

EPIPHYTIC BIOMASS AND NUTRIENT STATUS OF A COLOMBIAN UPPER MONTANE RAIN FOREST

ROBERT G. M. HOFSTEDE
JAN H. D. WOLF

University of Amsterdam, Department of Systematics, Evolution and Paleobiology,
Hugo de Vries-laboratory, Kruislaan 318, 1098 SM Amsterdam, The Netherlands

DAVID H. BENZING

Oberlin College, Department of Botany, Oberlin, Ohio 44074

ABSTRACT. A mature *Weinmannia mariquitae* tree that constituted part of the upper canopy layer and its epiphytic load were examined to determine the composition and importance of these two compartments in the forest ecosystem.

Extrapolation from this specimen and two other trees representing the relatively epiphyte-free middle and lower stories indicated that 44 tons ha⁻¹ of epiphytic biomass and suspended soil, a quantity that exceeds by at least three fold that reported from other sites, occurs in the studied Colombian rain forest. Epiphytic materials equivalent to 12% of the biomass of the *W. mariquitae* specimen, a higher proportion than any previously recorded, was present on this single phorophyte. Additionally, green biomass produced by epiphytes (ca. 20 kg dry wt) exceeded that of their support by one third. This tree and its associated epiphytic load contained 2,360 g N, 215 g P, 1,350 g K and 99 g Ca of which 51, 58, 80 and 72%, respectively, were present in the phorophyte. Water extractable P was concentrated in higher levels in the suspended than in the terrestrial soil. Unprecedented accumulations of dead vegetation and living bryophytes present in the canopy of this forest are promoted by low temperatures, continuous high humidity, low air turbulence, and certain aspects of forest structure. Low concentrations of certain nutrients in living foliage at the site appear to reflect the generally oligotrophic conditions that in part are imposed by slow mineralization of organic matter. However, the amounts of nutrient capital and green tissue present in suspended biomass and its location in the canopy insures a substantial role in the overall nutrient economy and productivity of the inclusive forest ecosystem.

A notable characteristic of wet tropical upper montane and subalpine rain forests is the presence of abundant nonvascular epiphytes, especially bryophytes and their partially decomposed remains (Grubb *et al.* 1963, Van Reenen & Gradstein 1983; FIGURE 1). These plants, and the less common vascular epiphytes associated with them, influence nutrient and water budgets and biogeochemical cycles and productivity in inclusive ecosystems (Nadkarni 1986, Pócs 1980, Veneklaas 1990, Veneklaas *et al.* 1990), but information on the magnitudes of these influences and important mechanisms is scarce. Earlier studies (Benzing 1981, Benzing & Seeman 1978, Gentry & Dodson 1987, Nadkarni 1984) dealt with the epiphytic compartments in communities at lower (warmer) elevations. The purpose of the study reported here was to determine how much of the biomass, nutrient capital and green tissue located in the canopy of an upper montane rain forest is apportioned between trees and other materials suspended in their crowns. The results are considered along with those obtained elsewhere with respect to potential impacts of epiphytic biomass on important processes in upper montane forest ecosystems.

STUDY SITE

The study site is located on a 15° west facing slope near hacienda "La Sierra" in the municipality of Santa Rosa de Cabal, department of Risaralda (4°49'N; 75°29.5'W), at 3,700 m alt in the Central Cordillera of Colombia. A description by Cleef *et al.* (1983) is applicable to this and other forests bordering the subalpine dwarf forests on the humid slopes of the interandean valleys of the northern Andes.

Clouds envelop the study site for at least 6 daylight hr each day and relative humidity inside the forest rarely falls below 90% (FIGURE 2). Annual rainfall, measured in 1983, was approximately 1,250 mm and distributed bimodally over the year (FIGURE 3). Rainless periods exceeding a few days are rare and continuous, high atmospheric humidity further reduces the probability of severe drought. Daytime temperatures are low (2-6°C) and neither strong winds or evidence of their effects were observed.

