the bryophyte cover was rarely higher than 50%. Moreover, the variation of the relative epiphyte cover was higher in the lowland than in the montane sites. In the lowland forests, some trees were nearly free of epiphytes while others were covered almost as densely as trees in the mountains. In contrast, in Los Cedros and Otonga almost all canopy trees were well covered by epiphytes.

Bryophytes and humus together usually formed a rather distinct layer on the branches. In the montane forests this layer was significantly thicker, 2–14 cm, than in the lowland forests, where it was never found to be more than 2

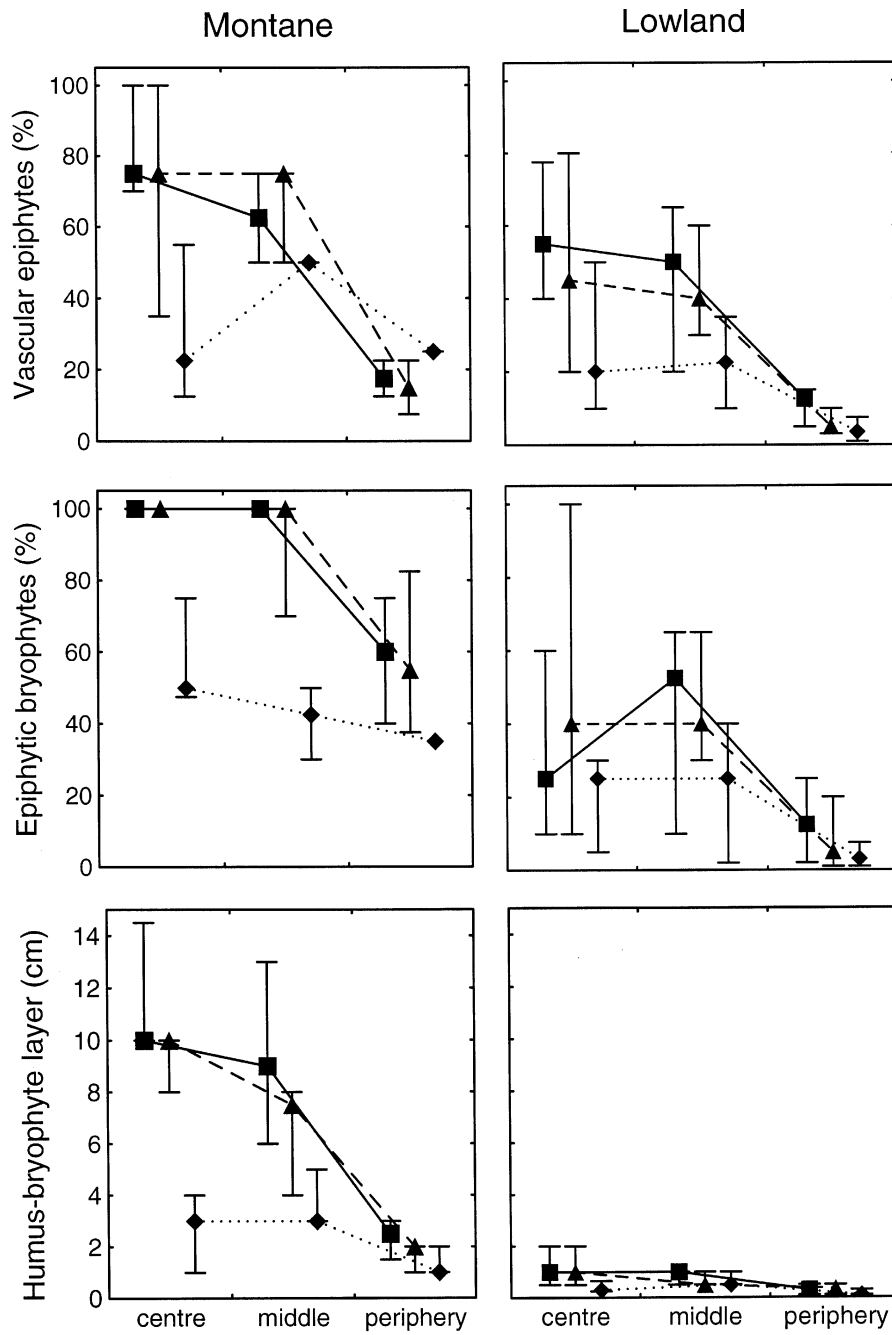


Figure 1. Branch cover of vascular epiphytes, epiphytic bryophytes, and thickness of humus-bryophyte layer at different crown sections (centre: branch diameter 18–40 cm, middle: 9–17.9 cm, periphery: 1–8.9 cm) and branch inclinations (horizontal: 0–30°, —■—; inclined: 31–60°, —▲—; vertical 61–90°, ···◆···) of montane (Los Cedros and Otonga) and lowland (Yasuni and Tiputini) forests. Values are medians ± quartiles. The number of trees was nine in the mountains and 10 in the lowlands.

cm (Mann–Whitney U-test: $P < 0.05$ at all crown positions; bottom of Figure 1).

Biomass of epiphytes and of dead organic matter

In all study sites, the total epiphytic biomass increased with branch diameter or decreased with distance from crown centre (Table 3). In the crown centre, branch sections of 100 cm carried loads of 1.2–2.0 kg epiphytic biomass in Otonga, 3–4, rarely up to 5 kg in Los Cedros, 0.7–1.0 kg in Yasuni, and 1.0–2.0 kg in Tiputini. This corresponds to 1.81 kg m⁻² branch surface in Otonga, 5.98 kg m⁻² in Los Cedros, 1.34 kg m⁻² in Yasuni, and 1.84 kg m⁻² in Tiputini (Table 3). On middle branches, the total epiphytic biomass was 0.91 kg m⁻² in Otonga, 3.42 kg m⁻² in Los Cedros, 0.80 kg m⁻² in Yasuni, and 0.88 kg m⁻² in Tiputini.

Before analysing altitudinal differences in epiphytic biomass at different crown positions, Mann–Whitney U-tests were performed for total epiphytic biomass and all fractions (as listed in Table 3), on the one hand between Los Cedros and Otonga, and on the other hand between Yasuni and Tiputini. Results showed that in none of the cases were there significant differences