Ecology, 72(6), 1991, pp. 2071–2082

FINE LITTER DYNAMICS WITHIN THE TREE CANOPY OF A TROPICAL CLOUD FOREST[1]

NALINI M. NADKARNI AND TERI J. MATELSON[2]
The Marie Selby Botanical Gardens, 811 South Palm Avenue, Sarasota, Florida 34236 USA

Abstract. Fine litter deposition and decomposition within the upper tree canopy was measured in a neotropical cloud forest to determine the potential nutrient input to epiphyte communities from intercepted tree litterfall. A comparable amount of fine litter passed through the canopy (752 $g \cdot m^{-2} \cdot yr^{-1}$) as arrived on the forest floor (820 $g \cdot m^{-2} \cdot yr^{-1}$), but $<1\%$ of the biomass and nutrients of this "gross litterfall" was retained within the upper tree canopy. The standing crop of litter in the canopy (≈ 170 g/m^2 of branch surface area, 8.8 g/m^2 of ground area) is equivalent to only 1% of the standing crop of litter on the forest floor. Measurements of leaf litter attrition (whole leaf loss from branches due to wind and other disturbances) with marked leaves documented that 70% of leaves deposited on branches are lost in the first 2 wk and nearly all are gone in 16 wk. Certain branch characteristics (branch angle, number of epiphyte stems and clumps) appear to affect the amount of litter retained at particular microsites. Decomposition of tethered, dead leaves within the canopy over a 12-mo period was half that of leaves on the forest floor (canopy litter turnover time = 2.8 yr). Assuming that litter accumulation within the canopy is at steady state, the biomass of fine litter retained and decomposed within the canopy was calculated as only 2.0 $g \cdot m^{-2} \cdot yr^{-1}$ and <0.02 $g \cdot m^{-2} \cdot yr^{-1}$ for all nutrients. Nutrient replenishment of epiphyte communities appears to be decoupled from the litterfall pathway, as input from litterfall retained within the canopy is small relative to epiphyte productivity and nutrient requirements reported in other studies.

Key words: canopy; decomposition; detritus; epiphytes; litterfall; Monteverde, Costa Rica; nutrient cycling; tropical cloud forest.

INTRODUCTION

In many tropical and temperate forest canopies epiphytic plants comprise a considerable portion of total aboveground biomass and plant species diversity (Madison 1977, Pócs 1980, Nadkarni 1984, 1985, Gentry and Dodson 1987). Because epiphytic plants have no direct vascular connection to the bank of nutrients in the forest floor, they must rely upon morphological and physiological attributes such as litter-impounding pools, foliar trichomes, insectivory, myrmecochory, and poikilohydric foliage to acquire and conserve nutrients in an environment that may deliver nutrients only sporadically and in dilute concentrations (Janzen 1974, Benzing and Seeman 1978, Huxley 1980, Benzing 1981, 1983, Nadkarni 1981). Some specialized epiphytes gain nutrients exclusively from precipitation and dry deposition (Sheline et al. 1976, Benzing 1981, Benzing and Pridgeon 1983), but many epiphytes have no apparent specialized adaptations for directly obtaining nutrients from atmospheric sources. These epiphytes, such as woody shrubs in the Ericaceae, have well-developed root systems, which penetrate the dead organic matter and "crown humus" (Jenik 1971) that accumulates as mats on upper branch surfaces.

[1] Manuscript received 17 November 1989; revised 18 November 1990; accepted 14 December 1990; final verson received 4 February 1991.

[2] Present address: Monteverde, Apartado 10165, San José 1000, Costa Rica.

Potential sources of nutrients for epiphytes include an array of both autochthonous and allochthonous sources (Table 1). The relative contribution of each of these sources to tropical epiphyte communities is unknown. From an ecosystem standpoint, it is important to distinguish between these two source types in forests where nutrient availability may limit productivity of the overall system (Grubb 1977, Vitousek 1984). If epiphytes were to obtain all of their nutrients from autochthonous sources, then they would simply be diverting nutrients from the tree-to-ground flux pathway for some length of time; they would not increase the total pool, but merely change the form or compartment in which nutrients are stored. Alternatively, if they were to sequester nutrients from outside the system, this would potentially increase the total nutrient input to the ecosystem in addition to altering the form and location of these nutrients.

In this paper, we quantify the nutrient dynamics of one potential autochthonous source of nutrients to the epiphyte community, the abscised plant litter that is intercepted within the upper tree canopy by inner branches and their epiphytes. Other than notations on the presence of dead leaf litter held as "suspended" or "arboreal" leaf litter in tropical forests with respect to bird foraging (e.g., Remsen and Parker 1984), we found no published measurements on the amounts, characteristics, or dynamics of suspended leaf litter within tree crowns. Plant litterfall is one of the most important

components of the biogeochemical cycle of forest ecosystems and is the most frequently measured transfer in studies of nutrient cycling (Proctor 1984, Vitousek 1984, Vitousek and Sanford 1986). Fine litter dynamics within the canopy may be critical for epiphyte productivity and may differ from litter dynamics on the forest floor for three reasons. First, canopy litter may be ephemeral, as it can be removed from branches by within-canopy disturbances such as wind, rain, and arboreal animal activities. In contrast to fallen leaves on the forest floor, which can shift their position on the ground with only minor consequences for plants rooted in soil (Orndorff and Lang 1981, Welbourn et al. 1981), movement of dead leaves in the canopy may remove a potentially substantial contribution to epiphyte nutrition. Second, leaf litter in the canopy may be deposited in smaller amounts than is leaf litter in the forest floor due to lack of input from subcanopy and understory vegetation. Third, decomposition rates of litter deposited and retained within the canopy may differ from litter on the forest floor due to microclimate and substrate differences between the canopy and forest floor, as well as differences in community structure and density of macroinvertebrate detritivores and microbial decomposers.

We quantified the biomass and nutrient dynamics of fine litter on interior branches of tree crowns in a neotropical cloud forest where live and dead epiphyte biomass is high. In this paper, we report on (1) the phenology, components, and biomass of tree and epiphyte fine litter (foliage, small stems, reproductive parts, bryophytes, and miscellaneous) that falls within the canopy; (2) the biomass and nutrient loss from fine litter that becomes potentially available to branch-dwelling epiphytes, calculated from direct measurements of fine litter standing crop, from an index of fine litter attrition with marked leaves, and from rates of fine litter decomposition; and (3) structural characteristics of branches than may affect microsite variation in fine litter capture and retention.

Materials and Methods

Study site

Field research was conducted in the Monteverde Cloud Forest Reserve (MVCFR), in west-central Costa Rica (10°18′ N, 84°48′ W), from June 1987 to June 1990. The study area is in tropical lower montane wet forest (1550 m elevation) in the biotic community recognized by Lawton and Dryer (1980) as Leeward Cove Forest, with a broken canopy 12–25 m in height and a density of ≈150 trees/ha (>10 cm dbh). The understory is fairly open, with a poorly developed herbaceous layer. Many treefalls and gaps in various stages of recovery are evident.