The three tiers of the multilayered canopy occur at 10-15, 6-10, and 2-6 m (FIGURE 4). *Weinmannia mariquitae* Szyszyl. (Cunoniaceae) contributed 60% to the coverage of the upper canopy



FIGURE 1. The sampled *Weinmannia mariquitae* tree in the upper canopy layer.

layer. Dominant epiphytic bryophytes are *Po-rotrichodendron superbum* Tayl., *Lepicolea pruinosa* (Tayl.) Spruce, and *Plagiochila fuscolutea* Tayl. on the trunks and inner branches and *Herbertus subdentatus* (Steph.) Fulf., and *Leptoscyphus jackii* (Steph.) Grolle on the middle and outer branches. Loosely packed individuals (the tall turf of Mägdefrau 1982) may create a 25 cm thick layer that encircle smaller branches. A variety of filmy (*Hymenophyllum*) and non-filmy (*Elaphoglossum*) ferns and some flowering plants

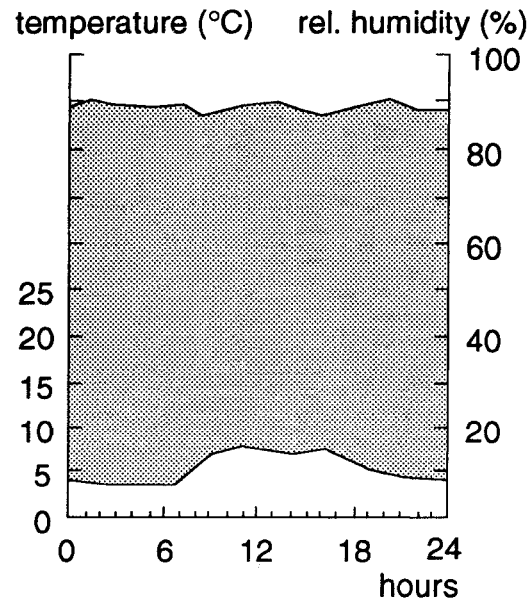


FIGURE 2. Mean temperature (bottom line) and relative humidity (upper line) fluctuations during the course of the day at the site, based on hourly readings during three weeks in May 1986.

(Ericaceae, Orchidaceae) root in the mats of suspended soil and living thallophytes. Smaller stems at the crown periphery are densely colonized by macrolichens belonging to the genera *Hypotrachyna*, *Usnea*, and *Oropogon*, and the pendent bryophyte *Frullania peruviana* Gott. Wolf (1993) provides a more comprehensive description of the epiphytic communities in the forest type.

METHODS

A mature *Weinmannia mariquitae* specimen chosen as representative of the trees forming the upper canopy layer was subdivided into trunk-foot, trunk, inner, middle and outer branches according to Johansson (1974). A rope ladder

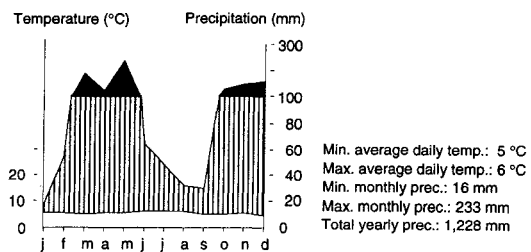


FIGURE 3. Climate diagram from climate station "La Sierra" at a site near ours, based on data from 1983 (Witte in press).

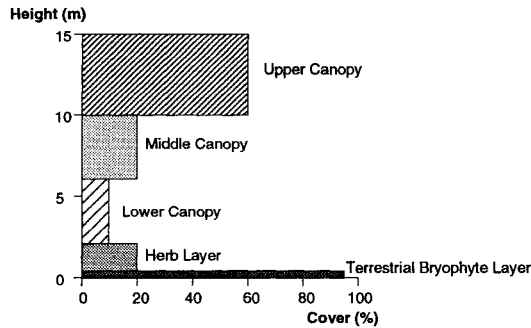
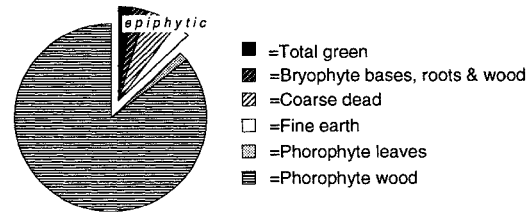


FIGURE 4. Structure diagram of the studied forest.

