

Epiphyte biomass and nutrient capital of a moist subtropical forest in north-eastern Taiwan

CHIA-CHUN HSU*, FU-WEN HORNG†¹ and CHEN-MENG KUO*

* *Department of Botany, National Taiwan University, Taipei, Taiwan*

† *Taiwan Forest Research Institute, 53 Nan-Hai Road, Taipei 100, Taiwan*

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ABSTRACT. A plot of 1200 m² was selected to represent the average epiphyte abundance of a moist subtropical broadleaved forest at Fushan in north-eastern Taiwan. In this plot, all epiphytes of 18 sample trees with dbh > 5 cm were removed and weighed to estimate their biomass and nutrient content. We found that the biomass of epiphytes and their associated detrital matter in this plot was 3360 kg ha⁻¹. The nutrient capital of the epiphytes (kg ha⁻¹) was: N = 42.4, P = 1.9, Mg = 5.5, Na = 1.3, Ca = 14.5 and K = 28.9. Although the epiphytic biomass constituted less than 2% of the total above-ground biomass of the forest, the epiphytes comprised about 21–43% of the total foliage nutrient capital of the ecosystem. Because nutrients contained in epiphytes and tree foliage are more readily available to other organisms than those in woody components, epiphytes may play a greater role in ecosystem nutrient cycling than their relatively small biomass would suggest.

KEY WORDS: Bryophytes, Fushan, hardwood forest, pteridophytes

INTRODUCTION

The effect of epiphytes on ecosystem-level functions has been increasingly studied for the past two decades. Many of the past studies focused on the role of epiphytes in biomass accumulation and nutrient cycling in ecosystems; however, most of the data on the role of epiphytes in ecosystems came from moist temperate and tropical regions (Denison 1973, Edwards & Grubb 1977, Golley *et al.* 1971, Hofstede *et al.* 1993, Nadkarni 1984*a, b*; Pike 1978, Pócs 1980). Relatively few studies provided detailed information on phorophyte surface area, epiphytic biomass and nutrient capital of the forest ecosystem.

Because of their efficiency in intercepting and retaining nutrients from the atmosphere, epiphytes can be important participants in the nutrient cycling in

¹ Corresponding author. Email: horng@serv.tfri.gov.tw

an ecosystem (Benzing 1990, Pócs 1976). Although epiphytes comprise a very small proportion of the total forest biomass, their contribution to productivity and nutrient capacity can be similar to or even greater than that of the phorophyte foliage in the ecosystem (Hofstede *et al.* 1993, Nadkarni 1984a, b).

The Fushan Experimental Forest is located in a subtropical region in north-eastern Taiwan. Because of its warm and continuously humid environment, epiphytes make up a conspicuous portion of this moist broadleaved evergreen forest. There are more than 100 species of epiphytes in this forest, which combined with its frequently cloudy weather pattern, shows a similar physiognomy to that of tropical cloud forests. Consequently, we hypothesized that epiphytes may contribute to a relatively similar pattern of biomass and nutrient accumulation as their counterparts in tropical moist cloud forests.

The purpose of the study was to estimate the amount of biomass and nutrient capital in the epiphytes and their associated detrital matter in this moist subtropical broadleaved evergreen forest. In addition, their relative contribution to the total above-ground ecosystem was calculated. The results were compared with epiphytic loads in tropical, subtropical and temperate forest ecosystems.

STUDY SITE

The study site was located in the Fushan Experimental Forest (24°46'N, 121°43'E), approximately 35 km from Taipei City in north-eastern Taiwan. The forest has been a long-term ecological research site of the National Science Council since 1990 (Figure 1).

The total area of the forest is 1098 ha, and ranges from 400 to 1400 m elevation. The climate is warm and humid with heavy rain and fog in the winter as a result of north-east monsoons. It is frequently struck by strong typhoons in summer and early autumn. During 1993–1997, the average annual temperature was 18.2 °C, and the average annual precipitation was 3600 mm with 221 rainy days. There is no dry season. The average annual relative humidity was 96%.