The climatic regime is strongly dominated by the trade winds, which produce moisture-bearing clouds throughout the year. During the April–November rainy season the trade winds lessen in velocity but still contribute substantial moisture to the Monteverde area. Convectional thunderstorms bring almost daily rain during May to October. Measured annual rainfall is 2500 mm/yr (33-yr average), but total deposition is undoubtedly much higher due to the input of mist-bearing winds (Hartshorn 1983). Only few quantitative wind data for the region are available (Lawton 1980; Instituto Meteorológico, San José, Costa Rica), and these are for areas at different exposures and elevations than the research plot. We estimate from visual observation and measurements nearby that windspeed above the canopy over our study area during the study period ranged between ≈5 and 50 km/h, and during storms exceeded 100 km/h.

Table 1. Potential sources of nutrient input to epiphyte communities in forest ecosystems.

Autochthonous sources	Allochthonous sources
I. Soil-rooted phytomass	I. Atmospheric
A. intercepted litterfall	1. wet deposition
B. bark decomposition	2. dry deposition
C. leachate of live foliage	3. gaseous input (including nitrogen fixation)
II. Animal defecation and death	

The epiphyte community of the Monteverde Cloud Forest has been described by Nadkarni (1986). Branch surfaces in the crown interior of nearly all mature trees support thick mats of epiphytes (bryophytes, herbs, woody shrubs, and hemi-epiphytes), and interwoven root–humus mats up to 25 cm thick (Fig. 1). The greatest accumulations of humus are found on junctions of large branches. Outer branches and branch tips are partially to completely covered with bryophytes and small herbaceous plants, with very little or no accumulated humus. Relative to the forest floor, the upper tree canopy experiences more wind (Lawton 1980), more frequent mist deposition, higher air temperature maxima, and more frequent wetting/drying cycles (N. M. Nadkarni and T. J. Matelson, *unpublished data*).

In April 1987, we established a 2-ha intensive research plot in which we measured tree diameter at breast height (dbh) and assessed "climbability" and epiphyte cover of mature trees. We assigned all trees over 10 cm dbh to an epiphyte cover class using a subjective quartile index (1 = 0–25% cover, 4 = 75–100% cover, including vascular and nonvascular epiphytes) and to a "climbability" class of 1–4 (class 3 and 4 trees were safely climbable with our methods). Of these, we selected a random subsample of the largest size class of trees (dbh > 45 cm) in the two highest epiphyte cover and climbability classes for sampling, which consisted of 14 trees in 9 genera of the most common families of trees in this forest (Lawton and Dryer 1980) (Table 2). Although the number of trees we sampled was small (8% of trees in the study site), we have climbed and measured in ≈30 other trees of

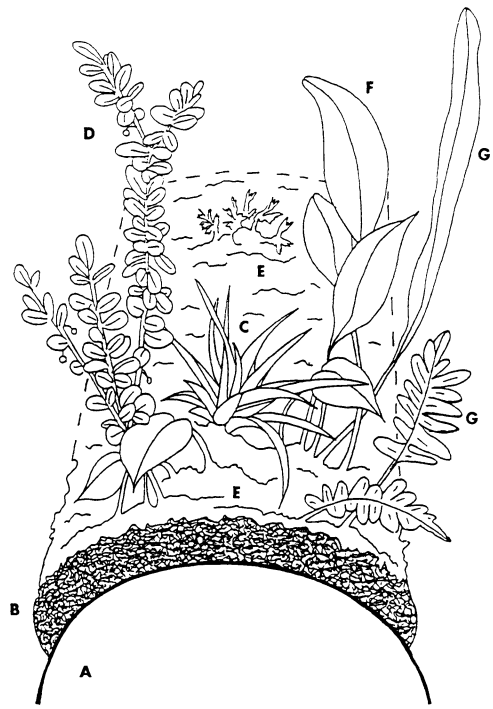

FIG. 1. Schematic of typical epiphyte mat on branch interior of mature trees in the Monteverde Cloud Forest study site. A = branch cross section, B = accumulated dead organic matter and crown humus, C = tank bromeliad, D = woody ericaceous shrub, E = filmy ferns, F = herbaceous orchid, G = fern frond.

the same size class in the study area during the course of our research, and have observed similar patterns. Trees were permanently rigged with mountain-climbing equipment, following Perry (1978) and Nadkarni (1988).

General approach

The standard method for quantifying fine litter input to the forest floor is to measure fallen abscised material with traps (buckets or boxes with screens), which are regularly collected at fairly short intervals. Collected materials are dried, weighed, analyzed for nutrient content, and extrapolated to an area basis. When considering litter dynamics in the canopy, however, collectors within tree crowns are useful only to measure "gross fine litterfall," the amount of litter falling through the canopy, as such collectors would greatly overestimate "net fine litterfall," the amount of litter that would naturally remain there long enough to potentially contribute nutrients to epiphytes through leaching and/or mineralization. The difference between gross and net fine litterfall in the canopy is due to two sources of loss not encountered in forest floor litterfall studies: (a) loss of litter as it passes through the canopy and does not land on branches at all, and (b) loss of litter that has been deposited on branches and is subsequently removed by wind or other canopy disturbances. In addition, measurement of canopy litterfall in collectors can be problematic because of high winds and potential loss of liter from them. Therefore, the amount of fine litterfall accumulated in canopy collectors is not analogous to material accumulated in forest floor collectors, and litterfall input to canopy communities cannot be measured directly. We used canopy buckets, corrected for wind loss with marked leaves, to estimate gross fine litterfall.

TABLE 2. Characteristics and sampling regime of sample trees used in the study. GL = gross fine litter collection in buckets; SL = standing crop of branch litter; KA = leaf attrition from canopy disturbance; KD = tethered litterbag decomposition.

Tree taxon	dbh (cm)	Measurements made			
		GL	SL	KA	KD
Ficus tuerckheimii	238.0	*	*	*	*
Ficus tuerckheimii	192.3				*
Ficus yoponensis	184.5				*
Ocotea tonduzii	100.0				*
Ocotea tonduzii	111.0		*	*	
Ocotea tonduzii	125.0		*	*	
Ocotea tonduzii	130.0		*		
Nectandra sp.	119.0		*		
Beilschmidea sp.	113.5	*			*
Pouteria sp.	70.1	*	*	*	
Meliosma ideopoda	92.0		*	*	
Dussia macrophyllata	112.5		*	*	
Matayba sp.	60.5		*	*	
Quercus sp.	121.0		*		

In an ecosystem that is in steady state, fine litter input to the forest floor (I) has frequently been calculated indirectly by measuring the fine litter standing crop (X_L) and its decomposition rate (the annual fractional mass loss rate, K), and estimating I as X_L times K (e.g., Edwards 1977, modified from Olson 1963). The assumption of a steady-state situation is not unreasonable on large branches in the crown interior of this old-growth forest. We calculated canopy net fine litterfall indirectly, using measurements of standing crop of fine litter (termed "canopy standing litter, X_{CL}") on branch segments and rates of litter loss as described below.