was used to remove the entire epiphytic mass and all phorophyte foliage. Wood in the trunk and branches was also sampled. Collected, suspended materials were segregated into 1) living, green vegetation (further subdivided into bryophytes, lichens, ferns and flowering plants), 2) living, nongreen material (subdivided into bryophyte shoot bases, and vascular plant roots and woody stems) and 3) dead material (further subdivided into fine, highly decomposed litter called fine earth by Klinge (1963) and coarser debris consisting of recognizable plant organs). Samples were oven dried at 70°C for 48 hours and weighed. Epiphytic loads on a *Hesperomeles lanuginosa* and a *Miconia* specimen that were representative of the middle and lower canopy tiers, respectively, were examined by the same procedures.

Ten random samples of each component of the epiphytic biomass that had been removed from each sector in the *W. mariquitae* tree and wood, bark, and leaves and terrestrial soil (upper 10 cm) were subjected to chemical analysis at the Hugo de Vries-laboratory. Assayed ferns, flowering plants, and lichens were drawn from collections that included plants harvested from the entire tree. One aliquot of each milled sample was digested in a solution of 4% salicylic acid in conc H_2SO_4 for total N analysis (colorimetrically at 660 nm with a Technicon-II auto analyser). A second aliquot was ashed at 400°C and dissolved in HCl (1.0 N) prior to P determination (colorimetrically at 660 nm with a Technicon-II auto analyser). A third digest was prepared to detect Ca and K using a spectrophotometer. Three samples of terrestrial soil and suspended soils from each of the sectors in the tree were extracted with deionized H_2O and the filtrates analyzed for pH, total P, Ca and K as described above. Ammonium, nitrate and nitrite were analyzed colorimetrically at 660 nm with a Technicon-II auto analyser.

The surface area of the bark was measured directly by determining the length and diameter of all trunk and branch segments (10–70 cm

FIGURE 5. The apportionment of biomass comprising a *Weinmannia mariquitae* tree in the upper canopy layer.

length). The more numerous branchlets were divided into two size classes, those with diameters of <0.5 cm and >0.5 cm. One hundred branchlets of known weight and surface area from each size class were used as references to calculate surface areas for entire classes. Trunk and branch masses were determined from the volume values using the specific gravities of blocks of wood that were obtained by submergence in H_2O . Separate dry/fresh wt ratios were applied to the trunk/branch material and both branchlet sizes.

RESULTS

Almost 115 kg of epiphytic biomass, including 20.4 kg of green tissue, was suspended in the *Weinmannia* tree (TABLE 1, FIGURE 5). Phorophyte foliage weighed 15.5 kg; wood comprising the trunk and crown accounted for an additional 755 kg. The five different fractions making up the epiphytic biomass varied. Accumulations were much greater on the sloping trunk base than on the upper trunk or branches. Fine earth was most abundant on the trunk base (FIGURE 6). The proportion of living compared to total suspended material was highest on the outer branches and also substantial on the trunk where the epiphyte layer was thinner than on the more heavily colonized middle and inner canopy and trunk base. Epiphytic biomass per tree in the middle and lower tiers were relatively modest, 2.29 and 0.31 kg. Mean biomass per surface area of the sampled trees from the upper and middle canopy was 32.7 and 8.9 g·dm² respectively.

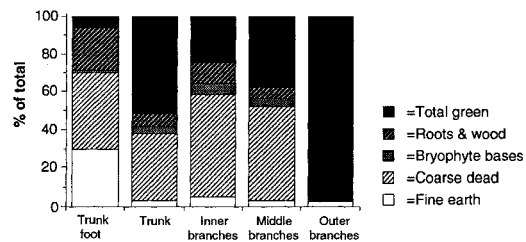


FIGURE 6. The distribution of the different epiphytic components within the tree.

TABLE 1. Apportionment and biomass (kg dry weight) of the different components of a *Weinmannia mариquitae* tree in the upper canopy layer and its epiphytic load.

