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Biomass and Nutrient Dynamics of Epiphytic Litterfall in a Neotropical Montane Forest, Costa Rica[1]

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ABSTRACT

To investigate the importance of the epiphyte community to ecosystem nutrient cycling, we assessed the standing crop, input rates, and turnover rates of litterfall derived from epiphytic material and compared them to litterfall derived from terrestrially rooted material in a neotropical cloud forest in Monteverde, Costa Rica. The standing crop of fallen epiphytic material in 1988 was 0.5 t ha^{-1} and 0.3 t ha^{-1} in 1990. Annual input of fallen epiphytic material was 0.5 t ha^{-1}, more than two times as much as has been reported for other tropical cloud forests. This is equivalent to 5–10 percent of total fine litter at the site (7.5 t ha^{-1}). Nutrient input from fallen epiphytic material was (kg ha yr^{-1}): N, 7.5 (7% of nutrient transfer via total fine litter); P, 0.5 (8%); Ca, 4.2 (4%); Mg, 0.8 (5%); and K, 0.1 (1%). Assuming a steady state condition in this old-growth forest, epiphyte-derived litter biomass had a higher annual decay rate (K_1 = 1.3) than did litter derived from terrestrially rooted plants (0.7). However, turnover time ($1/K_1$) of all nutrients except K in fallen epiphytic material was four to six times slower than for nutrients in terrestrially rooted material; K was tenfold faster. Over half of the fallen epiphytic material was collected in less than 2 percent of the collections, indicating the deposition of epiphytic material is highly sporadic in space and time and must be measured at the appropriate spatial scale.

RESUMEN

Con el objetivo de conocer la dinámica del flujo de nutrientes en hojarasca caida se han investigado la cantidad, la rápidez de deposición y el ciclaje de la hojarasca caida de las plantas epifíticas en un bosque nublado neotropical en Monteverde, Costa Rica y éstos se han comparado con la dinámica de la hojarasca caida en otros bosques nublados tropicales. La cantidad de hojarasca caida fué de 0.5 t ha^{-1} en 1988 y 0.3 t ha^{-1} en 1990. La deposición de epifitas caidas fué de 0.5 t ha^{-1} y mostró un patrón estacional de nutrientes de hojarasca menuda fué (kg ha año N, 7.5; P, 0.5; Ca, 4.2; Mg, 0.8; y K, 0.1. Asumiendo una condición estable dentro de este bosque de gran edad, las epifitas caidas tendrían una rápidez de descomposición (K_1 de 1.3), mas rapido del material de que tiene las raices dentro de la tierra (0.7). Pero el ciclaje anual de epifitas caidas para N, P, Ca, y Mg fué mucho mas despacio (4–6×) de hojarasca caida de los arboles. La deposición de material epifítica es muy esporádica en espacio y tiempo, y deberia ser medida en escala apropriado.

THE DEPOSITION, DECOMPOSITION, AND MINERALIZATION of fallen litter represents a major pathway for transferring nutrients and energy from vegetation to soils and is the most frequently measured nutrient flux in forest ecosystems (Bray & Gorham 1964; Proctor 1983; Vitousek 1982, 1984; Vitousek & Sanford 1986). Nearly all litterfall studies have focused on the biomass and nutrient composition of "fine litter" deposited by terrestrially rooted trees and understory plants, as their abscissed leaves, twigs, and reproductive parts constitute the major component of labile nutrients in most forest types.

In many tropical moist forests, however, live epiphytes and associated dead organic matter on branches and trunks constitute a considerable part of the above-ground biomass and nutrient pools, up to 45 percent of the foliar mineral capital (Grubb 1977, Pocs 1980, Grubb & Edwards 1982, Nadkarni 1984). Nutrients from live and dead epiphytic material are released into the nutrient cycles of terrestrially rooted vegetation by three pathways: epiphyte mats on host tree branches and trunks are permeated by host tree canopy roots (Nadkarni 1981); epiphyte mats are leached by precipitation, and the nutrients are transferred to the forest floor via stemflow and throughfall; and epiphytic material falls to the forest floor and decomposes. Various processes cause epiphytic material to fall to the forest

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floor, including senescence, wind, disruption by birds and mammals, and the falling of supporting branches and whole trees.