In the canopy, intercepted litter loss is made up of two components: (a) "attrition" of leaves due to within-canopy disturbances (wind, rain, animal movements), and (b) loss of mass and nutrients of leaves remaining on branch surfaces due to decomposition. The amount of nutrients released from within-canopy litter that is potentially available to the epiphyte community is that which is deposited on branches and which remains in the canopy long enough to become available by mineralization and/or by leaching. We calculated an index of leaf attrition (L_a) experimentally, by measuring rates of disappearance of marked leaves that we placed on branch segments. We measured leaf

TABLE 3. Characteristics of branch segments used for collection of: (a) canopy standing litter, and (b) index of leaf attrition rate.

Characteristic	Mean	SE	Maximum	Minimum
a) Canopy standing litter				
Length (cm)	52.0	2.5	120.0	20.0
Width (cm)	30.8	1.8	101.0	15.0
Angle (°)	25	2.5	75	0
Height of epiphytes (cm)	18.7	1.5	60.0	4.0
No. of epiphyte stems (per dm^2)	2.1	0.2	10.1	0.6
No. of epiphyte clumps (per dm^2)	0.4	0.04	3.2	0
b) Index of leaf attrition rate				
Length (cm)	56.2	3.0	120.0	26.0
Width (cm)	29.9	2.1	70.0	11.0
Angle (°)	25	2.9	75	0
Height of epiphytes (cm)	17.9	1.9	60.0	0
No. of epiphyte stems (per dm^2)	1.7	0.2	7.1	0
No. of epiphyte clumps (per dm^2)	0.2	0.02	0.6	0

decomposition (L_d) directly, by measuring changes in biomass and nutrient content of abscised litter in tethered litterbags within the canopy at intervals over 1 yr (equivalent to the annual fractional mass loss, K_d, the term often used as an index of decomposition rate). These two rates were multiplied to provide an estimated rate of biomass and nutrient flux from litter within the canopy. This rate was then multiplied by the biomass of canopy standing litter, and the flux was summed for each time interval for an estimate of net potential input to canopy communities. A summary of this approach is presented below.

Based on the assumption that inner branch communities of the canopy of this mature forest are in a steady state:

$$\text{annual potential fine litter input} = [(X_{CL}) \times (L_a \times L_d)]$$

over a 12-mo period, where X_{CL} = biomass of canopy standing litter, L_a = leaf attrition rate, and L_d = seasonal leaf decomposition rate.

This should be considered as potential, rather than actual input to epiphyte communities, as some portion of this flux could be taken up by microorganisms, immobilized on exchange sites, or be transported to the forest floor via throughfall or stemflow.

Phenology and composition of gross fine litterfall

Gross fine litterfall was collected within the canopy with plastic buckets (55 cm tall, 40 cm diameter) tied on top of large branches in each of three of the sample trees (15 collectors total) at heights ranging between 15 and 24 m above the forest floor. Collectors were located in the crown interior, within 3 m from the central trunk, below the main overarching outer "dome" of leaves of the upper tree crown. Holes were punched in the bucket bottoms and the bottoms covered with 2-mm nylon mesh to retain fine litter but to allow water to drain. Accumulated litter was collected at 2–3 wk intervals from 20 June 1987 to 9 May 1988, and separated into the following components: leaves, stems, reproductive parts, bryophytes, and miscellaneous. All separated samples were oven-dried at ≈60°C for 24 h and weighted. For each component and each collection interval, samples were bulked into three composites, and subsamples were analyzed for nutrients.

Wind in the canopy could blow leaves from canopy buckets, which would result in an underestimate of gross litterfall. We monitored loss of leaves from each bucket by placing 10 marked leaves in each bucket and recording how many remained after 14 d. There is a high variability of leaf size, mass, and shape in this forest, so we used leaves of various species that fell within the midrange of size and mass (≈5–10 cm in length, 2–4 g dry mass). The time period for these measurements (1 April 9–May 1988) was during the transition from the dry to the wet season, and encompassed a range of windy and windless days.

Biomass and composition of standing fine litter

Standing crop of fine litter within the canopy was measured by sampling the fine litter resting on branches in crown interiors at two times during the study period. In May 1988, we collected accumulated fine litter on 29 segments of accessible branches within 3 m of the central trunk in seven of the sample trees (Table 2) for a general estimate of within-canopy standing crop. The branch segments encompassed the variation in branch angle, branch width, and epiphyte cover that exists within inner tree crowns.

To investigate specific effects of substrate size and characteristics on litter accumulation, we measured fine litter on 69 other segments in 11 of the sample trees in May 1990. We recorded angle from horizontal, branch width and length, height of epiphytic plants, number of stems and number of clumps of epiphytes (Table 3a). Standing litter was separated into compo-

nents as for gross litter, except that leaves were subdivided into three categories: epiphyte leaves, tree leaves, and unknown leaves. The ratio of epiphytic and tree leaves in the unknown leaf category was assumed to be the same ratio as for the identified leaves. We multiplied this ratio by the biomass of the unknown leaf category and allocated the calculated amounts to the epiphyte and tree leaf categories. Samples were oven-dried and weighed separately for each branch segment. Material was bulked by tree and subsamples analyzed for nutrients (1988 samples only). The effects of branch characteristics on biomass of canopy standing crop were tested with simple multiple regression with the SYSTAT statistical package (SYSTAT 1984)

Leaf litter attrition (L_a)

To determine an overall index for the rate at which fine litter is removed from branches by wind and animal activity, we selected 15 branch segments that encompassed the variation within tree crowns from seven trees (Table 2). From 18 June 1988 to 10 January 1989, 10 marked leaves were placed on each branch segment, and the number remaining after 14-, 33-, and 71-d intervals was counted. A total of 135 collections (1350 leaves) was made. Because of the patterns of leaf loss we observed, we calculated rates of loss for 0–2 and 2–10 wk separately by deriving regressions of the percentage of marked leaves remaining on the branch plots.

To investigate the effects of particular substrate characteristics on the rate of leaf attrition, we performed similar experiments in May 1990, on 35 branch segments in 8 trees. We measured length, width, angle, number of stems, number of clumps, and height of epiphytes (Table 3b) of the segments. After 31 d, the number of marked leaves remaining was recorded. The effects of these branch characteristics were tested with multiple regression as for canopy standing litter.