	Trunk foot	Trunk	Inner branches	Middle branches	Outer branches	Total
Epiphytic						
Living						
Green						
Bryophytes	3.88	0.14	4.27	4.89	1.59	14.77
Lichens	0.03	0.01	0.10	0.17	1.59	1.90
Ferns	0.15	0.01	1.19	0.83	0.00	2.18
Flow. plants	0.59	0.00	0.63	0.29	0.00	1.51
Total green	4.65	0.16	6.19	6.18	3.18	20.36
Non-green						
Roots & wood	15.39	0.02	2.92	0.85	0.00	19.18
Bryoph. bases	1.04	0.01	1.22	0.86	0.00	3.13
Total non-green	16.43	0.03	4.14	1.71	0.00	21.31
Total living	21.08	0.19	10.33	7.89	3.18	42.67
Dead						
Coarse dead	27.60	0.11	13.40	7.88	0.08	49.07
Fine earth	21.14	0.01	1.40	0.60	0.08	23.23
Total dead	48.74	0.12	14.80	8.48	0.16	72.30
Total epiphytic	69.82	0.31	25.13	16.37	3.26	114.97
g dm ⁻² bark surface area	137.8	4.0	130.4	32.4	1.5	32.7
Phorophyte						
Wood						755.13
Leaves						15.38

Concentrations of nutrients in the biomass of epiphytes growing on the lower trunk of *W. mариquitae* generally exceeded those in plants anchored elsewhere in the canopy (TABLE 2). Nitrogen was most concentrated in nonliving components of the epiphytic biomass; green material, including phorophyte foliage, was generally richest in K. Calcium and P exhibited no consistent trends. Nonfilmy ferns were exceptionally well provisioned with Ca and K (11.7 and 8.1 g/kg respectively). Except for Ca and N, which were more concentrated, quantities of the four elements in phorophyte foliage were similar to those in the bryophytes. Ammonium was the predominant form of N in suspended and terrestrial soil (TABLE 3). The two types of soil were distinguished most clearly by extractable P which was at least 20 fold more concentrated in samples from the canopy. Among suspended soils, that on middle branches was generally the most fertile, although NH₄⁺ was most concentrated in material from the trunk base.

Apportionments of nutrient capital through the canopy were calculated by multiplying nutrient concentration with biomass values with one exception. Because so little material covered the trunk surface, concentrations from samples collected from middle branches were used to cal-

culate the nutrient status of trunk epiphytes. Tree and associated suspended materials together contained 2,360 g N, 215 g P, 1,350 g K, and 1,005 g Ca of which 49, 42, 20, and 28% were present in the second compartment. Phorophyte foliage accounted for 156 g N, 14 g P, 77 g K, and 99 g Ca, values that in every instance were below those recorded for the epiphytic biomass (FIGURE 7). A large proportion of the total nutrient capital located in the epiphytic load resided in the material collected from the base of the trunk. Thirty-four percent of the N contained in above ground biomass was contained in the dead portion of the epiphytic biomass.

Numbers of trees comprising the upper, middle and lower canopy tiers were 424, 802 and 1,140 ha⁻¹ respectively. The estimated epiphyte load for the entire forest was 44 tons ha⁻¹ after correction for the 140 trees of the upper canopy layer that had erect trunks with relatively modest epiphytic growth on the base.

DISCUSSION

Surveys of tropical forest biomass that have recorded epiphytic material have been conducted in Costa Rica, Jamaica, Panama, New Guinea, and Tanzania (TABLE 4). However, temper-

TABLE 2. Nutrient concentrations (mg g^{-1} dry weight) of the wood, bark and leaves of a *Weinmannia mariquitae* tree in the upper canopy layer and of the different epiphytic components it supported. Samples are bulked from 10 sub-samples and analyzed in triplicate. Standard deviations in italics.