A plot of 1200 m² (20 m × 60 m) was set out on an acidic soil with a slightly inclining slope at 750 m elevation. The forest canopy here is about 8–15 m high and is a mixed broadleaved forest dominated by Lauraceae and Fagaceae. Common canopy trees include *Castanopsis carlesii* (Hemsl.) Hayata var. *sessilis* Nakai (Fagaceae), *Machilus thunbergii* Sieb. & Zucc., *Machilus zuihoensis* Hayata (Lauraceae), *Engelhardtia roxburghiana* Wall. (Juglandaceae), *Meliosma squamulata* Hance (Sabiaceae), *Diospyros morrisiana* Hance (Ebenaceae), *Schefflera octophylla* (Lour.) Harms (Araliaceae) and *Pyrenaria shinkoensis* (Hayata) Keng (Theaceae). The understorey vegetation consists mainly of *Blastus cochinchinensis* Lour. (Melastomataceae), *Alsophila podophylla* Hook. (Cyatheaceae), *Diplazium dilatatum* Blume (Athyriaceae), *Lasianthus* spp. (Rubiaceae), *Calanthe formosana*

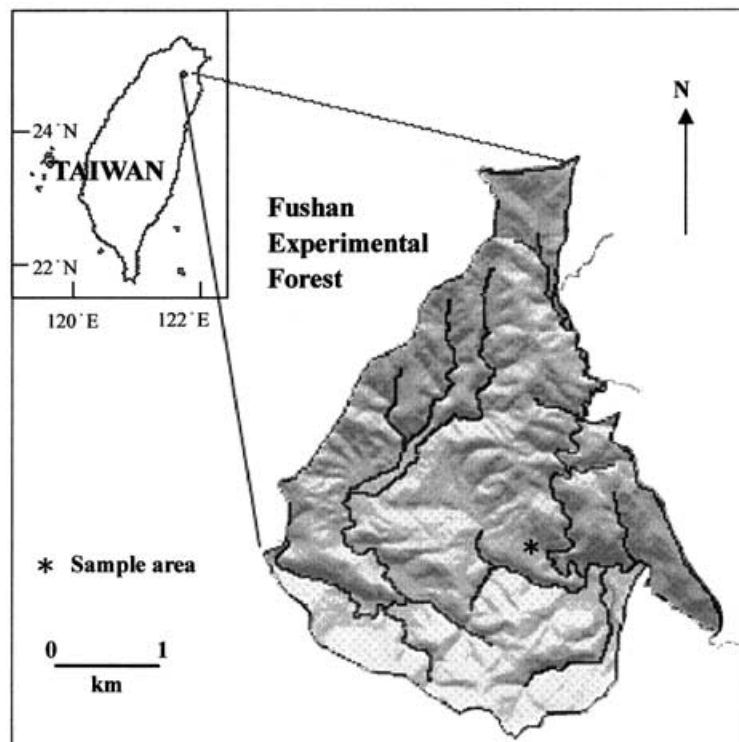


Figure 1. Location of study area (black lines inside boundary are rivers).

Rolfe (Orchidaceae), and *Cephalantheropsis gracilis* (Lindl.) S. Y. Hu (Orchidaceae).

METHODS

Epiphytes located on small trees (dbh < 5 cm) were very small and infrequent, so were disregarded. All 147 trees with dbh > 5 cm in the plot were grouped into five classes by 10-cm increments in dbh. In each class, 4–6 sample trees were selected randomly, with 21 trees in total.

Each phorophyte was subdivided into five sections to indicate epiphyte location on the tree: trunk base up to 3 m above the ground, the trunk, the main branching point, the lower canopy (the primary branch), and the upper canopy (modified from Johansson 1974). For some old trees with the first main branching point lower than 3 m above the ground, all large forks were considered the main branching point (Figure 2). In addition, the main branching point was defined as the portion within 50 cm of the inversion point.