Leaf litter decomposition (L_d)

Litter decomposition rates were measured for abscised leaves enclosed in mesh bags that were tethered to the tops of branches and collected at 1–3 mo intervals for 12 mo. We used the naturally occurring litterfall that was collected in ground-level buckets at the study site between 28 May and 8 September 1987. It was air-dried and bulked, and 5–7 g weighed samples of leaf litter were placed in polyester mesh bags (15 × 15 cm, 2 mm mesh). Ten replicates of the litterbag contents were oven-dried and weighed for dry mass calculations and determination of original litter nutrient content. Litterbags were secured with wire on branches 15–23 m above the forest floor in four of the sample trees (Table 2). Seven replicates were retrieved at each collection time. Litterbags were transported to the laboratory and gently sprayed with water to remove accumulated particulates; any roots that had grown into the bag were removed. The remaining litter was oven-dried at 60°C for 24 h and weighed. For each collection, the remaining litter was bulked into three composite samples for nutrient analysis.

For each litterbag sample, the nutrient concentrations of the material remaining at the time of collection were multiplied by the biomass of the remaining material divided by the original litter mass. This product was expressed as a percent of the original nutrient content of each litterbag. The mean percentage remaining was calculated from the seven replicates for each collection period. A linear regression was performed using the natural logarithm of the mean dry mass remaining over time to calculate K, the annual fractional loss rate, following the formula:

$$\ln(X_t/X_0) = -K_d t,$$

where x_t and x_0 are the mass remaining at time t and time 0, respectively (Olson 1963).

Nutrient analysis

Subsamples of dried standing litter and fine litter were ground in a Wiley Mill to pass a 425-μm mesh screen. Total elemental composition of samples was determined by a modified Kjeldahl wet digestion procedure. The digestion system consisted of a mixture of sulfuric acid with hydrogen peroxide, selenium as a catalyst, and lithium sulfate for temperature elevation (Parkinson and Allen 1975). A commercial block digester (Technicon BD-40) was employed, and samples were maintained at 340°C for 2 h after clearing (Nelson and Sommers 1980). Samples ($\approx$300 mg) were digested in triplicate. Solutions of organic N (urea, niacinamide) and organic P (phytic acid) compounds were used as standards throughout the study. A modified indophenol blue colorimetric method (Scheiner 1976) and a molybdenum blue procedure (Watanabe and Olsen 1965) were used to determine ammonium and phosphate in digests. Cations were analyzed using the same digested solutions on a Varian AA6 atomic absorption spectrophotometer.

Results

Gross fine litterfall

The fine litter loss from collectors due to wind was highly variable, with a mean of 74% of marked leaves retained during 2-wk intervals (Fig. 2). Because these measurements were made under a variety of wind conditions, we assumed that litter loss from buckets would show similar trends throughout the year. We also assumed the same loss rate would apply for all fine litter components, and corrected the percent of litter that would be lost due to wind for each bucket using that particular collector's loss rate.

Total gross fine litterfall falling through the canopy was 752 $\pm$ 61.2 g·m^{-2}·yr^{-1} (mean $\pm$ SE, 229 collections total), an amount comparable to fine litterfall deposited on the forest floor in this forest during the same time period (820 $\pm$ 36.2 g·m^{-2}·yr^{-1}, N. M. Nadkarni and

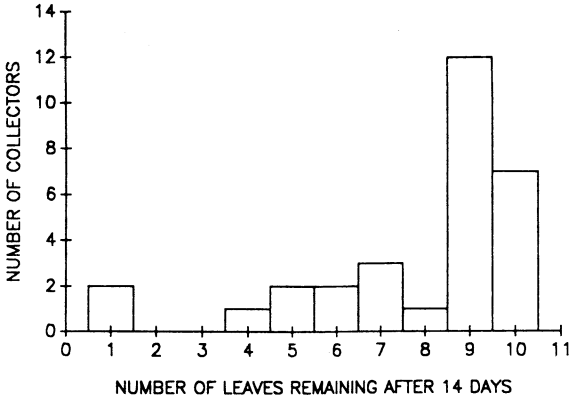

FIG. 2. Histogram of loss of marked leaves in canopy litterfall collectors from 1 April to 9 May 1988, expressed as number of leaves remaining (of 10 marked leaves placed in buckets) after 14 d. This yields the probability of loss used to correct gross litterfall estimations from canopy buckets.

T. J. Matelson, *unpublished data*). These amounts fall within the range of fine litterfall estimates in other tropical montane forests (500–1100 $g \cdot m^{-2} \cdot yr^{-1}$) (Edwards 1977, Tanner 1980*a*, Proctor 1984, Vitousek and Sanford 1986). Litter was deposited all year, but there was a major pulse of all constituents from mid-January through mid-March (Fig. 3), which coincided with extremely strong winds at that time (exceeding 100 km/h, Monteverde Weather Station for the Instituto Meteorológico, San José, Costa Rica). The variability in gross fine litterfall biomass was quite high (mean standard error per collection was ≈10–40% of the mean per collection interval), but within the range reported in other studies over a comparable ground area (Klinge and Rodriques 1968, Dwyer and Merriam 1981, Merriam et al. 1982, Cuevas and Medina 1986). Gross fine litter was dominated by leaves (59% of total) (Fig. 4), in proportions comparable to those of litter samples in other tropical cloud forests (Bray and Gorham 1964, Tanner 1980*a*, *b*, Proctor 1984).

Nutrient concentrations in gross fine litterfall (Table 4a) were comparable or slightly higher than those in other tropical cloud forests (Tanner 1977, Vitousek and Sanford 1986). Distinct seasonal patterns of nutrient concentrations were not apparent, except for Ca and Mg, which were lower in the dry season than in the wet and misty seasons (Fig. 5). The amount of nutrients contained in gross fine litterfall was comparable to that falling to the forest floor in this and other tropical montane forests (Tanner 1980*a*, Grubb and Edwards 1982, Vitousek and Sanford 1986). Over half of the nutrients (52–70%) were contained in the leaf component (Table 5).

TABLE 4. Nutrient concentration of: (a) gross fine litterfall, and (b) canopy standing litter components collected during the study period. For gross fine litter, $N = 9$ bulked samples; for standing crop, $N = 8$ bulked samples. Data are means, with SE in parentheses.