	Total N (mg g^{-1})	SD	P (mg g^{-1})	SD	K (mg g^{-1})	SD	Ca (mg g^{-1})	SD
Epiphytic								
Trunk foot								
Bryophytes	8.33	<i>0.72</i>	1.16	<i>0.05</i>	5.94	<i>0.21</i>	3.37	<i>0.09</i>
Bryoph. bases	8.48	<i>0.53</i>	0.83	<i>0.11</i>	2.84	<i>0.09</i>	4.09	<i>0.05</i>
Roots	12.38	<i>0.75</i>	0.83	<i>0.04</i>	1.83	<i>0.11</i>	1.39	<i>0.03</i>
Coarse dead	11.11	<i>0.92</i>	0.93	<i>0.05</i>	0.93	<i>0.02</i>	3.11	<i>0.04</i>
Fine earth	14.33	<i>1.29</i>	1.19	<i>0.09</i>	0.28	<i>0.02</i>	1.39	<i>0.11</i>
Inner branches								
Bryophytes	5.87	<i>0.55</i>	0.73	<i>0.02</i>	5.62	<i>0.12</i>	2.53	<i>0.08</i>
Bryoph. bases	6.06	<i>0.32</i>	0.56	<i>0.02</i>	2.85	<i>0.08</i>	3.51	<i>0.09</i>
Roots	12.68	<i>0.22</i>	0.56	<i>0.06</i>	2.49	<i>0.24</i>	3.45	<i>0.10</i>
Coarse dead	8.53	<i>2.19</i>	0.54	<i>0.05</i>	0.38	<i>0.03</i>	3.33	<i>0.06</i>
Fine earth	10.76	<i>0.30</i>	0.66	<i>0.02</i>	0.50	<i>0.02</i>	4.69	<i>0.08</i>
Middle branches								
Bryophytes	6.40	<i>0.21</i>	0.71	<i>0.05</i>	3.68	<i>0.11</i>	1.80	<i>0.08</i>
Bryoph. bases	5.96	<i>0.09</i>	0.55	<i>0.02</i>	2.00	<i>0.24</i>	2.09	<i>0.04</i>
Roots	7.03	<i>0.39</i>	0.62	<i>0.03</i>	1.92	<i>0.10</i>	2.14	<i>0.36</i>
Coarse dead & fine earth	8.12	<i>0.45</i>	0.62	<i>0.03</i>	0.65	<i>0.03</i>	2.80	<i>0.16</i>
Outer branches								
Bryophytes	6.65	<i>0.49</i>	1.02	<i>0.02</i>	2.20	<i>0.07</i>	2.44	<i>0.01</i>
General								
Lichens	6.37	<i>0.12</i>	0.58	<i>0.13</i>	1.83	<i>0.03</i>	1.72	<i>0.06</i>
Filmy ferns	9.15	<i>0.21</i>	1.11	<i>0.04</i>	2.70	<i>0.08</i>	1.63	<i>0.04</i>
Nonfilmy ferns	8.30	<i>0.00</i>	0.85	<i>0.05</i>	11.65	<i>0.04</i>	8.11	<i>1.24</i>
Flowering plants	7.05	<i>1.06</i>	0.88	<i>0.08</i>	6.08	<i>0.30</i>	3.62	<i>0.06</i>
Phorophyte								
Leaves	10.20	<i>1.22</i>	0.90	<i>0.03</i>	5.03	<i>0.12</i>	6.45	<i>0.23</i>
Bark	3.00	<i>0.21</i>	0.27	<i>0.04</i>	2.84	<i>0.04</i>	6.76	<i>0.00</i>
Wood	1.30	<i>0.08</i>	0.14	<i>0.03</i>	1.27	<i>0.05</i>	0.54	<i>0.01</i>

atures reflecting altitude differences of at least 1,300 m and other factors distinguish all of these sites from ours and could influence proportional sizes of epiphytic loads. Lower evaporative demand and decomposition slowed by cool temperatures probably contributed to the greater development of the epiphytic biomass at the Colombian location. Relative humidities below 70% substantially diminish photosynthesis in

many hepatics (Hosokawa *et al.* 1964); low temperatures have less effect on carbon gain (Dilks & Proctor 1975). Hepatics appear to be especially well suited for life under continuously cool and humid conditions and regularly relegate mosses and vascular epiphytes to secondary status in cool montane forests (Van Reenen & Gradstein 1983, Gradstein *et al.* 1989). A wood core taken at breast height from the sampled *Weinmannia*

TABLE 3. Concentrations (mg kg^{-1}) of H_2O -extractable nutrients of suspended soil and terrestrial soil. Samples are bulked from 10 sub-samples and analyzed in triplicate. Standard deviations in italics.