A nail ladder and mountain-climbing equipment were used to remove the entire epiphytic mass from each tree. Epiphytes on twig tips were sampled by cutting off one complete branch and extrapolating to estimate the amounts for

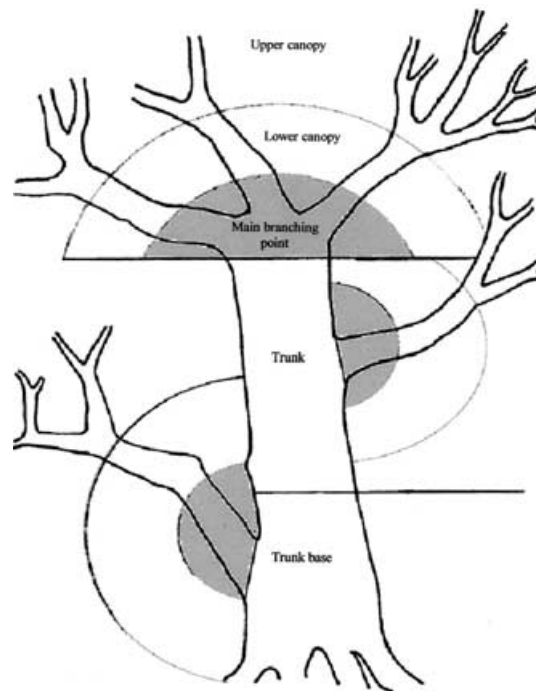


Figure 2. Epiphyte location for old trees having the first main branching points below 3 m from the ground. By considering the characteristics of forks and organic detritus, all large forks were assigned to the main branching point.

all branches of a phorophyte. Because only a small amount of moss was present on twig tips, such an estimation was considered reasonable.

The surface area of the phorophyte was measured by determining the length and diameters both ends of all trunk and branch segments. These segments were assumed to be tapered cylinders, and their surface area calculated accordingly.

Dry weight to substrate surface area ratios for bryophytes were calculated from the mean value of five 200 cm² (10 cm × 20 cm) randomly selected samples in each component of a phorophyte. This was multiplied by the total surface area of each component of the phorophyte obtaining total bryophyte biomass.

Epiphytes were separated into (1) bryophytes, (2) filmy ferns (Hymenophyllaceae), (3) bird's nest ferns, (4) all other ferns, (5) epiphytic vines, (6) hemi-epiphytic vines, (7) flowering plants and (8) accumulated detritus and suspended soil. Flowering plants were divided into roots, stems and leaves. Ferns were divided into root–stems and leaves. The bird's nest ferns were divided into leaves, trapped litter, root–stems, organic substrate and fine roots.

All epiphytic samples were weighed in the field, and taken to the laboratory for dry-weight determination. One random subsample of mixed bryophytes was selected on each tree sampled. Three random subsamples of organs of each

species were oven-dried at 65 °C for 48 h and ground into a size smaller than 0.5 mm for nutrient determination. A sample (20 g) of ground material was then oven-dried at 105 °C for biomass determination.

Subsamples were taken and digested in different ways for nutrient analysis following Page (1982).

(1) Total nitrogen. Subsamples of epiphytes and suspended soil were digested in a sulphate acid mixture with copper sulphate and selenium at 420 °C. Total nitrogen was analysed with an auto-analyser.

(2) Phosphorus, potassium, calcium, magnesium and sodium. Epiphyte samples were burnt to ash at 490 °C. The ash and suspended soil were extracted with acid as described above. Elements were determined by inductive-coupled plasma (ICP).

After the biomass and nutrient content of each subcomponent were determined, they were used to estimate the total epiphytic biomass and nutrient content of each sample tree. Regression analyses were applied to obtain relationships between phorophyte dbh and their epiphytic biomass. The data of three trees were not used because they were partially dead or bordered the forest path. The regression equation then was used to estimate the total epiphytic biomass and nutrient content of the plot.