Component	Concentration (mg/g)				
	N	P	Ca	Mg	K
a) Gross litterfall					
Leaves	15.3 (1.3)	0.6 (0.02)	14.7 (1.0)	2.1 (0.03)	3.5 (0.3)
Stems	6.5 (0.4)	0.5 (0.02)	9.6 (0.0)	0.9 (0.2)	1.7 (0.1)
Reproductive	8.6 (0.6)	0.9 (0.01)	19.0 (2.8)	2.7 (0.4)	8.9 (0.7)
Bryophytes	10.6 (0.2)	0.9 (0.01)	9.5 (0.2)	1.7 (0.2)	6.9 (0.1)
Miscellaneous	11.2 (0.2)	0.2 (0.04)	10.2 (0.4)	1.5 (0.2)	3.5 (0.5)
b) Canopy standing litter					
Leaves	17.6 (0.6)	0.7 (0.04)	12.7 (1.3)	1.7 (0.2)	1.3 (0.2)
Stems	11.3 (0.5)	0.4 (0.07)	13.1 (1.4)	1.3 (0.3)	1.4 (0.3)
Reproductive	18.9 (1.5)	1.1 (0.1)	5.2 (0.7)	1.6 (0.9)	4.6 (1.3)
Bryophytes	13.0 (0.8)	0.9 (0.09)	10.6 (0.6)	1.9 (0.2)	4.2 (0.7)
Miscellaneous	18.6 (1.3)	1.1 (0.07)	13.5 (1.6)	1.9 (0.3)	2.3 (0.4)

TABLE 5. Mean biomass and nutrients in gross fine litterfall passing through the canopy, collected with canopy buckets and corrected for loss of leaves due to wind (see *Results: Gross fine litterfall*).

Source	Bio-mass	Nutrient content ($g \cdot m^{-2} \cdot yr^{-1}$)				
		N	P	Ca	Mg	K
Leaves	440	6.7	0.3	6.5	0.9	1.5
Stems	109	0.7	0.1	1.0	0.1	0.2
Reproductive	83	0.7	0.1	1.6	0.2	0.7
Bryophytes	24	0.3	0.02	0.2	0.04	0.2
Miscellaneous	96	1.1	0.02	1.0	0.1	0.3
Total	752	9.5	0.5	10.3	1.3	2.9

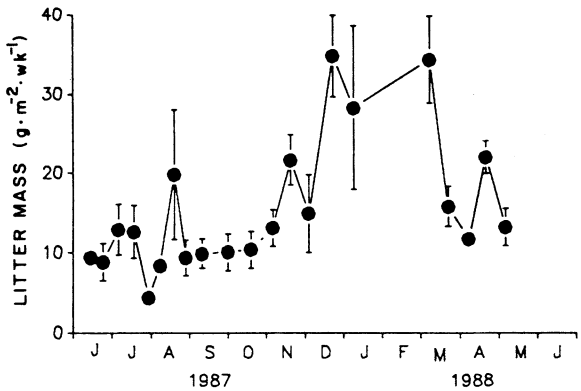

FIG. 3. Gross fine litterfall within the canopy from 20 June 1987 to 19 May 1988. Values (means ± 1 SE) are corrected for wind-blown loss from buckets (see *Materials and Methods: Phenology and composition of gross fine litterfall*).

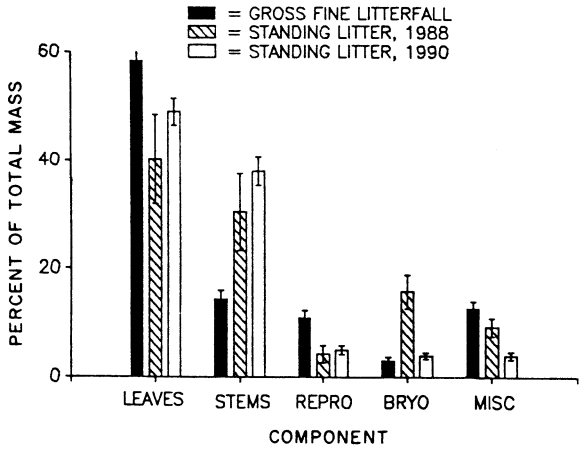

FIG. 4. Composition of gross fine litterfall and canopy standing litter. Gross fine litterfall is the average composition during the study period. REPRO = reproductive parts (flowers and fruits); BRYO = moss and other bryophytes; MISC = miscellaneous.

Canopy standing litter

The mean biomass of standing litter was ≈170 g/m² branch surface area. There was no significant difference in biomass of standing crop of intercepted fine litter on tree branches between the 1988 and the 1990 sampling periods (Student's t test, $t = 0.267$, df = 28, $P = .79$). There was no significant effect of individual tree (one-way ANOVA), indicating that among-tree variation exceeded within-tree variation ($F = 1.303$, df = 58, $P = .251$). The composition of the standing crop of litter was similar to that of gross fine litter, but had a higher proportion of stems and a lower proportion of reproductive material. Epiphyte leaves in the 1990 samples made up 17% of the total biomass of standing litter (35% of leaf biomass) (Fig. 4).

The distribution of the biomass of canopy standing litter was extremely variable (range = 4.5–1268 g/m²; standard error was ≈20–30% of the mean). Based on the 1990 values, we found a significant effect of branch characteristics on total biomass of canopy litter ($P = .04$, $r^2 = 0.27$). The number of stems, the number of clumps, and the angle from horizontal had significant effects ($P = .01$, .03, and .001, respectively), but width of branch and height of epiphytes had no significant effect ($P = .15$ and .85, respectively).

The nutrient concentration of standing litter was comparable to gross fine litter for leaves, but slightly higher in N for other components and lower in Ca for reproductive parts (Table 4). The mean nutrient concentration of each component was multiplied by mean biomass for total nutrient capital in standing litter; leaf litter contained the largest amount of nutrients, from 25 to 46% of standing litter nutrient pool (Table 6).

Leaf litter attrition (L_a)

Considerable attrition of litter deposited on branch surfaces occurred within a short time period in the canopy (Fig. 6). Approximately 70% of the leaves were lost within 4 wk. It appears that most leaves are removed rapidly, as there was only a 10% difference between the amounts lost between 2 and 10 wk. Using simple linear regression, the equations for leaf attrition are:

$$\text{0–2 wk:} \quad y = -33.5x + 100 \quad (r^2 = 0.99),\ n = 397$$

$$\text{2–10 wk:} \quad y = -1.019x + 35.27 \quad (r^2 = 0.99),\ n = 953$$

where y = the percent leaves remaining, x = the number of weeks, and n = the number of leaves.

TABLE 6. Biomass (mean and 1 SE) and nutrient pool of canopy standing litter in May 1988 and May 1990. Sample number = 29 branch segments on 7 trees (1988) and 69 branch segments on 11 trees (1990).