	pH	NO_2	SD	NO_3	SD	NH_4	SD	PO_4	SD	K	SD	Ca	SD
Suspended soil													
Trunk foot	3.7-4.1	1.0	<i>0.4</i>	1.5	<i>0.3</i>	78.6	<i>16.9</i>	100.7	<i>48.3</i>	115.7	<i>38.1</i>	33.8	<i>12.7</i>
Inner branches	3.9-4.7	0.7	<i>0.3</i>	0.7	<i>0.2</i>	41.3	<i>19.0</i>	128.3	<i>9.2</i>	197.5	<i>51.5</i>	72.9	<i>25.7</i>
Middle branches	4.2-4.3	2.4	<i>1.5</i>	1.2	<i>0.8</i>	34.3	<i>27.0</i>	144.3	<i>2.6</i>	323.7	<i>2.8</i>	81.9	<i>2.1</i>
Terrestrial soil													
	3.9-4.1	0.9	<i>0.2</i>	1.3	<i>0.5</i>	92.8	<i>6.2</i>	5.0	<i>1.4</i>	179.3	<i>9.4</i>	53.0	<i>10.9</i>

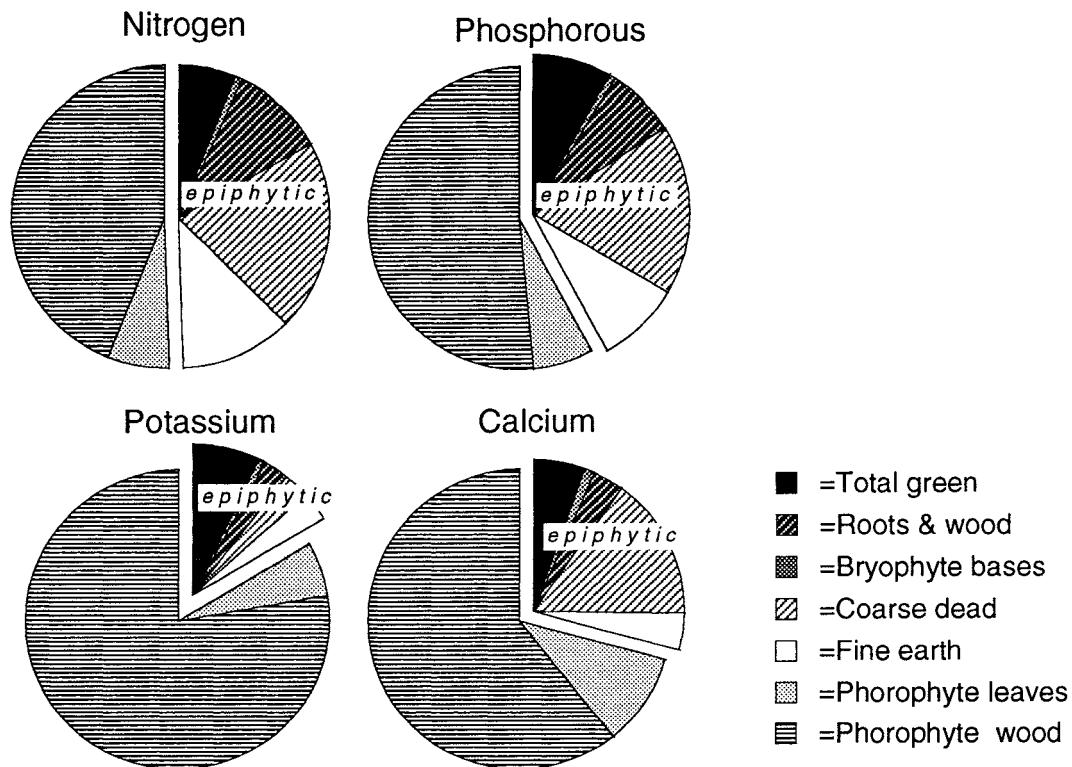


FIGURE 7. The apportionment of some macronutrients comprising a *Weinmannia mariquitae* tree in the upper canopy layer and its epiphytic load.

mariquitae specimen yielded a ^{14}C date of 215 ± 15 yr, sufficient time to build up substantial biomass.