The contribution of the epiphyte community to nutrient transfer in tropical forests is poorly understood. Epiphyte biomass and nutrient pools have been measured in only a small number of forests; the few measurements made of nutrient fluxes from epiphytes to the forest floor have been primarily limited to temperate or boreal forests (Pike *et al.* 1977, Pike 1978, Rhoades 1978, Carroll 1980, Reiners & Olson 1984, Esseen 1985, Nadkarni 1985). The few reports in which epiphyte litterfall has been reported in tropical forests have been anecdotal or based on small collectors designed to trap tree fine litter (*e.g.*, Tanner 1980, Songwe *et al.* 1988, Veneklaas, 1991). As a consequence, estimates of the total input of nutrients to the forest floor are probably inaccurate in forests where epiphytes are a substantial canopy component. Epiphytic material that has fallen and mineralizes on the forest floor may have particular ecological relevance because some of the nutrient capital of epiphytes (*e.g.*, N in cloud forest ecosystems) is derived from atmospheric sources, which represents, at least in part, "new" nutrient sources being channelled into and recycled within the forest ecosystem (Clark & Nadkarni 1990, Nadkarni & Matelson 1991).

In this study, we quantify the dynamics of fallen epiphytic material in a tropical cloud forest in Monteverde, Costa Rica. We focus on fallen live and dead epiphytic material (hereafter designated as **EM**) which consists of live epiphytic vascular and nonvascular plants, associated detritus, microbes, invertebrates, fungi, and "crown humus" (*sensu* Jenik 1973). We differentiate EM from terrestrially rooted material (hereafter **TM**) which is considered in a separate paper (Nadkarni & Matelson, in press). We are confident that this separation is meaningful at this site, as other measurements we have made (Nadkarni and Matelson 1991) demonstrate that only negligible amounts of TM litterfall are retained on epiphyte mats in the canopy because of frequent within-crown disturbances such as wind and animal movements. This contrasts with anecdotal observations of other montane cloud forests (J. Wolf, pers. comm.), where tiny leaflets of overstory dominants such as *Weinmannia* sp. are inextricably bound in epiphyte mats and such separation would not be possible. We report: EM standing crop biomass, composition, and nutrient pools on the forest floor; input of EM biomass, composition, and nutrients to the forest floor; and rates of EM biomass and nutrient turnover. We compare these with epiphyte and terrestrial plant fine litter dynamics measured in this and other wet tropical montane forests, and discuss the ecological significance of this material.

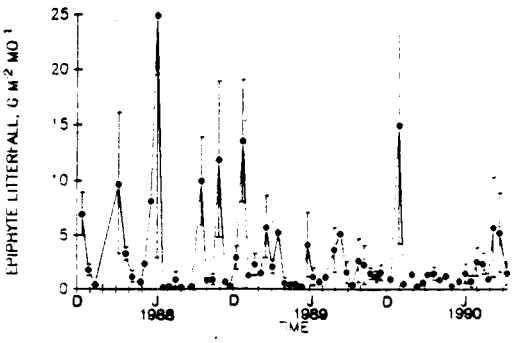

FIGURE 1. Epiphyte litter (g m^{-2} mo^{-1}) collected from 5 m × 5 m plots and fine litter collectors between 7 December 1987 and 6 September 1990. Error bars represent one standard error of the mean.

METHODS

STUDY SITE.—Fieldwork was conducted from 1 April 1987 to 6 September 1990 in the Monteverde Cloud Forest Reserve (MVCFR), a lower montane moist forest along the Cordillera de Tilarán, Costa Rica (10°12′N, 84°42′W). The study area (1480–1520 m) is in the Leeward Cloud Forest described by Lawton and Dryer (1980), and is composed of trees 15–30 m in stature, with a well-developed subcanopy, a moderately rich shrub layer, and a sparse herbaceous community. Soils are derived from volcanic rhyolites, and are moist or wet all year long.

The climate of Monteverde has been roughly divided into three seasons. The **misty-windy season** (November–January) is characterized by advective clouds and precipitation dominated by mist borne by the northeast tradewinds. During the **dry season** (February–April), cloud water and mist deposition occur, but measurable precipitation is low; bouts of strong wind abate at the end of this season. The **wet season** (May–October) is characterized by abundant convective precipitation and low wind speeds, which originate in the Pacific-side lowlands. Annual precipitation is recorded as 2000–2300 mm, but actual wet deposition is no doubt higher because of the large amount of wind-driven mist and fog that occur throughout the year (Lawton and Campbell 1984). Temperature is quite consistent all year, with diurnal ranges exceeding yearly ranges (14.8°C to 20.7°C), and a yearly mean of 17.7°C. Wind occurs throughout the year, but it is particularly

strong during the misty and dry seasons (J. Campbell, pers. comm.).