between Yasuni and Tiputini ($P > 0.1$). However, in some cases significant differences in epiphytic biomass were detected between Los Cedros and Otonga (lichens, humus, total biomass and dead organic matter; $P < 0.05$) while in most cases differences were not significant (monocots, dicots, pteridophytes, bryophytes, green parts of vascular epiphytes, vascular epiphytes including roots, and litter; $P > 0.05$).

Therefore, in the latter case values for Los Cedros and Otonga were combined to compare montane and lowland sites by using Mann–Whitney U-tests. In the montane sites there were significantly more bryophytes ($P < 0.002$ at all branch positions) and dicots ($P = 0.001$ on middle branches), and significantly less monocots ($P < 0.02$ on middle and central branch positions) than in lowland sites. While bryophytes only contributed to less than 5% of the epiphytic biomass on middle and inner branches and up to 42% on periphery branches in the lowland forests, in Los Cedros and Otonga about 10–25% of the biomass on the larger branches and up to 70% in the periphery were bryophytes (Table 3). Altitudinal differences in biomass of pteridophytes, vascular epiphytes and litter at all branch positions were not significant ($P > 0.3$).

In the case of lichens, humus, dead organic matter and total epiphytic biomass Los Cedros and Otonga had to be compared separately with the two lowland sites. In Los Cedros there was significantly more humus, dead organic matter and total epiphytic biomass than in Yasuni and Tiputini ($P < 0.004$). Also, in Otonga the biomass of humus and dead organic matter as well as the total epiphytic biomass was larger than in the lowland sites, however, these differences were not significant ($P > 0.1$). The biomass of lichens was never more than 0.01 kg m⁻² and usually did not contribute to more than 1% of the total epiphytic biomass. Only in the periphery of Tiputini trees, where the total

Table 3. Composition and distribution of epiphytic biomass per branch surface (kg m^{-2}) on different branch sections at the four study sites. Numbers are medians and percentages of total epiphytic biomass and sample numbers are in parentheses. Diameters are 1–8.9 cm for inner, 9–17.9 cm for middle and 18–40 cm for outer branches.