Nadkarni (1984) analyzed the epiphytic mat on a *Clusia alata* tree in a lower montane rain forest (1,700 m) at the Monteverde Cloud Forest Reserve, Costa Rica, where annual temperatures range between 15–18°C (climate type G9, Herrera 1985). Although canopy surfaces supported

much accumulated biomass only 20% of this material was present on the trunk of the *Clusia alata* tree compared to 61% for our sampled *Weinmannia*. Total epiphytic load was greater at Monteverde (141.1 vs. 114.9 kg), but the area available for epiphyte colonization was also greater (92.9 vs. 35.2 m²). Moreover, we counted 424 trees ha⁻¹ (dbh > 45 cm; crown diameter > 6 m) and many had closely placed, sloping trunk

TABLE 4. Epiphytic biomass values of some tropical rain forests. Abbreviations: LMRF = Low Montane Rain Forest, UMRF = Upper Montane Rain Forest (Grubb *et al.* 1963).

Reference	Location	Altitude (m)	Epiphytic biomass		
			(kg/tree)	(g/dm ²)*	(tonnes/ha)
LMRF					
Golley <i>et al.</i> (1971)	Panama	250–600	—	—	1.4
Pócs (1980)	Tanzania	1,415	—	—	2.1
UMRF					
Tanner (1980)	Jamaica	1,615	—	—	2.8
Nadkarni (1984)	Costa Rica	1,700	141.9	15.3	4.7
Pócs (1980)	Tanzania	2,120	—	—	13.7
Edwards and Grubb (1977)	New Guinea	2,500	—	—	5.2
Veneklaas <i>et al.</i> (1990)	Colombia	3,370	—	—	12
This study	Colombia	3,700	115	32.7	44

* = mean biomass (g dm⁻² bark surface area).

TABLE 5. Nutrient concentrations (mg g^{-1}) of tree leaves (A) and epiphytes (B) of some tropical montane rain forests. Abbreviations: LMRF = Low Montane Rain Forest, UMRF = Upper Montane Rain Forest, SARF = Sub Alpine Rain Forest (Grubb *et al.* 1963, Grubb 1977).

A					
Reference	Location	Total N	P	K	Ca
LMRF					
Grubb (1977)	Malaya	13.8	0.7	7.7	2.1
Tanner (1977)	Jamaica (Gap)	17.6	1	14.9	12.6
UMRF					
Grubb (1977)	Australia	11.1	0.48	6.2	6
	Malaya (mean)	9.8	0.33	6.4	5.3
	Puerto Rico	9.7	0.53	3.9	7.6
Edwards and Grubb (1977)	New Guinea	14.2	0.84	10.1	10.9
Tanner (1977)	Jamaica (Mor)	10.5	0.5	5.5	6.2
	Jamaica (Mull)	16.1	0.7	12.3	9.3
	Jamaica (Wet slope)	12.7	0.8	14.9	11.4
Veneklaas (1990)	Colombia	14.7	0.90	6.1	—
This study	Colombia	10.2	0.90	5.03	6.45
SARF					
Grubb (1977)	New Guinea	9.7	0.54	6.4	9.7

B				
Epiphytic component	Total N	P	K	Ca
Nadkarni (1984)				
Bryophytes	16.9	0.62	3.66	1.37
Dead organic matter	19.9	0.66	1.73	2.23
Ferns	15.8	0.44	6.08	5.27
Flowering plants	14.2	0.79	18	9.5
This study				
Bryophytes	7.06	0.86	5.34	2.66
Dead organic matter	11.21	0.80	0.54	2.92
Ferns (mean)	8.73	1.00	7.22	4.87
Flowering plants	7.05	0.88	6.08	3.62

bases, an elfin character (Leigh 1975). Fewer, larger trees (25 ha^{-1} , diam 121 cm at 3 m) characterized the Monteverde forest. Epiphyte mats were especially thick (130.4 g dm^{-2}) on inner branches at the Colombian site compared to those at Monteverde (22.9 g dm^{-2}) perhaps in part because disturbance is infrequent. Winds up to 100 km hr^{-1} occur at Monteverde (Lawton & Dryer 1980) and probably dislodge much more suspended materials than does the considerably calmer atmosphere at the Colombian site.