RESULTS

A total of 115 kg of epiphytic biomass was removed from 18 sampled phorophytes. The dbh of the phorophytes and the epiphytic biomass were highly correlated ($r^2 = 0.87$; $P < 0.05$) (Figure 3). Based on the regression equation and the dbh of the remaining 126 trees in the sample plots, the total epiphytic biomass was estimated to be 403 kg in the sampled plot (1200 m²). The epiphytic biomass for the entire forest was estimated to be 3360 kg ha⁻¹.

The epiphytic biomass constituted less than 2% of the total above-ground biomass (including woody material), but it is equivalent to about 43% of the biomass of total foliage in the ecosystem (Table 1). Green tissues of epiphytes represented 64.2% of the total epiphytic biomass (Table 2), whereas in the phorophytes, photosynthetic tissues constituted 2.1% of the total biomass of the phorophytes.

The epiphytic biomass varied widely depending on location in the phorophyte canopy (Figure 4). Occurrence of epiphytic biomass was 16, 36, 24, 21 and 3% on the trunk foot, trunk, main branching point, lower canopy and outer canopy respectively. On the main branching point and in the lower canopy, about 60–70% of the total epiphytic biomass consisted of bryophyte mats. Ferns, especially *Pyrrhosia lingua* (Thunb.) Farw. (Polypodiaceae), were most abundant (40%) in the outer canopy. Bird's nest ferns occurred in the lower levels of the phorophyte canopies, but were most abundant (25%) on the trunk. Epiphytic vines were evenly distributed in each area of the phorophyte canopy, comprising about 10% of the epiphytic biomass. Hemi-epiphytic vines were most abundant (30%) in the outer canopy.

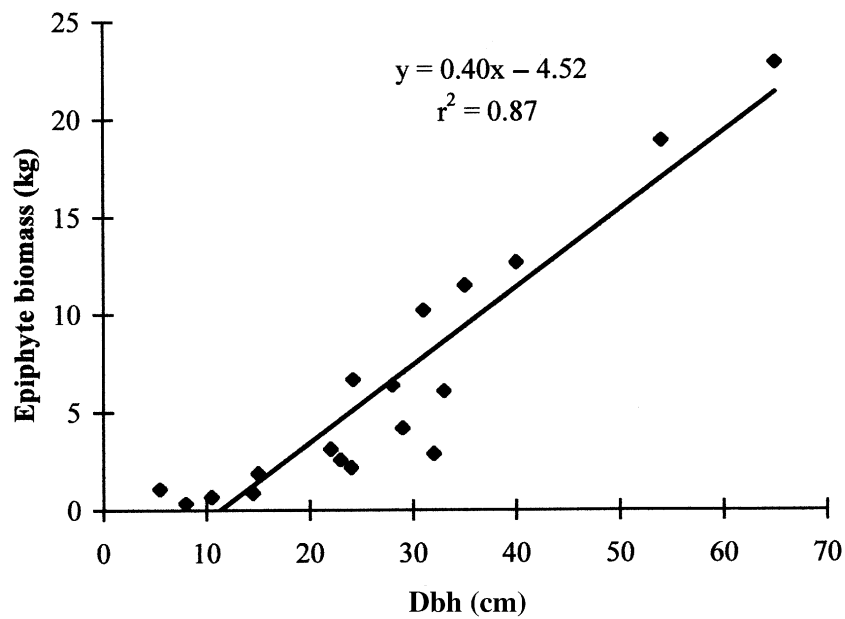


Figure 3. Relationship between total epiphyte biomass and dbh of 128 trees at Fushan in north-eastern Taiwan.

Table 1. Proportion of total biomass in the Fushan subtropical forest comprising epiphytes. The epiphytic biomass for the entire forest was estimated to be 3360 kg ha⁻¹. Data of biomass other than epiphytes are from Lin *et al.* (1994).

