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Biomass and Nutrient Dynamics of Fine Litter of Terrestrially Rooted Material in a Neotropical Montane Forest, Costa Rica¹

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ABSTRACT

To investigate the dynamics of nutrient transfer in fine litter, we assessed the forest floor standing mass, input rates, and turnover rates of litter derived from terrestrially rooted material in a neotropical cloud forest in Monteverde, Costa Rica and compared them to litter dynamics in other tropical cloud forests. The mean standing crop of fine litter was 10.1 t ha⁻¹, and showed no striking seasonal differences but apparent annual differences. Input of fine litter was 7.0 t ha⁻¹ y⁻¹ and showed a strong seasonal pattern, with greatest amounts of fine litter falling during the dry season. Nutrient input from fine litter was (kg ha⁻¹ y⁻¹): N, 93; P, 6; Ca, 115; Mg, 15; and K, 12. Assuming a steady state condition in this old-growth forest, fine litter had an annual decay rate (K_d) of 0.69 and a turnover time ($1/K_d$) of 1.4 years. About 25 percent of N and 42 percent of P were retranslocated from foliage prior to abscission. Litter nutrient fluxes were high and nutrient use efficiency was low compared to other tropical montane forests, indicating that N and P may not be as limiting in this forest as in other montane forests.

RESUMEN

Con el objetivo de conocer la dinámica de la transferencia de nutrientes por hojarasca, se han investigado la masa de la capa de hojarasca, la tasa de deposición y la tasa de reciclaje de la hojarasca fina de las plantas que tienen raíces terrestres en un bosque nublado neotropical en Monteverde, Costa Rica y éstos se han comparado con la dinámica de la hojarasca en otros bosques nublados tropicales. La masa de la capa de hojarasca fue de 10.1 t ha⁻¹ y no mostró diferencias estacionales obvias pero sí diferencias significativas anuales. La deposición de hojarasca fina fue de 7.0 t ha⁻¹ año⁻¹ y mostró un patrón estacional; la cantidad de nutrientes depositada en la hojarasca fina fue (kg ha⁻¹ año⁻¹): N, 93; P, 6; Ca, 115; Mg, 15; y K, 12. Asumiendo un equilibrio dentro de este bosque, la hojarasca fina tendría una velocidad de descomposición (K_d) de 0.69 con una tasa de reciclaje anual ($1/K_d$) de 1.4 años. El follaje de las especies representativas mostraron realocación de N de 67 por ciento y de P de 76 por ciento. El flujo de nutrientes por medio de hojarasca fue alto y la eficiencia del uso de los nutrientes fue baja en comparación con otros bosques montañosos tropicales, indicando que quizás la disponibilidad de N y P en este bosque no está tan limitada como en otros bosques montañosos.

Key words: cloud forest; Costa Rica; fine litter; montane forest; Monteverde Cloud Forest Preserve; nutrient dynamics; seasonality; tropics.

THE DEPOSITION AND SUBSEQUENT DECOMPOSITION OF FINE LITTER represents a major pathway for transferring carbon and most nutrients from vegetation to soils and is the most frequently measured nutrient flux in forest ecosystems (Bray & Gorham 1964, Brown & Lugo 1982, Proctor 1983, Vitousek 1984, Vitousek & Sanford 1986). Measurements of fine

litter have also been used in conjunction with nutrient concentrations of litter to assess the nutrient status of forest ecosystems (Hirose 1975, Vitousek 1982).

Litter dynamics may be especially important in tropical montane forests because nutrients, particularly P and N, may be limiting to forest productivity (Grubb 1977; Tanner 1980a, 1985), and litterfall is the major path of flux for those nutrients (Vitousek & Sanford 1986). There have been few montane forest studies, however, that have measured fine litter and its constituents for periods of more than one year (Proctor 1983). The slow rate of litter decomposition in montane forests, relative

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to rates in tropical lowland forests, has been attributed to a number of factors. These include the high frequency of misty conditions, low air and soil temperatures, lack of drying-rewetting cycles, a high degree of sclerophylly, and waterlogged soils (Vitousek 1984, Grubb 1977, Tanner 1981, Leigh 1975, Edwards 1982). Nutrients and carbon in montane forests may be bound in organic forms for long periods of time and thus may accumulate on the surface of the mineral soil which can lead to the development of a root mat near the soil surface (Ovington & Olson 1970, Edwards & Grubb 1977, Grimm & Fassbender 1981, Tanner 1985) as occurs in oligotrophic lowland forests (Cornforth 1970, Cuevas & Medina 1986).