Standing crops of epiphytic biomass reported by Veneklaas *et al.* (1990) for a montane forest with a similarly high tree density of 420 ha^{-1} (dbh > 10 cm), but taller stature (up to 25 m) with less epiphytic biomass on the often upright trunks, and by Pócs (1980) for a continuously moist, mossy forest in Tanzania (2,120 m) also exceeded those at Monteverde. In fact, the total dry weight of the microepiphytes in Pócs' mossy forest approximates that of our forest when the

masses of the bryophytes bases and green tips are summed (Pócs: $10,096 \text{ kg ha}^{-1}$; this study: $9,197 \text{ kg ha}^{-1}$). However, amounts of humus distinguish the two communities (Pócs: 26% of total epiphytic biomass; this study: 63%) as does the forest structure. Trees at Pócs site were seldom more than 4–6 m tall and generally lacked trunks where most of the litter had accumulated in our forest. Additionally, heavier rainfall at the Tanzanian site (ca. $3,000 \text{ mm yr}^{-1}$) could wash much decomposed material out of the canopy.

Substantially lower accumulations of epiphyte biomass in a premontane forest in Panama (Golley *et al.* 1971) and in upper montane forests in New Guinea (Edwards & Grubb 1977) and Jamaica (Tanner 1980) may result from higher temperatures that promote decomposition (Swift *et al.* 1979) and exacerbate the effects on productivity of the occasional dry spells (up to three weeks in New Guinea).

Concentrations of foliar Ca and P (TABLE 2) fell within the ranges reported by Grubb (1977), Tanner (1977), and Edwards and Grubb (1977) for other montane rain forests (TABLE 5A). Potassium and N concentrations were generally lower and possibly related to leaf type. Pachyphyllous leaves, such as those encountered at our site, possess structural features appropriate for cool, humid habitats (Grubb 1977). Ratios of N and K-rich cytoplasm to Ca-rich cell walls are low, a condition that contributes to N economy, leaf durability and probably reduces vulnerability to herbivore and decomposers. Although scarcities of P often are believed to limit growth in tropical forest ecosystems we observed no evidence of P insufficiency. Similar concentrations

of P in epiphyte and phorophyte foliage occur despite the much lower abundance of extractable P in terrestrial compared to suspended soils. Differences in P use efficiency between these two compartments may exist depending on the photosynthetic performance and the longevity of green tissues present there.

Concentrations of Ca, P, and K in the different fractions of the epiphyte biomass were similar to those reported by Nadkarni (1984, TABLE 5B) as were inputs of the same nutrients in precipitation (Monteverde: N: 12.3, P: 1.8, K: 3.7, Ca: 4.2 kg·ha⁻¹·yr⁻¹; Colombia N: 12.2, P: 0.48, K: 6.9, Ca: 7.37 kg·ha⁻¹·yr⁻¹; Veneklaas 1990). Nutrient capital suspended on the sampled *Clusia alata* (Ca: 460, K: 678, N: 3,062, P: 97 g) exceeded our values for the *Weinmannia mariquitae* tree because nutrient concentrations and the size of the epiphyte load were larger at Monteverde.

CONCLUSIONS

The *Weinmannia* tree at our Colombian site supports much more living and dead organic material per unit bark surface than did the *Clusia alata* tree surveyed at Monteverde (Nadkarni 1984) suggesting that this Andean forest is characterized by unusually large loads of suspended soil and plant material perhaps three or more times than that at other locations studied. Extraordinary development of epiphytic biomass at the Colombian location is probably fostered by numerous factors, most notably by low temperatures, continuous high humidity, low wind speeds, extended tree age, and the sloping orientation and high density of tree trunks. Epiphytic biomass at this site is important for two reasons: 1) the presence of 28, 20, 49, and 42% (respectively) of the total above ground pools of Ca, K, N and P in that compartment, and 2) its capacity to dominate nutrient cycling and strongly influence productivity in the ecosystem. Ion fluxes among all compartments and the photosynthetic contributions of green tissue throughout the community must be determined to fully evaluate the importance of epiphytism in this upper montane rain forest. Information on the potentially diverse and abundant fauna (Paoletti *et al.* 1991) that utilize canopy resources is also essential for a full accounting of the impacts of epiphytes on their communities.

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