Forest component	Biomass (t ha ⁻¹)	Epiphyte biomass (%)
Total above-ground	290	1.2
Tree	271	1.2
Above-ground foliage	7.8	43

Average nutrient concentrations of epiphytes varied according to life form and organ (Table 3). Nutrient concentrations of green tissues, including phorophyte foliage, were far higher than those of woody boles and branches of the phorophytes. Concentrations of N, P and Mg in the green tissues of the epiphytes were similar to those of the phorophyte foliage; however, Ca and K concentrations of epiphytic green tissues generally far exceeded those of phorophyte foliage.

The nutrient capital (in kg ha⁻¹) of epiphytes in the entire forest was estimated by multiplying the nutrient concentrations by the epiphytic biomass: N = 42.4, P = 1.9, Mg = 5.5, Na = 1.3, Ca = 14.5 and K = 28.9 (Table 4). Although the nutrients contained in the epiphytes comprised less than 5% of those in the total above-ground biomass (including woody material), the mineral capital contained in epiphytes constituted 21–43% of that in the above-ground non-woody foliage.

Table 2. Composition of epiphytic biomass removed from 18 trees at Fushan in north-eastern Taiwan.

Plant material	Biomass (kg)	Proportion of total epiphytic biomass (%)
Living		
Green		
Leaves of vascular epiphyte	14.3	12.4
Bryophyte	59.6	51.8
Total green	73.8	64.2
Non-green		
Roots–stems of ferns	3.3	2.9
Roots of flowering plants	0.8	0.7
Stems of flowering plants	25.2	21.9
Total non-green	29.3	25.5
Total living	103.2	89.7
Dead		
Organic substrates of bird's-nest ferns	9.8	8.5
Litter collected by bird's-nest ferns	2.1	1.8
Total dead	11.8	10.3
Total epiphyte	115.0	100

DISCUSSION

In previous studies, the epiphytic biomass for the entire ecosystem was roughly estimated based on data collected for only one to three representative trees (Hofstede *et al.* 1993, Nadkarni 1984*a, b*). In contrast, we determined the epiphytic biomass for trees. Furthermore, our sampled trees included every class of dbh; thus, we could examine the relationship between epiphyte loads and the dbh of phorophyte.

The data best fitted a linear regression with $r^2 = 0.87$, and the estimated epiphytic biomass of our sample plot is 403 kg. If the mean epiphytic biomass of each dbh class (5–10, 10–20, 20–30, 30–40 and > 40 cm) was used separately to estimate epiphytic biomass by multiplying the corresponding biomass for each class with the number of trees in each class, the result was 402.7 kg, which is close to that estimated with the linear regression. It appears that phorophyte dbh is a good predictor of epiphytic biomass in this forest.

A wide range of epiphytic biomass has been reported in temperate and tropical ecosystems in past studies (Table 5). For example, the epiphytic biomass in a Colombian upper montane rain forest (Hofstede *et al.* 1993) reached a peak of 44 t ha⁻¹, which is almost 10 times that of the Fushan forest. At 3700 m elevation in the Central Cordillera of Colombia (annual rainfall 1250 mm, temperature 2–6 °C, no dry season), lower evaporative demand and decomposition rates resulting from cool temperatures probably contribute to the greater development of epiphytic biomass of this forest. The relatively old-growth phorophytes in Colombia (424 trees ha⁻¹; dbh > 45 cm) have sufficient time to build up substantial epiphytic biomass. There are fewer large trees (50 trees ha⁻¹, dbh > 45 cm; 1225 trees ha⁻¹, dbh > 10 cm) in the Fushan forest. Additionally, heavier rainfall (3800 mm y⁻¹) and frequent typhoons probably deplete