	Otonga		Los Cedros		Yasuni		Tiputini	
	(kg m^{-2})	%	(kg m^{-2})	%	(kg m^{-2})	%	(kg m^{-2})	%
Inner branches (n)	(5)		(5)		(2)		(5)	
Living biomass	0.87	48	2.57	43	0.76	57	0.92	50
Vascular epiphytes	0.59	33	1.87	31	0.75	56	0.89	48
Green	0.40	22	0.57	10	0.48	36	0.51	28
Monocots	0.27	15	0.08	1	0.39	29	0.43	23
Dicots	0.06	3	0.34	6	0.01	1	0.01	1
Ferns	0.07	4	0.15	3	0.09	6	0.07	4
Non-green	0.19	11	1.30	21	0.27	20	0.38	20
Roots	0.19	11	0.74	12	0.27	20	0.38	20
Ericaceae bulbs	0.00	0	0.56	9	0.00	0	0.00	0
Cryptogams	0.28	15	0.70	12	0.01	1	0.03	2
Bryophytes	0.28	15	0.70	12	0.01	1	0.03	2
Lichens	0.00	0	<0.01	0	0.00	0	0.00	0
Dead biomass	0.94	52	3.41	57	0.58	43	0.92	50
Litter	0.07	4	0.15	3	0.04	3	0.07	4
Semi-humus	0.18	10	0.41	7	0.04	3	0.19	10
Humus	0.69	38	2.85	47	0.50	37	0.66	36
Total	1.81		5.98		1.34		1.84	
Middle branches (n)	(7)		(9)		(5)		(13)	
Living biomass	0.63	50	1.39	42	0.42	53	0.38	50
Vascular epiphytes	0.31	25	0.67	20	0.39	49	0.34	45
Green	0.24	19	0.23	7	0.29	37	0.27	35
Monocots	0.05	4	0.04	1	0.24	30	0.16	21
Dicots	0.03	2	0.17	5	<0.01	1	0.01	1
Ferns	0.16	13	0.02	1	0.05	6	0.10	13
Non-green	0.07	6	0.44	13	0.10	12	0.07	10
Roots	0.07	6	0.30	9	0.10	12	0.07	10
Ericaceae bulbs	0.00	0	0.14	4	0.00	0	0.00	0
Cryptogams	0.32	25	0.72	22	0.03	4	0.04	5
Bryophytes	0.32	25	0.71	22	0.03	4	0.04	5
Lichens	0.00	0	0.01	<1	<0.01	<1	<0.01	<1
Dead biomass	0.64	50	1.88	58	0.37	47	0.38	50
Litter	0.03	2	0.05	2	0.05	6	0.01	1
Semi-humus	0.06	5	0.22	7	0.06	8	0.06	8
Humus	0.55	43	1.61	49	0.26	33	0.31	41
Total	1.27		3.27		0.79		0.76	
Outer branches (n)	(5)		(4)		(3)		(4)	
Living biomass	0.39	87	0.75	41	0.17	89	0.09	56
Vascular epiphytes	0.07	16	0.21	11	0.09	47	0.05	31
Green	0.05	11	0.08	4	0.06	31	0.04	25
Monocots	<0.01	<1	0.02	1	0.06	31	0.0	16
Dicots	0.05	11	0.01	<1	0.00	0	0.0	16
Ferns	<0.01	<1	0.05	3	<0.01	<1	0.02	13
Non-green	0.02	5	0.13	7	0.03	16	0.01	6
Roots	0.02	5	0.13	7	0.03	16	0.01	6
Ericaceae bulbs	0.00	0	0.00	0	0.00	0	0.00	0
Cryptogams	0.32	71	0.54	30	0.08	42	0.04	25
Bryophytes	0.32	71	0.53	30	0.08	42	0.03	19
Lichens	0.00	0	0.01	<1	<0.01	<1	0.01	6
Dead biomass	0.06	13	1.07	59	0.02	11	0.07	44
Litter	<0.01	<1	<0.01	<1	0.00	0	<0.01	<1
Semi-humus	0.01	2	0.20	11	<0.01	<1	0.01	6
Humus	0.05	11	0.87	48	0.02	11	0.06	38
Total	0.45		1.82		0.19		0.16	