The epiphytes of Monteverde are diverse and abundant (Nadkarni 1986). Unlike some other wet tropical forests, (*e.g.*, Sanford 1969) the species of host tree does not appear to be an important determinant of epiphyte biomass and organic matter accumulated on mature trees (Lawton and Dryer 1980). Branch surfaces in the crown interior of nearly all mature trees support thick mats of epiphytes (bryophytes, herbs, woody shrubs, and hemiepiphytes), and an interwoven root-humus mat up to 25 cm thick, with the greatest humus accumulations on junctions of large branches. Outer branches and branch tips are partially or completely covered with liverworts and mosses and small herbaceous plants, and they support little accumulated humus. Fallen EM is evident on the forest floor.

In April 1987, a 2 ha study area (divided into 20 m × 20 m quadrats) was established within the 20 ha Research Area of the MVCFR. The study area encompassed a variety of slopes (5% to 20%) and level areas, several current and recovering gaps (25 m^2 to 225 m^2 in area), and appeared representative of that forest type. We marked and measured all trees >10 cm diameter at breast height (dbh) in the study area; canopy height was 18–25 m; mean tree dbh was 65.5 cm.

LITTER MEASUREMENTS

STANDING CROP.—We measured standing crop of EM on the forest floor with plots and belt transects. In May 1988, we used 11 randomly located plots (5 × 5 m) within the study area and four 1 × 100 m belt transects around the perimeter of 1 ha of the study area. In May 1990 we used three 1 × 100 m belt transects in areas not previously sampled. All materials that were clearly epiphytic in origin were collected and weighed in the field; these included clumps of bryophytes, bromeliads, herbs, woody epiphytic shrubs, and mats of interwoven roots, humus, and live plants. Because we could not positively identify the origin of individual leaves (epiphyte vs. tree) after they had fallen to the forest floor and mixed thoroughly with the leaves from TM, we did not collect any individual fallen leaves from the plots or belts, so our estimates of EM are conservative.

Samples were taken to the field laboratory and separated to vascular plants, bryophytes, and dead organic matter (detritus and humus). These were dried in an oven at *ca* 60°C to constant weight (48 to 72 hr). At each collection, ten samples of each component were randomly chosen, subsampled, ground with a Wiley Mill to pass through a 40-mesh screen, and transported to the University of California, Santa Barbara for nutrient analysis.

LITTER PRODUCTION.—We used two methods to measure input of EM to the forest floor. To collect the large discrete pieces of EM that would not fit into standard litterfall traps, we collected newly fallen EM from ten 5 × 5 m plots, approximately twice per month (mean interval length = 15 days; std = 5.3 days) from 7 December 1987 to 6 September 1990. Eleven additional plots of the same size were established on 9 May 1988, and monitored for EM litterfall until the end of the study. The understory within the plots (plants <2 m in height) was cleared, and re-cleared monthly, so that EM could be easily seen and collected. Material collected included intact epiphyte mats attached to fallen branches and whole trunks, whole epiphytic plants, and plant parts of sizes greater than *ca* 20 cm^2 that were clearly epiphytic in origin and unattached to branches. As with standing crop, it was not possible to distinguish between individual leaves, stems, or roots regarding origin from epiphytes vs. trees, so our values underestimate total EM input and are conservative.

The fresh weight of EM from each plot was recorded and the collected material from each plot was dried and weighed as for the standing crop. The amount of EM components (vascular plants, bryophytes, and dead organic matter) was measured by choosing ten random plots per collection interval and separating, drying, and weighing the material. Between 8 February 1988 and 1 January 1989, three composited subsamples of each component from each sampling date were ground and stored for nutrient analyses.