	Biomass (g/m² of branch area)		1988 Nutrient capital (g/m² of branch area)				
Component*	1988	1990	N	P	Ca	Mg	K
Leaves	63.7 (4.9)	79.3	1.1	0.04	0.8	0.1	0.1
TM	n.m.	53.6 (8.0)	...	...	...	...	...
EM	n.m.	25.7 (5.0)	...	...	...	...	...
Stems	48.8 (2.0)	76.7 (23.4)	0.6	0.02	0.6	0.1	0.1
Repro	6.8 (0.4)	6.2 (1.8)	0.1	0.01	0.04	0.01	0.03
Bryo	25.2 (0.9)	3.7 (0.6)	0.3	0.02	0.7	0.05	0.1
Misc	14.8 (0.9)	9.1 (3.1)	0.3	0.02	0.2	0.02	0.03
Total	159.3 (50.9)	175.0 (31.9)	2.4	0.1	2.3	0.3	0.4

* Leaves: TM = leaves of terrestrially rooted plant material; EM = epiphytic material; Repro = reproductive material; Bryo = mosses and other bryophytes; Misc = miscellaneous. n.m. = not measured.

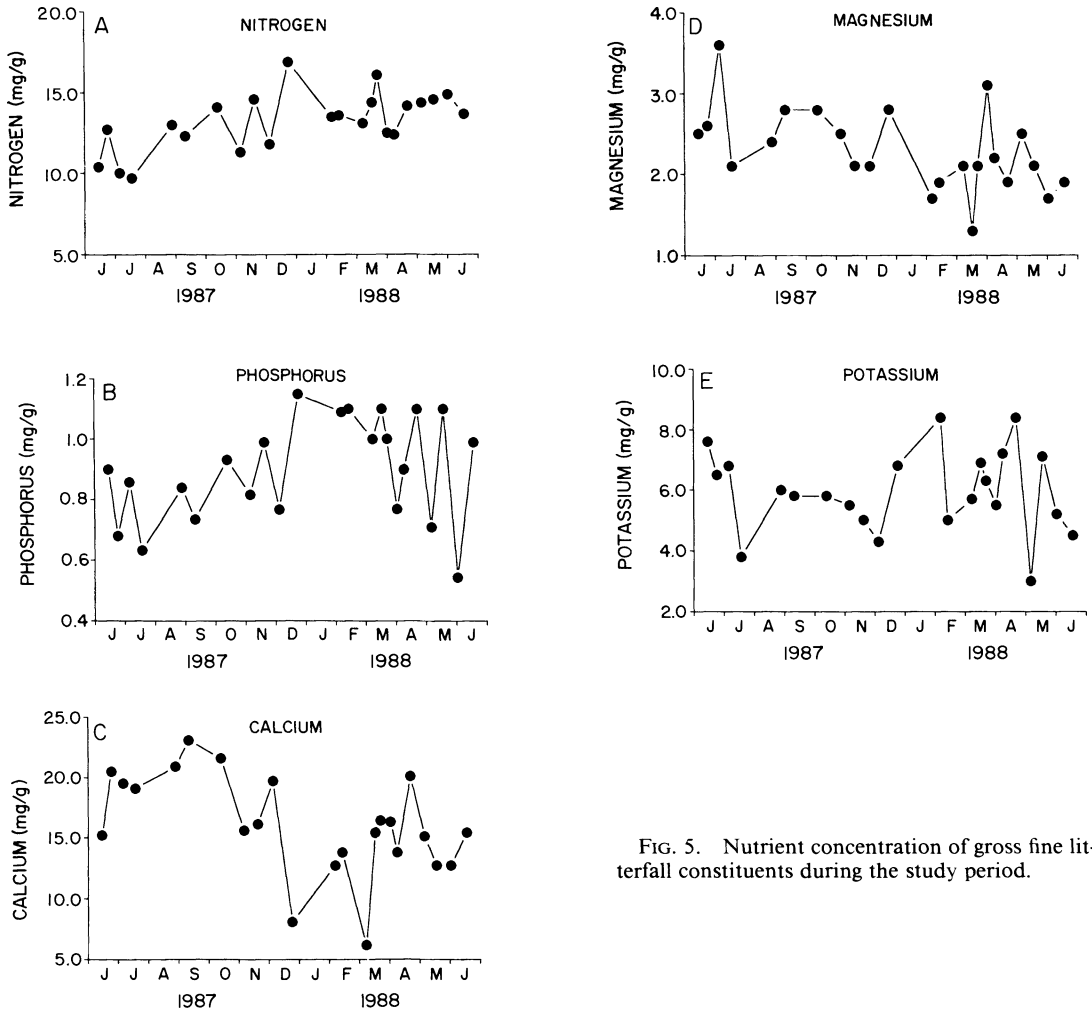

FIG. 5. Nutrient concentration of gross fine litterfall constituents during the study period.

The leaf attrition rate experiments in 1990 corroborated the 1988 measurements. The amount of remaining leaves after 31 d ($\bar{X} \pm 1$ SE = 26 ± 4%) was within 2% of the amount predicted by the 1988 regressions. Based on ANOVA, there was no significant tree effect on the rate of leaf attrition ($F = 1.79$, df = 27, $P = .13$)

The overall effect of the branch characteristics we measured had a significant effect on the percent of leaves remaining ($P = .001$, $r^2 = 0.49$). The width of the branch had a significant effect ($P = .002$), but angle, height, number of stems, and number of clumps had no significant effects ($P = .12$, .49, .10, and .59, respectively).

There was no significant correlation of the percent of leaves remaining with the biomass of standing litter ($P = .11$, $r^2 = 0.07$). We explain this lack of correlation by noting that the rate of fine litter accumulation is a combination of both the probability that a leaf lands on a branch surface and that the leaf remains after it has landed. We were not able to measure the amount of litter input to particular branch segments; this would depend upon the surroundings of the branch segment (e.g., proximity of large branches, degree of protection from wind), rather than the physical characteristics of the branch segment itself.

Litter decomposition (L_d)

After 12 mo, ≈70% of the litter biomass inside the tethered litterbags remained (Fig. 7A, open circles). The regression of percent biomass loss with time was significant ($P < .03$, $F = 8.72$). The annual fractional litter loss (K_d) was 0.36, with 64% of the variance explained by an exponential model. Based on the model, leaf litter turnover time is 2.8 yr, which is considerably slower than decomposition rates on the forest floor of the study area (time = 1.4 yr; N. M. Nadkarni and T. J. Matelson, *unpublished data*) and in leaves on the forest floor in other tropical montane and cloud forests (Wiegert and Murphy 1970, Edwards 1977, La Caro and Rudd 1985).