epiphytic biomass was very small, the lichens became relatively more important and contributed to 6%.

On the central and middle branch sections of the lowland as well as the montane forests about half of the biomass was living and the other half was dead material (Table 3). In the crown periphery, the proportion of living biomass was much larger than that of dead material, with the exception of Los Cedros, where this proportion was the same in all crown positions.

Furthermore, the epiphytic biomass was compared with the number of epiphyte species. The epiphytic biomass of each tree was characterized by the average dry weight of total epiphytic biomass on middle branch sections and correlated with species number of vascular epiphytes of the same tree. Spearman's rank correlation showed no significant relationships between them ($P > 0.1$).

DISCUSSION

The number of vascular epiphytic species found on the trees in the four montane and lowland forests in Ecuador (9–54 species per tree) may be compared with the numbers recorded from other neotropical forest trees, however, the species numbers vary tremendously not only between sites but also between trees within sites: 8–107 in Veracruz, Mexico (Valdivia 1977), 33–65 in Saül, French Guiana (Freiberg 1996a), 15–72 in Les Nouragues, French Guiana (Freiberg 1999; M. & E. Freiberg, unpubl. data). This variability can be explained by the manifold influencing parameters. These are climate factors (amount and seasonality of precipitation, temperature, wind, frequency of fog), phorophyte characteristics (e.g. species, age, height, diameter of crown, bark, leafing phenology), geographical position (latitude, altitude, exposition, inclination) and sampling methods with different precision (Hietz & Wolf 1996).

Among these parameters, altitude has been analysed frequently. In contrast to earlier findings (Benzing 1983, Gentry & Dodson 1987a, Grubb *et al.* 1963, Ibisch *et al.* 1996, Sugden & Robins 1979) and our hypothesis, in the present study there were only small, non-significant differences between montane and lowland forests comparing vascular epiphyte diversity. However, species numbers in the cited literature are referred to in areas of ≥ 0.1 ha up to landscape size, while in the present study species numbers per tree are given. On the one hand, this result can signify that the hypothesis does not apply to the present study sites. On the other hand, the fact that in the four study sites the species numbers per tree are not significantly different, does not necessarily imply that the species numbers per hectare are similar as well. Where species number per tree in Otonga and Los Cedros varied from one tree to another to a greater extent than in Yasuni and Tiputini, in the first regions the species number per hectare might be distinctly higher than in the latter regions, although species numbers per tree were recorded as the same.

While total species numbers per tree were not significantly different between study sites, we did detect altitudinal differences in the occurrence of some families. However, comparison with other regions show that epiphytic Ericaceae are not generally absent in or epiphytic Cactaceae restricted to lowland forests (Freiberg 1999, Ibisch 1996).

With few exceptions, the orchids contributed essentially (20–50%) to the number of vascular epiphyte species. Reports from other regions (42–50%, Biedinger & Fischer 1996; 45–65%, Freiberg 1996a; 51%, Freiberg 1999; 45%, ter Steege & Cornelisson 1989) are within this range.

As a consequence of the hypothesis that both epiphyte diversity and biomass are higher in the montane than in the lowland forests, it would be expected that these parameters are positively correlated with each other. However, in the present study they were not. Many species do not directly depend on the humus biomass. Nevertheless, a significant relationship might be detected if biomass were to be correlated only with species of certain humus demanding life-forms.