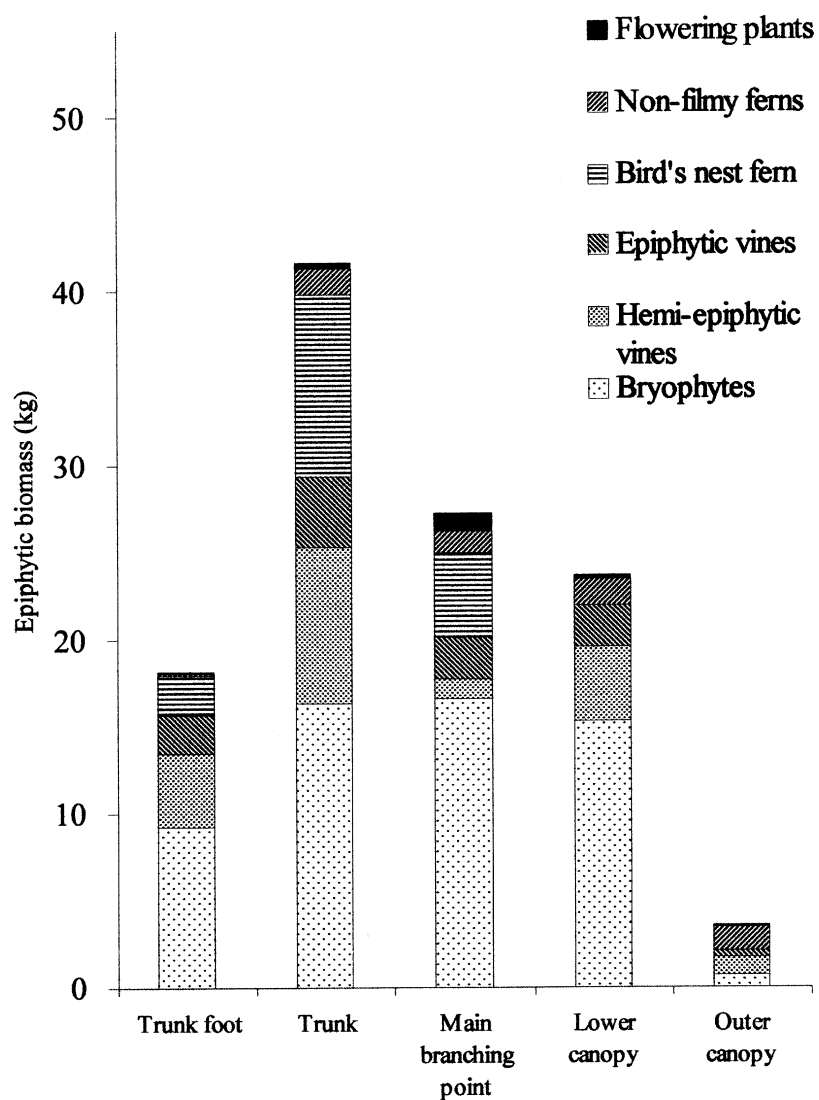


Figure 4. Distribution and composition of epiphytic biomass removed from 18 trees at Fushan in north-eastern Taiwan. Total epiphytic biomass is 115 kg.

throughfall nutrient availability and dislodge suspended organic matter of the canopy, which would reduce the accumulation of epiphytic biomass at Fushan.

Nevertheless, the estimate of 3.4 t ha^{-1} for the epiphytic biomass in the moist subtropical broadleaved evergreen forest of Fushan is within the range of those for tropical rain forests. The most important regional environmental determinant of epiphyte success, however, is less closely linked to the total annual rainfall than to rainfall distribution throughout the year (Gentry & Dodson 1987). The warm and continuously humid environmental conditions at Fushan are

Table 3. Nutrient concentrations of epiphytes (mean \pm SD) (mg g^{-1}). n is number of epiphyte species, except for bryophytes and suspended soil which are replicated subsamples. Data of phorophytes are from Lin *et al.* (1996).