To measure EM that fell in the form of smaller pieces, we used collectors that were established to collect TM fine litterfall on the forest floor. On 20 June 1987, 23 fine-litter collectors were installed at random locations. These collectors were plastic buckets (sides = 55 cm high, 44 cm diameter) mounted on wooden stakes 1 m above the forest floor. Holes in each bucket bottom were covered with 2 mm nylon mesh to retain fine litter while allowing free passage of water. Collections were made twice monthly (Nadkarni and Matelson, in press). Because we could be certain that only the bryophytes were of epiphytic origin, we added to our estimate of total EM only this component of the materials falling into the bucket collectors. This was an underestimate because an unknown portion

of the fine litter (other than bryophytes) collected by the buckets would have been from epiphytic plants. Nutrient content of bryophytes was analyzed as for EM litter from the plots.

NUTRIENT ANALYSIS.—Total elemental composition of samples was analyzed by a modified Kjeldahl procedure (Parkinson & Allen 1975) following digestion (Technicon BD-40) of *ca* 300 mg samples. Solutions of organic N (urea, niacinamide) and organic P (phytic acid) compounds were digested and analyzed throughout the study period to establish validity and precision of N and P analyses. Pretreatment for recovery of nitrate was not incorporated in the protocol; separate analysis of NO_3 (extractable 1 N KCl) was performed on materials and was typically less than 3 percent of total N. A modified indophenol blue colorimetric method (Kempers 1974) and a molybdenum blue procedure (Watanabe & Olsen 1965) were used to determine NH_4 and PO_4 digests respectively. Cations were analysed on a Varian AA6 atomic absorption spectrophotometer.

RESULTS

STANDING CROP.—Fallen EM appeared on the forest floor in four forms: intact mats of live and dead epiphytes attached to treefalls and large branchfalls; unattached mats, sloughed from branches and trunks, which varied greatly in size; individual bromeliads, orchids, and other vascular epiphytes which reached the ground intact; and small fragments of vascular epiphytes and clumps of bryophytes.

Biomass of standing crop from the 5 × 5 m plots and belt transects were very similar; the difference between the means was less than 5 percent. In 1988, the mean biomass of standing crop was 50 g m^{-2} (SEM = 16.0); in 1990, the mean was 27 g m^{-2} (SEM = 14.3). There was a great deal of spatial variation in the amount of standing crop; biomass over both the sample dates ranged between 3.3 g m^{-2} and 81.9 g m^{-2} in our plots. Composition of standing crop was dominated by dead organic matter (58% ± SEM = 4), followed by bryophytes (22% ± 5), and vascular plants (20% ± 1). The nutrient pool of standing crop on the forest floor (Table 1A) was calculated by multiplying the biomass of each component (mean of the 1988 and 1990 measurements) by the nutrient concentration of that component (Table 2A).

LITTER PRODUCTION.—The biomass of EM input from plots during the study period was 350 kg ha^{-1} yr^{-1} (SEM = 60.2). Input was highly variable spatially, with biomass from individual plots ranging between 0 and 232 g m^{-2} per collection period (the latter is equivalent to 6.1 t ha^{-1} yr^{-1}). Standard deviations for a given collection interval were between 6 percent and 360 percent of the mean. EM input measured with the fine litter collectors (bryophyte category) was 140 kg ha^{-1} yr^{-1}, which is equivalent to 2 percent of the total TM fine litter (Nadkarni & Matelson, in press). Bryophyte input into these collectors was less spatially variable than EM litter to the plots; standard deviations for a given collection period were only 2 percent to 16 percent of the mean. This bryophyte component was added to plot collection input for a mean total annual EM input of 0.5 t ha^{-1}.

Input of EM was also temporally sporadic. There did not appear to be seasonal differences for any of the years (Fig. 1), but greater amounts fell in 1988–1989 than in 1989–1990 (Fig. 1). The highest values of EM litterfall occurred during 1988 windstorms which were the most severe recorded in the past fifteen years (J. Campbell, pers. comm.).

Of our 1234 collections of individual plots, 99 percent contained bryophytes, 62 percent contained vascular plants, and 56 percent contained dead organic matter. Composition of EM input to the forest floor on a dry weight basis was bryophytes, 76 ± 0.9 percent; dead organic matter, 13 ± 0.6 percent; and vascular plants, 11 ± 0.8 percent. There did not appear to be any seasonal differences in composition.