The results on bryophyte cover and thickness of humus-bryophyte layer supported the expectations. Thicker horizontal branches had significantly higher bryophyte cover and thicker humus-bryophyte layers than thin peripheral and vertical branches. Moreover, values were higher in the mountains than in the lowlands. Surprisingly, the cover of vascular epiphytes was only slightly and not significantly higher in the montane than in the lowland sites. The values for the thickness of the humus-bryophyte layer in the four forests of the present study match with data from Colombia (Wolf 1993). There, the thickness of the living bryophyte layer on central and middle branch sections increases with increasing altitude from 0–2 cm at 1000 m asl to 1–15 cm at 3500 m. The smaller abundance of bryophytes in the lowland may be caused by microclimatic conditions, which do not allow sufficient net photosynthesis (Frahm 1987). Field studies show that lowland bryophytes have high respiration rates at night due to high temperatures. This nocturnal carbon loss cannot always be compensated during the day, because then bryophytes often dry out, leading to a reduced carbon gain through photosynthesis (Zotz 1999).

Beside the thickness of the humus-bryophyte layer, epiphytic biomass was generally higher on thick central branches than in the periphery (Table 3). Moreover, the proportion of biomass fraction changed with distance from crown centre. While on middle and central branches a large fraction of the biomass was dead, the proportion of living biomass was higher in the periphery. The same phenomenon has been found in Monteverde, Costa Rica, where on the inner and middle branches about half of the biomass was living and the other half was dead organic matter (Nadkarni 1984), and in the periphery 70% of the epiphytic biomass were living bryophytes. This is due to a shorter surface availability of branches in the periphery, where dead organic matter simply did not have enough time to accumulate. While the biomass and the proportion of

vascular epiphytes was higher in the crown centre, bryophyte biomass did not change with branch diameter and its proportion was higher in the periphery (Table 3). This can be explained by the fact that bryophytes are early colonizers on young branches, covering them rather quickly, while most vascular epiphytes need dead organic matter, bryophytes and/or more time to establish.

Comparing montane and lowland forests, most biomass fractions as well as total epiphytic biomass were lower in Yasuni and Tiputini than in Otonga and Los Cedros. This is most profound for bryophytes, dead organic matter and total epiphytic biomass. Figure 2 presents a comparison of the results of the present study with data reported from other forests at different altitudes in Central America and northern South America. In contrast to the hypothesis that epiphytic biomass increases with increasing altitude, the biomass of green parts of vascular epiphytes was more or less the same in all four study sites. This is supported by the comparison with data from other regions which shows that the values resemble each other very closely (Figure 2). On central branches in eight forest sites from 40–3700 m asl the biomass of green vascular epiphytes was between 0.4 and 0.9 kg m⁻², while at the same sites the biomass of epiphytic bryophytes increased from nearly zero at 40 m up to almost 3.0 kg m⁻² at 3700 m. Middle branches featured the same tendency (right side of Figure 2).

Looking at different fractions of vascular epiphytes in the four present study sites, differences between montane and lowland forests were not significant for pteridophytes, but there were significantly more dicots in the mountains and significantly more monocots in the lowland. This might be due to the fact that typical morphological adaptations of epiphytes (velamen radicum of orchids, absorptive trichomes of bromeliads, water-storage tanks, secondary homorhizy) are very common in monocots, but nearly missing in dicots. Therefore, monocots are better able to deal with the typical water stressed habitat of the lowland canopy than dicots. Due to a wetter environment in the canopy of montane forests, these adaptations are not as advantageous as in the lowland, so that the less adapted dicots are able to compete and become more abundant than monocots.