	Total N	P	Mg	Na	Ca	K	n
Epiphyte							
Bryophyte	18.6 \pm 2.60	1.07 \pm 0.26	1.08 \pm 0.38	0.16 \pm 0.05	5.41 \pm 3.03	20.1 \pm 3.44	21
Woody epiphyte							2
leaf	10.9 \pm 3.10	0.66 \pm 0.18	3.95 \pm 3.18	0.50 \pm 0.14	7.74 \pm 0.20	8.52 \pm 6.12	
root	6.80 \pm 2.80	0.51 \pm 0.20	3.77 \pm 3.00	0.34 \pm 0.31	4.80 \pm 1.62	16.2 \pm 2.99	
stem	6.20 \pm 2.10	0.17 \pm 0.23	0.33 \pm 0.42	0.13 \pm 0.15	1.76 \pm 2.46	1.92 \pm 2.51	
Hemi-epiphyte vine							6
leaf	23.8 \pm 2.20	1.31 \pm 0.49	4.47 \pm 0.99	0.64 \pm 0.30	9.41 \pm 3.37	21.9 \pm 10.9	
stem	10.4 \pm 4.10	0.49 \pm 0.28	1.09 \pm 0.52	0.32 \pm 0.27	5.31 \pm 4.08	7.70 \pm 3.31	
Epiphytic vine							4
leaf	8.50 \pm 0.80	1.13 \pm 0.52	9.39 \pm 6.39	1.45 \pm 1.08	16.5 \pm 13.4	30.2 \pm 9.44	
stem	16.1 \pm 9.00	0.41 \pm 0.40	1.71 \pm 1.67	0.24 \pm 0.23	5.71 \pm 5.86	7.03 \pm 6.06	
Bird's nest fern							3
leaf	17.2 \pm 5.90	0.68 \pm 0.26	3.83 \pm 1.26	1.03 \pm 0.65	12.9 \pm 7.07	29.8 \pm 12.2	
fine roots	18.9 \pm 2.60	0.96 \pm 0.18	1.25 \pm 1.06	0.23 \pm 0.27	3.08 \pm 1.36	1.83 \pm 1.47	
substrates	23.1 \pm 3.00	0.23 \pm 0.25	0.44 \pm 0.20	0.08 \pm 0.05	1.45 \pm 0.90	0.68 \pm 0.41	
litter trapped	16.7 \pm 2.40	0.82 \pm 0.17	2.10 \pm 0.45	0.23 \pm 0.09	9.69 \pm 2.75	2.63 \pm 0.89	
root-stem	16.3 \pm 4.30	0.72 \pm 0.39	2.35 \pm 1.28	0.81 \pm 0.52	5.63 \pm 3.23	9.36 \pm 7.42	
Filmy fern	19.7 \pm 3.20	0.80 \pm 0.19	1.25 \pm 0.78	0.16 \pm 0.01	2.38 \pm 0.41	2.63 \pm 2.08	3
Non-filmy fern							11
leaf	12.3 \pm 3.90	0.66 \pm 0.56	2.33 \pm 1.93	0.31 \pm 0.25	2.86 \pm 2.43	12.4 \pm 10.5	
root-stem	9.00 \pm 1.60	0.40 \pm 0.34	0.97 \pm 0.82	0.13 \pm 0.10	1.90 \pm 1.82	3.30 \pm 2.74	
Orchid							4
leaf	14.8	1.10	2.92	0.32	8.98	13.0	
stem	6.90	0.53	1.86	1.18	3.05	14.1	
Suspended soil	18.7 \pm 2.30	0.82 \pm 0.09	0.73 \pm 0.33	0.13 \pm <0.01	3.61 \pm 1.23	1.20 \pm 0.30	3
Phorophyte							
Bole	1.66	0.32	0.55		1.73	1.58	
Small branches	4.71	0.35	0.67		2.33	3.28	
Leaves	24.2	1.37	3.95		5.43	12.8	

Table 4. Nutrient capital (kg ha^{-1}) of epiphytes, total above-ground biomass and total above-ground foliage. Proportions of epiphyte nutrient capital are presented in parentheses. Data other than for epiphytes are from Lin *et al.* (1996).