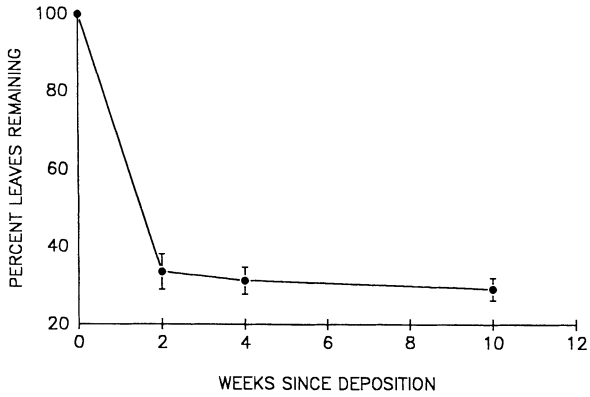

FIG. 6. Rates of leaf loss from branch surfaces from wind, based on marked-leaf experiments within the canopy during 1988. Large amounts of loss of leaves deposited on branches occurred within days of deposition, with slower attrition occurring between 2 and 10 wk. The calculated rates of leaf loss are in the text (*Results: Leaf litter attrition* [L_a]) for these two time intervals. Error bars are ± 1 SE; total number of marked leaves was 1350.

Changes in nutrient content during the field incubation differed with each nutrient (Fig. 7B–F). For all nutrients except N, there was net mineralization over the 12-mo period. The high calculated net increase in N in litter is presumably due to immobilization of N from surrounding crown humus by microbes or from atmospheric deposition. In contrast, K was mineralized or leached very rapidly, with 90% lost from the bags within the 1st mo.

Potential net litter input in the canopy

The combination of leaf attrition by disturbance and slow decomposition rates within the canopy yields only small amounts of nutrients from abscised leaves that become potentially available to the epiphyte community (Fig. 7A–F). Net loss from litter (calculated by multiplying mean values of the canopy standing litter by leaf attrition rates, L_a, and decomposition rates, L_d, and summed over the entire year) is only 2.0 $g \cdot m^{-2} \cdot yr^{-1}$ of biomass and <0.02 $g \cdot m^{-2} \cdot yr^{-1}$ for all nutrients. The calculated nutrient flux (in grams per square metre per year) from litter within the canopy was: N, −0.22, P, 0.001, Ca, −0.01, Mg, 0.01, K, 0.02. Positive values (for P, Mg, K) indicate net potential input to epiphyte communities, and negative values (N, Ca) indicate net immobilization of litter from the surroundings. Comparing potential net litter input with the gross litterfall (Table 5), <1% of biomass and all nutrients contained in the gross fine litterfall remains on branches long enough to potentially contribute to the nutrient pools available to epiphyte communities via mineralization.

DISCUSSION

In most terrestrial systems, the major portion of the nutrients required for net primary production is replenished via the litterfall pathway, especially for N, P, and Ca. Within mature tree crowns in tropical cloud forests, where vascular plants, bryophytes, root mats, and humus occur, nutrients are bound in organic matter as they are in the forest floor below. However, the amount of intercepted tree litterfall on inner branches is extremely small (approximately <1% estimated in this study) relative to the amount of gross litterfall that passes through the canopy. The reasons for low litter interception and high litter attrition include disturbances such as wind, falling branches, impact of rain, and animal activities such as monkeys and rodents moving along branches, and birds foraging in accumulated leaf litter. These disturbances cause substantial leaf litter displacement before the nutrients contained in the intercepted litter can be mineralized and thus made available for epiphyte uptake. The wind regime in this forest is typical for other tropical montane forests affected by the tradewinds, and so the high rate of leaf attrition (due at least in part to high winds) can probably be generalized to other such forests.

The few leaves that do remain in the canopy decompose very slowly, which may at least in part be due to dry environmental conditions and low densities of canopy macroinvertebrates (Nadkarni and Longino 1990). The amounts of nutrients released from fine litter in the canopy must be considered only potentially available for uptake by epiphytes because the mineralized nutrients may be immobilized by microorganisms or leached to other parts of the ecosystem, and therefore be temporarily or permanently diverted from epiphytes.

The source of some of the fine litter deposited within the canopy is from epiphytes themselves. We found that 35% of the canopy standing leaf litter (the only component we could reliably identify) was epiphytic in origin. If we assume the most conservative estimate (i.e., all other components were entirely derived from terrestrially rooted material), then at least 17% of the total standing crop was epiphytic in origin. This indicates that a substantial amount of "recycling" of nutrients within the epiphyte community may occur. The initial nutrient source of these recycled leaves is unknown, so we are unable to partition that input more precisely into allochthonous or autochthonous sources.

Whether or not the small amount of fine litter that enters the epiphyte community (<2.0 $g \cdot m^{-2} \cdot yr^{-1}$) is sufficient to satisfy the nutrient requirements of plants growing in the canopy is unknown, as there are few published estimates of epiphyte productivity or annual nutrient requirements (Pike 1978), and we could find none for epiphytes in tropical cloud forests. Productivity data for the plant communities that are most comparable are epiphytes in temperate old-growth moist coniferous forest (260 $g \cdot m^{-2} \cdot yr^{-1}$, Pike 1978), and temperate forest floors dominated by bryophytes (166 $g \cdot m^{-2} \cdot yr^{-1}$, Rieley et al. 1979). Productivity of the shrub community of temperate heath forests, which