As part of an ecosystem-level study on cloud forest nutrient cycles, we studied the litter dynamics for a 36-month period in a cloud forest of Monteverde, Costa Rica. In this paper, we describe the dynamics of fine litter. This litter includes abscised leaves, small stems (<3 cm in diameter), and reproductive parts of trees and understory plants rooted in the forest floor and soil. We report forest floor standing litter mass, composition, and nutrient content; biomass and nutrients of litter components deposited to the forest floor; biomass and nutrient turnover of litter, assuming a forest in steady state; and calculations of nutrient use efficiency and retranslocation as indicated by element/biomass ratios of leaf litter and nutrient concentrations of live foliage for the most common tree species in the forest. We compare these with data from other wet tropical montane forests and discuss the temporal and spatial dynamics of fine litter. Elsewhere, we report similar information on litter derived from epiphytic plants in the canopy of this forest (Nadkarni & Matelson 1992).

MATERIALS AND METHODS

STUDY SITE.—Fieldwork was conducted from 1 April 1987 to 7 July 1990 in the Monteverde Cloud Forest Reserve (MVCFR), a lower montane wet forest along the Cordillera de Tilarán, Costa Rica (10°12'N, 84°42'W). The study area was in Leeward Cloud Forest described by Lawton and Dryer (1980). This area, composed of trees 15–30 m in stature, has a well-developed subcanopy, a moderately rich shrub layer, and a sparse herbaceous community. The epiphyte community is extremely diverse and abundant (Nadkarni 1986a). Branch surfaces in the crown interior of nearly all mature trees support thick mats of epiphytes (bryophytes,

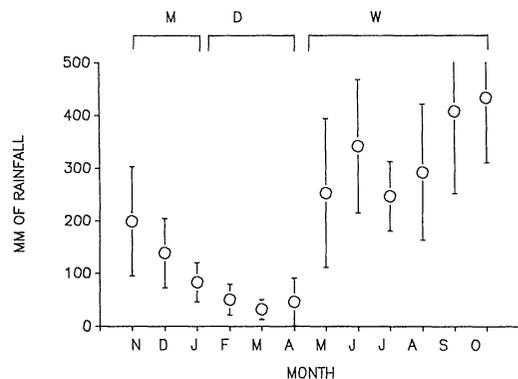


FIGURE 1. Mean monthly rainfall for Monteverde, averaged over measurements from 1953 to 1989. Rain gauge was located 2 km from the study site. Error bars are one standard error of the mean. Seasons are indicated at the top of the graph: M = misty-windy season; D = dry season, W = wet season.

herbs, woody shrubs, and hemi-epiphytes), and an interwoven root-humus mat up to 25 cm thick. Fallen epiphytic material is evident on the forest floor. The soil is classified as a Typic Dystrandept, derived from volcanic rhyolites, and is moist or wet throughout the year. A well-defined root mat lies atop the A horizon of the soil; 50 to 70 percent of fine root biomass in the soil is in the upper 10 cm of the soil profile (Vance & Nadkarni 1990).

Temperature is consistent all year with a yearly mean of 17.7°C and a range of 14.8°C to 20.7°C. Annual precipitation is recorded as 2000–2600 mm, but actual wet deposition is probably much higher because of the prevalence of wind-driven mist and fog that occurs throughout the year (Lawton & Campbell 1984). The climate of Monteverde has been roughly divided into three seasons (Fig. 1). The misty-windy season (November–January) is characterized by advective cloud cover and precipitation dominated by mist borne by the northeast tradewinds. During the dry season (February–April), advective cloud water and mist deposition occur, but measurable precipitation is low; bouts of strong tradewinds abate at the end of this season. The wet season (May–October) is characterized by low wind-speeds and convective precipitation, much of which originate in the Pacific-side lowlands.