According to the hypothesis, one would rather expect that the epiphytic biomass would be higher in Otonga than in Los Cedros, but, the total epiphytic biomass, dead organic matter, and bryophyte mass were distinctly higher in Los Cedros than in Otonga. Possible causes might be climatic differences, although, at first sight, the climate (temperature, precipitation) appears to be comparable at both sites, but the lack of long-term climate data does not allow an interpretation. However, differences in topography of montane forests may result in distinct small-scale differences in the local climate regime (wind influencing evaporation, frequency of fog, seasonality, exposition, wind shade), so that even neighbouring slopes or valleys have very different local climate and consequently different epiphyte biomass.

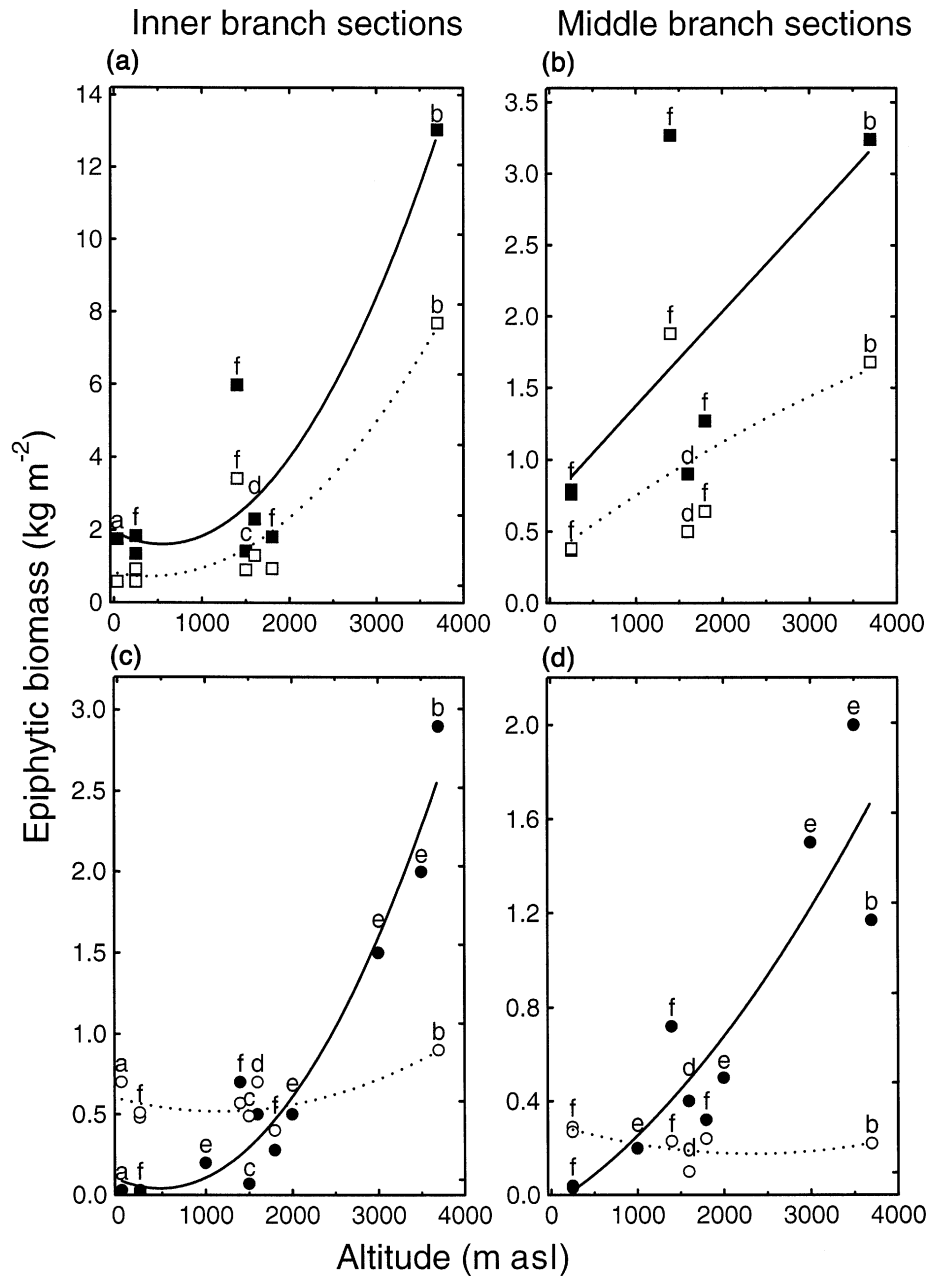


Figure 2. Comparison of data on epiphytic biomass (kg m^{-2}) on (a, c) inner and (b, d) middle branches of the present study with values from other studies at different altitudes above sea level. Small letters indicate sites as follows: a, Aratai, French Guiana, 40 m (Freiberg 1999); b, Colombia, 3700 m (Hofstede *et al.* 1993); c, Monteverde, Costa Rica, 1500 m (Ingram & Nadkarni 1993); d, Monteverde, Costa Rica, 1600–1800 m (Nadkarni 1984); e, Colombia, 1000, 2000, 3000, 3500 m (Wolf 1993); f, Yasuni and Tiputini, 250 m, Los Cedros, 1400 m, Otonga, 1800 m. Ecuador, (this study). —■— total epiphytic biomass, —□— dead organic matter, —●— non-vascular epiphytes, —○— vascular epiphytes, which include only green parts, with exception of Nadkarni (1984).

The accumulation of epiphytic dead organic matter (humus and semi-humus) is influenced by opposing processes. It depends on the equilibrium between production and decomposition of biomass. On the one hand, the degree of humus accumulation depends on the type and amount of organic matter provided. Origins for material are fallen leaves, fruits, flowers, and twigs of phorophytes and epiphytes, dead bryophytes, bark, detritus, dead animals and micro-organisms, and dust. On the other hand, the decomposition depends on various factors such as microclimate, the presence of decomposers and microbial activity.