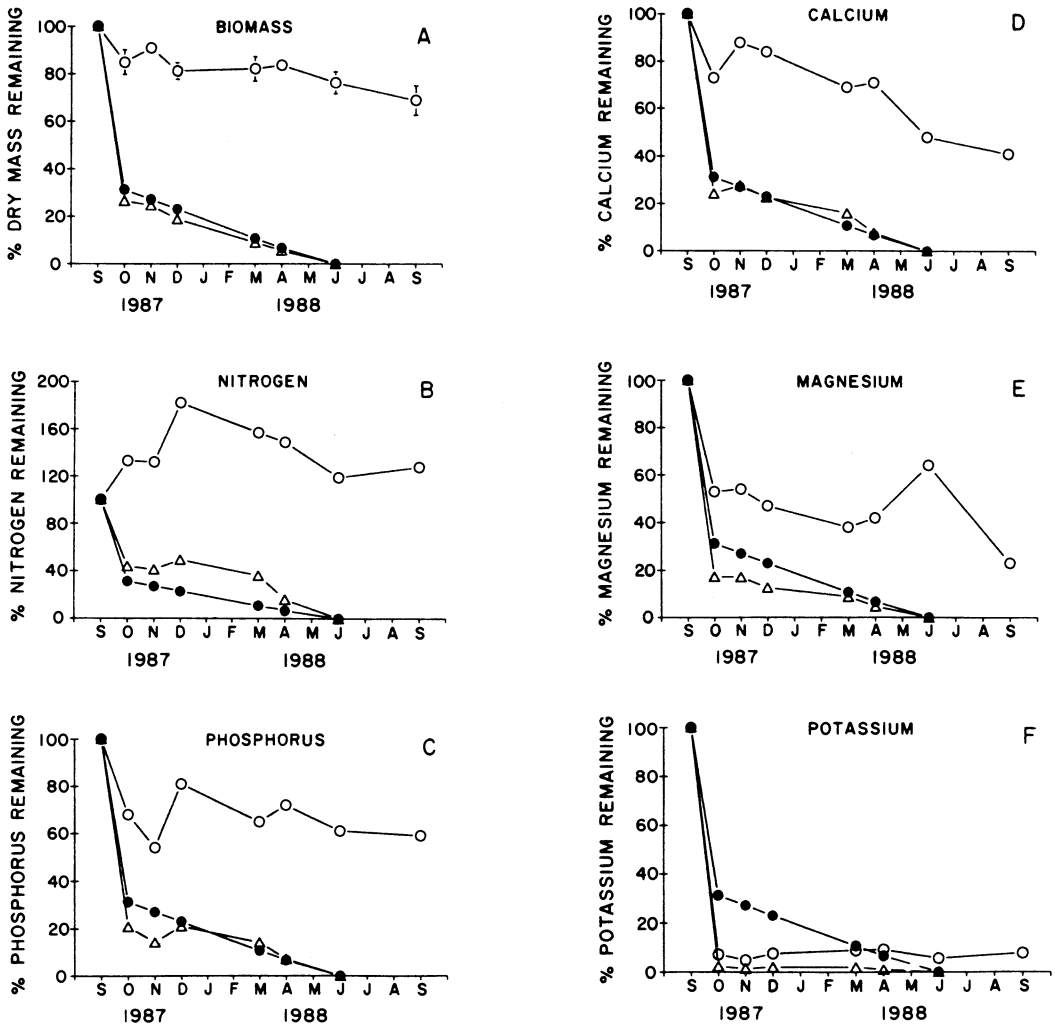

FIG. 7. Measured and calculated rates of biomass and nutrient change of intercepted litterfall of litter material in tethered bags in the canopy, as a percent of original mass or amount of nutrients from September 1987 to September 1988. O shows the percentage of the original biomass (mean ± 1 SE) and nutrient content of the original material contained in tethered litterbags. ● shows calculated amounts of leaves remaining after leaf attrition (loss of whole leaves from the canopy (L_a). △ are amounts of material remaining as a function of the integration of leaf attrition and leaf decomposition (L_d).

are dominated by woody ericaceous shrubs growing upon histosols as are inner branches of trees in the study site, is 160–380 $g \cdot m^{-2} \cdot yr^{-1}$ (Whittaker 1963). These estimates far exceed the input from intercepted host tree litterfall in our study (2.0 $g \cdot m^{-2} \cdot yr^{-1}$). This suggests that if epiphytic productivity at our site is of the same order of magnitude or greater than in the studies cited above, then epiphytes are decoupled from the litterfall pathway with respect to nutrient inputs. However, we must await studies that quantify epiphyte production and nutrient uptake in this forest type before we can determine the extent to which epiphytes depend upon fine litter nutrients in the canopy.

Abscised litterfall that is intercepted, however, may be more important for some members of the epiphyte community than the small overall amount we report implies. As one might expect, we found that certain branches (those with low angle from horizontal, numerous stems, and many clumps of plants) retained relatively more intercepted litter than did branches with steeper angles, and those without as much surface irregularity. The retention of litter may promote higher nutrient input at certain sites, thereby creating positive feedback for fine litter accumulation and plant growth. We presume that such input would be most important for epiphytes without morphological adaptations for acquiring atmospheric nutrients (e.g., sclerophyllous woody epiphytic shrubs). This variability in litter retention warrants further field measurements to assess the amount of captured litter associated with particular elements of the epiphyte community.

Since the replenishment of nutrients to many cloud forest epiphytes appears to be only partially derived from litterfall decomposition, the balance must be de-

rived from the other sources outlined in Table 1. Two sources, foliar leachate (autochthonous) and atmospheric deposition (allochthonous), seem the most likely candidates for most of the balance. Nutrients derived from foliar leachates (especially mobile nutrients K and NO_3) may be important, as throughfall concentrations collected at the forest floor are occasionally lower than in bulk precipitation (K. Clark, *personal communication*), indicating that at least some of the canopy components are "scavenging" nutrients from bulk precipitation. The majority of host tree foliage, however, is sclerophyllous, with waxy cuticles, and many cloud forest trees retranslocate high proportions of N and P, which presumably minimizes water and nutrient transfer through foliage (Grubb 1977, Tanner 1980*a*, *b*).

Atmospheric deposition is an allochthonous source that is likely to contribute nutrients to all epiphytes. On outer branches, poikilohydric epiphytes such as bryophytes and filmy ferns capture atmospheric nutrients and incorporate them into their biomass. When they die, their detritus contributes to the development of humus buildup, which no doubt increases nutrient retention. The epiphytes that occupy inner branch areas and that do not have morphological adaptations for direct atmospheric uptake must acquire nutrients by root uptake from nutrients sequestered in the accumulated mats. These plants may obtain at least some of their nutrients by physically intercepting precipitation (especially wind-blown mist) with their shoots and channeling it to the humus mats that are permeated with their root systems. Understanding the ultimate nutrient sources of canopy solutions and sinks of nutrients by quantifying the uptake and release of specific canopy components is needed to differentiate these two sources.

Based on estimates of average branch surface area (estimated from length and diameter of branches of trees visible from our rigged trees; 6.5 m^2/tree) and density of large trees ($\approx$80 trees/ha) in our site, the branch surface area within inner tree crowns on which canopy standing litter collects is $\approx$520 m^2/ha. Assuming that trees of this size collect similar amounts of branch litter to our sample trees, and that the amounts collected on outer branches and trunks are negligible, the total standing crop of litter in the canopy is probably $\approx$8.8 g/m^2 of ground area. This represents 1% of the standing litter on the forest floor (880 g/m^2; N. M. Nadkarni and T. J. Matelson, *unpublished data*). Other forests, especially humid tropical forests where wind is less important, may support larger proportions of intercepted fine litter.

Acknowledgments

We thank the staff of Monteverde Cloud Forest Reserve, the Tropical Science Center, and the Monteverde community for use of the study area and logistical support. F. Setaro, K. Clark, W. Kuhn, and R. Khatir provided technical help in the laboratory. R. Solano, K. Williams, J. Gold, J. Crisp, and M. Arguedas provided field and laboratory assistance in Monteverde. J. Longino, E. Vance, S. Hart, and J. Damith gave assistance with analyses and ideas discussed in this paper. This research was funded by Research Grants and a Research Experience for Undergraduates Grant Supplement from the National Science Foundation (BSR86-14935 and BSR 90-18006), the Whitehall Foundation, the National Geographic Society Committee on Research and Exploration, and the UCSB Academic Senate. A portion of this research was completed while at the Department of Biological Sciences, University of California, Santa Barbara, California 93106 USA. P. Sollins, G. P. Robertson, and several anonymous reviewers gave helpful critical advice on the manuscript.

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