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 area encompassed a variety of slopes (5% to 20%) and level areas and several current and recovering gaps

(25 m²–225 m² in area), and it appeared representative of montane wet forest. 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.—Between 26 June 1987 and 31 July 1990, the forest floor standing litter was sampled at varying intervals ranging between 3 and 6 months. In the study area, all material on the forest floor to the F₁ layer (fermentation layer, where material was substantially broken down through biological or physical action) was collected from 23 random points using a 0.5 × 0.5 m frame. Materials were placed in bags, dried at 60°C for 72 hr, and weighed. Samples from each date were bulked into three composites and each sorted into four components: leaves, small stems (<3 cm diameter), bryophytes, and miscellaneous. Bryophytes, which were all clearly epiphytic in origin, were subtracted from the total. The miscellaneous category was made of finely broken plant fragments which could not be identified with certainty. Careful examination of a subset of samples revealed most of the miscellaneous litter was composed of reproductive parts (flowers and fruits), leaf and root fragments, pieces of bark, invertebrate frass, and humus-like material. Subsamples of each component from each sampling period were ground and analyzed for nutrients at the University of California, Santa Barbara (UCSB). The nutrient pool of standing crop on the forest floor was calculated by multiplying the nutrient concentration of each component by the mean biomass of each component and summing for a total for each time interval.

LITTER PRODUCTION.—On 20 June 1987, 23 litterfall collectors were installed at random locations within the study area. Collectors were plastic buckets (55 cm high, 44 cm diameter) mounted on wooden stakes 1 m above the forest floor. Holes in the bucket bottom were covered with 2 mm nylon mesh to retain litter while allowing free passage of water. Litterfall was collected every 5 days for the first 2 months of the study, but since we observed little change in leaves retained in collectors for longer intervals, we made collections twice monthly for the rest of the study. In order to ascertain that the litter was not underestimated due to wind loss, we placed marked leaves in the buckets (10 per bucket) and monitored rates of loss for 14-day intervals between 24 April and 23 May 1988. This period of time encompassed a range of windy and windless days. Of the 460 leaves monitored, only one leaf was lost

which confirmed that negligible leaf loss due to wind had occurred. To identify possible seasonal trends, we performed a Fourier transform of the litterfall data over all collectors for each sampling interval to create a time series in the frequency domain (SYSTAT, Evanston, Illinois).

Fine litter from each collector was dried at 60°C to constant weight (24–48 hr), weighed separately, and mixed randomly into three composites per collection interval. Each composite was separated and analyzed the same way as used for forest floor standing litter. Nutrient input from litterfall for the first 18 months of the study (for which nutrient concentrations were directly measured) was calculated by multiplying the nutrient concentration of each fine litter component by the corresponding component mass at each harvest and summing all components. As we did not detect strong seasonal or yearly trends in nutrient concentrations, we multiplied the same nutrient concentrations by the biomass of the components collected at the same time intervals for the subsequent years of the study and summed the values. These values were averaged to estimate a total annual deposition rate of nutrients.

LIVE FOLIAGE.—A random subset of fourteen climbable trees in the largest size class (>80 cm dbh) in the study plot was chosen for sampling live foliage of trees. These included species in seven genera (*Ficus*, *Ocotea*, *Beilschmiedia*, *Meliosma*, *Dussia*, *Pouteria*, and *Matayba*) which are among the six most common families of trees (Moraceae, Lauraceae, Sabiaceae, Fabaceae, Sapotaceae, and Sapindaceae) in this forest type (Lawton & Dryer 1980). The sample trees were rigged and climbed with mountain-climbing methods (Perry 1978, Nadkarni 1988).

Live foliage was collected from sample trees from 24 April 1988 to 14 January 1989 at intervals of 1 to 6 weeks (mean interval between collections = 11 days, SEM = 2.4 days; total number of collection dates = 19). At least four trees were sampled at each harvest, and live foliage was collected from at least two locations within accessible areas of the crowns of the sample trees. We collected mature foliage only; leaves that appeared to have emerged recently (indicated by light green color and proximity to bud) were not taken. Any visible frass or detritus was removed from leaf surfaces. Leaves were bagged separately by tree, dried, processed, and analyzed for nutrients as the litter samples were. We calculated the mean nutrient concentration of live foliage by averaging the nutrient concentrations of tissue from the individual sample trees.