Forest component	N	P	K	Ca	Mg
Epiphyte	42.4	1.9	28.8	14.5	5.5
Total above-ground biomass	951 (0.04)	66.6 (0.03)	616 (0.05)	816 (0.02)	196 (0.03)
Total above-ground foliage	146 (0.29)	9.0 (0.21)	69.7 (0.41)	33.9 (0.43)	19.2 (0.29)

most likely responsible for the great diversity and biomass of epiphytes at Fushan.

Comparison of epiphytic biomass to phorophyte foliar biomass reveals a different picture from the comparison to total above-ground biomass. The data for above-ground biomass are from Lin *et al.* (1994). They set up a 20-m \times 20-m plot at Fushan. All trees in the plot and all shrubs and herbs in the four 5-m \times 5-m subplots were removed and weighed. Unlike the long life of the woody

Table 5. Biomass of epiphytes in various ecosystems.

Ecosystem/location	Epiphytic biomass (t ha ⁻¹)	Source
Temperate		
Moist coniferous forest Olympic National Park, USA	6.9	Nadkarni (1984a)
Subtropical		
Dry forest Guanica, Puerto Rico	0.14	Murphy & Lugo (1986)
Moist broadleaved forest Fushan, Taiwan	3.4	This study
Tropical		
Lower montane rain forest Panama	1.4	Golley <i>et al.</i> (1971)
Upper montane rain forest New Guinea	5.2	Edwards & Grubb (1977)
Submontane forest Uluguru, Tanzania	2.1	Pócs (1980)
Elfin cloud forest Monteverde, Costa Rica	4.7	Nadkarni (1984b)
Upper montane rain forest Colombia	44	Hofstede <i>et al.</i> (1993)

components of phorophytes, the epiphytic biomass represents only several years of growth (Matelson *et al.* 1993). Live epiphytes fall to the forest floor because they are dislodged by wind or animals, or because they have poorly developed root systems or branches break. Other studies have indicated that epiphytes can contribute up to 8% of the total deposition of biomass and nutrients in fine litter in tropical montane cloud forests (Nadkarni & Matelson 1992). Fallen epiphytes finally die and decompose, releasing their nutrients.

In this forest, 90% of the epiphytic biomass consists of living organisms, only 10% is non-living (Table 2). This distinguishes this forest system from that of the tropical montane rain forest, where humus deposition in the canopy can comprise 26–63% of the epiphytic biomass (Hofstede *et al.* 1993, Nadkarni 1984b, Pócs 1980). The thin layer of organic matter found on phorophytes in the Fushan forest may be the result of heavy rainfall and a rapid decomposition rate. In total, green tissue comprises 64% of the epiphytic biomass, which is close to 15% of the total above-ground foliage. Thus, the epiphytes greatly increase the primary productivity of this ecosystem.

The vertical distribution of epiphytic biomass can reveal microhabitats at various locations on the phorophytes (Figure 4). Epiphytes that prefer the upper portions of their host tree canopies may have higher light requirements than those in the lower parts of the canopies, or they may be more tolerant of lower humidity, and/or greater degree of drought stress. The ecophysiology of such epiphytes requires further investigation.

Nutrient concentrations of the epiphytes are much higher than those of the woody component of trees, and are similar to those of the tree leaves. Because nutrient sources are limited in the arboreal environment, some epiphytes

possess specialized absorptive features which make them efficient at intercepting airborne nutrients (Benzing 1990). Epiphytes also increase the surface area of phorophytes for interception of water and nutrients during precipitation events.

The nutrient pools within canopy epiphytes in this study represented 21–43% of those in the above-ground foliage. In an upper montane rain forest in Colombia (Hofstede *et al.* 1993), nutrient capital located in the epiphytic load even reached 20–49% of total above-ground nutrients. Thus, epiphytes can expand both the nutrient storage and absorption capacity of tropical and subtropical forest ecosystems.

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