While the amount of biomass of vascular epiphytes was nearly the same at all altitudes, the biomass of epiphytic bryophytes was very low in the lowland forests. Therefore, in the lowland forests vascular epiphytes appear to be more important as a source for humus. Furthermore, high temperatures increase microbial and faunal decomposition activity in the lowland compared to the highland. Consequently, the equilibrium between accumulation and decomposition shifts to lower humus biomass in lowland than in montane forests. Bryophytes, together with low decomposition rates, are the best candidates to cause the high humus accumulation in montane forests. Litter as a source for humus is difficult to evaluate, because litter input highly depends on various factors like the phenology of the epiphytes, the phorophyte, and the surrounding trees, and is highly variable throughout the year. Therefore, it cannot be considered without detailed analysis of annual rhythms.

Despite its relatively low biomass (not more than 1%; Edwards & Grubb 1977, Murphy & Lugo 1986, Tanner 1980) compared with other forest compartments, the epiphytic organic matter plays an important role in the ecology of tropical rain forests. Studies of Pócs (1980) show that the epiphytic biomass can retain up to 15 000 litres of water ha⁻¹ in a submontane rain forest and even 50 000 litres ha⁻¹ in a mossy elfin forest. By absorbing precipitation water (rain and fog), epiphytes retain minerals effectively (Coxson & Nadkarni 1995). Moreover, epiphytic biomass influences the microclimate in the canopy (Freiberg 2000), which then affects phenomorphology of epiphytes (Freiberg 1996b).

ACKNOWLEDGEMENTS

We gratefully thank Dra Laura Arcos, Dr Giovanni Onore and Dr Renato Valencia of the Pontificia Universidad Católica del Ecuador, Martha Mondragon, Murray Cooper, and José Decoux of CIBT (Centro de Investigación de Bosques Tropicales, Quito), as well as Dr Gunter Reck, Dr Carol Walton and Kelly Swing of the Universidad San Francisco de Quito. Our very special thanks are meant for the Tapia family in San Francisco de las Pampas and for Iris. This investigation was supported by the German Research Foundation (DFG), grant nos. Fr 1150/3-1 and Fr 1197/1-1.

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