Individual collections of extremely large samples were infrequent; only 26 (2%) of all collections exceeded 10 g m^{-2} per collection interval (equivalent to 2.6 t ha^{-1} yr^{-1}). There was no apparent seasonal trend for these incidents of large EM deposition (Fig. 1); 2.3 per month occurred in the misty season, 0.6 per month in the dry season, and 2.0 per month in the wet season. These sporadic pulses of large EM comprised 53 percent of the total EM input. However, steady input of small amounts of material fell throughout the year; we recorded only 106 (8%) of the 1234 individual collections with no EM litter during the study period. The minimum total collection for a given time interval was equivalent to 25 kg ha^{-1} yr^{-1}.

Nutrient input via EM litter (Table 1B) was calculated by multiplying the nutrient concentration (Table 2) for each component at each collection period by the mean biomass of that component for that collection period. These inputs (kg ha^{-1} yr^{-1}) were: N, 7.5; P, 0.5; Ca, 4.2; Mg, 0.8; and K, 0.1 (Table 1B).

TABLE 1. *Summary of biomass and nutrient pools and transfers in fine litter during the study period.* **A.** *Biomass (t ha^{-1}) and nutrient pools (kg ha^{-1} yr^{-1}) in standing crop of epiphytic matter (EM) and terrestrial rooted material (TM).* **B.** *Biomass (t ha^{-1}) and nutrient transfer (kg ha^{-1} yr^{-1}) via litterfall in EM and TM.* **C.** Calculated annual decay constants (yr^{-1}) and turnover time (yr) based on a steady state assumption (K_1 = annual litter input/forest floor standing crop, turnover time = $1/K_1$). TM measurements were made at the same study area at the same time and are reported in Nadkarni and Matelson (in press).

		Nutrient				
	Biomass	N	P	Ca	Mg	K
		A. Standing crop				
EM	0.4	46	3	29	5	15
TM	10.1	159	7	213	17	16
Total standing crop	10.5	205	9	242	22	31
% EM of total standing crop	4	22	33	12	23	48
		B. Litterfall				
EM	0.5	7.5	0.5	4.2	0.8	0.1
TM	7.0	93	6	115	15	12
Total litterfall	7.5	100.5	6.5	119.2	15.8	12.1
% EM of total litterfall	7	7	8	4	5	1
		C. Annual decay constant and turnover time				
Annual decay constant (yr^{-1})						
EM K_1	1.3	0.16	0.17	0.14	0.16	10
TM K_1	0.7	0.6	0.9	0.5	0.9	0.8
Turnover time (yr)						
EM	0.8	6.3	5.9	7.1	6.3	0.1
TM	1.4	1.7	1.1	2.0	1.1	1.3

DISCUSSION

Fallen EM has been either entirely overlooked or inaccurately measured in nearly all nutrient cycling studies. Only a few tropical studies have estimated fallen EM input by separating EM from TM from material collected in fine litter collectors. In a tropical evergreen lowland forest in Cameroon, Songwe, Fasehun, and Okali (1988) found 105 kg ha^{-1} yr^{-1} from epiphytic mosses and ferns (0.8% of total fine litter). In a Jamaican montane forest, Tanner (1980) reported 4 to 180 kg m^{-2} yr^{-1} (0–3% of total fine litter) as EM (mainly bromeliads). In a lower montane rain forest, Veneklaas (in press) documented 220 kg ha^{-1} yr^{-1} of fallen vascular and non-vascular EM (3% of total fine litter) using 0.5 m × 0.5 m wire frames. If we had collected only the epiphytic material identified in our TM litterfall collectors, we would have underestimated EM by 72 percent, as only 14 g m^{-2} yr^{-1} in the bryophyte category fell into our collectors.

Our estimates of EM biomass and nutrient input are twice as high as those reported for other cloud forests. In our study site, the biomass of EM litterfall (0.5 t ha^{-1} yr^{-1}) is equivalent to 5–10 percent of the total fine litter biomass (7.5 t ha^{-1} yr^{-1}) (Nadkarni & Matelson, in press). The nutrient transfer via EM litterfall is up to 8 percent of the annual nutrient transfer in total fine litterfall (Table 1B).

If we assume that this old-growth, primary forest is in a steady state, then, over an annual cycle, litter decomposition equals litter deposition (Olson 1963). The annual decay rate (K_1) of this material is the annual litter input divided by the forest floor pool, and was calculated as 1.3 for EM biomass (Table 1C). The fractional turnover time ($1/K_1$) for EM biomass would be 0.8, or approximately 10 months. We found a more rapid decay rate and shorter turnover time for EM than measured for TM at the same time and place (K_1 = 0.7, $1/K_1$ = 1.4) (Nadkarni & Matelson 1991). However, we found a much slower decay rate for nutrients in EM litter (except K) than for nutrients in TM fine litter. Turnover time for all nutrients except K were four to six times longer for EM than TM. The turnover time for K was tenfold faster in EM than TM (Table 1C).

These results indicate that at least a portion of EM is recalcitrant and highly resistant to decomposition and mineralization. However, certain components of EM decompose very rapidly, while other components are more resistant to mineralization. Bryophytes appear to decompose very rapidly; input

TABLE 2. *Mean nutrient concentration (mg g^{-1}) (± SEM) of* **A** *standing crop and* **B** *litterfall of epiphytic components for 29 collection intervals between 16 May 1988 and 10 January 1989.*

Component	Nutrient				
	N	P	Ca	Mg	K
		A. Standing crop			
Total	18.4 (0.7)	1.3 (0.003)	11.9 (1.2)	1.9 (0.1)	6.0 (0.4)
		B. Litterfall			
Vascular plants	10.7 (0.7)	0.8 (0.5)	58.6 (0.9)	2.5 (0.3)	0.7 (0.1)
Bryophytes	15.8 (0.8)	1.1 (0.04)	8.4 (0.5)	1.7 (0.06)	0.3 (0.02)
Dead organic matter	15.5 (1.3)	0.7 (0.02)	10.8 (1.3)	1.2 (0.1)	0.2 (0.03)

was 76 percent of fallen EM, but only 22 percent of the EM standing crop, which suggests that this component decomposes quickly. The calculated decay rate for bryophytes is 4.3, with a turnover time of only 0.23 yr, or less than 3 months. Conversely, dead organic matter appears to have a much slower decay rate, comprising only 13 percent of input, but 58 percent of the EM standing crop; K_x for this material is 0.28, and the turnover time is 3.6 yr. Vascular plants are intermediate; K_x is 0.68 and turnover time is 1.5 yr. Further studies of particular components are needed to determine the timing of eventual nutrient mineralization and nutrient release from this material.

The patchy nature of the deposition of EM was manifested by our observation that over half of the EM fell in less than 2 percent of the collections. This has at least two implications for plants rooted in the forest floor. **First**, due to the "clumpy" nature of fallen epiphytes, nutrient deposition from EM concentrates input in particular but unpredictable locations. This contrasts to TM litter which is distributed fairly evenly across the forest floor. **Second**, nutrients deposited in EM that ride down tree- and large branchfalls co-occur with higher levels of light associated with resulting gaps. This pulse of nutrients released from EM may alter nutrient availability in the immediate vicinity of regenerating gap species.

Results from related research on litterfall from terrestrially rooted material at this site indicate that EM should be considered in future nutrient cycling studies in forests that support appreciable amounts of canopy epiphytes. We suggest three reasons to differentiate the contribution of epiphyte material and terrestrially rooted material. **First**, epiphyte material falls to the ground in large clumps, which include whole plants that are intertwined with a variety of materials such as nutrient-rich dead organic matter, and bryophytes. Bryophytes, which constitute over 75 percent of the EM litter, have higher nutrient contents than fallen TM leaf litter and apparently cycle their nutrients quickly (Table 2B) (Nadkarni & Matelson 1991). **Second**, in contrast to many tree species at our site whose abscissed leaves undergo considerable retranslocation before abscission (>25% N and 40% P) (Vitousek & Sanford 1986; Nadkarni & Matelson 1991), the foliage of EM may not go through retranslocation. This is because it is the unpredictable and sudden dropping of limbs and whole trees (rather than senescence of epiphytes themselves) that causes much of the EM to descend to the forest floor. **Third**, nutrient sources of epiphytes may partially or wholly differ from those of terrestrial plants. Forest plants that are rooted in the soil and the forest floor derive the majority of their nutrients from soil parent material whereas epiphytic plants (which have no vascular connection to the forest floor or to the vascular systems of their supporting host trees) derive at least a portion of their nutrients from atmospheric sources (Clark & Nadkarni 1990; Nadkarni & Matelson, 1991). Results from this study emphasize the need to make measurements with the appropriate means of sampling. Just as it would be inappropriate to measure elephants with mousetraps, so it is inappropriate to measure major branchfalls and treefalls with bucket collectors designed to collect leaf litter.

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