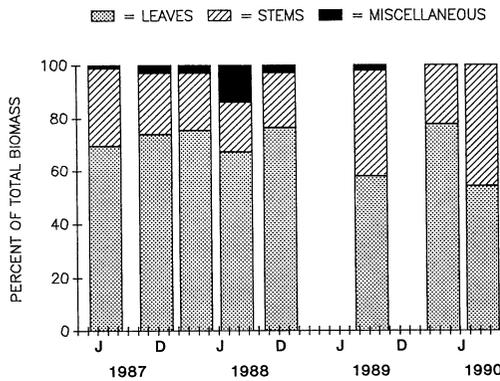


FIGURE 2. Composition of forest floor standing litter as a percent of total litter biomass during the study period.

NUTRIENT ANALYSIS.—Subsamples of forest floor standing litter, litterfall collected during the first 18 months of the study (20 June 1987 to 9 January 1990), and live foliage were ground in a Wiley Mill to pass a 40-mesh screen. Samples (*ca* 300 mg) were digested in an aluminum block digester (Technicon BD-40) following a modified Kjeldahl procedure with Se as a catalyst (Parkinson & Allen 1975). Solutions of organic N (urea, niacinamide) and organic P (phytic acid) compounds were analyzed throughout the study to confirm accuracy of the detection of N and P. Pretreatment for recovery of nitrate was not incorporated in the protocol; separate analysis of NO₃ (extractable in 1 N KCl) was performed on materials and was typically less than 3 percent of total N. A modified indophenol blue colorimetric method and a molybdenum blue procedure (Watanabe & Olsen 1982) were used to determine NH₄ and PO₄, respectively, in the digests. Cations were analyzed on a Varian AA6 atomic absorption spectrophotometer using an air acetylene flame.

RESULTS

LITTER MEASUREMENTS.—The mean total mass of the forest floor standing litter was 10.1 t ha⁻¹ (SEM ± 0.4), and varied considerably among collectors and seasons (range = 0.7 t ha⁻¹ to 13.0 t ha⁻¹). Standing litter differed significantly between sampling dates, based on a one-way ANOVA (*F* = 3.25; *df* = 166; *P* < 0.005). There was no effect of season in the total biomass of standing crop for any of the 3 years of the study (Table 1). However, there was an effect of year, with greater amounts of litter on the forest floor in 1988–1989. This coincided with

TABLE 1. Mean biomass (t ha⁻¹), SEM and number of samples taken by year and by season of forest floor standing litter produced by terrestrially rooted plants, based on a total of eight sampling times. The misty season is considered November to January, the dry season from February to April, and the wet season from May to October. Significantly different means (at the 0.05 level) occurred among years, but not among seasons.

Year	Mean litter mass by year		
	1977–88	1988–89	1989–90
Mean biomass	8.7	10.6	11.7
SEM	0.6	0.6	0.8
Number of samples	69	66	39

Season	Mean litter mass by season		
	Misty	Dry	Wet
Biomass	9.2	10.8	10.1
SEM	8.1	6.0	6.1
Number of samples	46	66	62

the aftermath of unusually high winds in the 1987–1988 misty-windy and dry seasons (pers. obs.).

The composition of standing crop varied considerably, with an overall mean (±SEM) percentage of constituents as: leaf litter, 71 percent (±17); stems, 27 percent (±17); and miscellaneous, 2 percent (±4). There was a greater proportion of stems (35%) in measurements taken during the wet season than during the dry (25%) and misty (22%) seasons (Fig. 2). Nutrient concentrations of components (Table 2) were comparable for other montane sites.

TABLE 2. Mean concentration (gm m⁻¹) of nutrients in components of forest floor standing litter. There were no significant differences among years or among seasons, so all concentrations are expressed as pooled means (± SEM). Misc = miscellaneous litter, unidentified parts plus reproductive parts.

Component	Nutrient				
	N	P	Ca	Mg	K
Leaves	16.2 (1.6)	0.7 (0.1)	20.7 (0.6)	1.8 (0.1)	1.7 (0.3)
Stems	15.4 (3.2)	0.6 (0.1)	24.8 (4.5)	1.3 (0.2)	1.4 (0.9)
Misc	12.1 (0.9)	0.7 (0.1)	8.2 (1.8)	1.5 (0.2)	1.7 (1.4)

TABLE 3. Mean nutrient concentration (mg g^{-1}) (\pm SEM) of components of litterfall from a montane tropical forest in Monteverde, Costa Rica.

Component	Nutrient				
	N	P	Ca	Mg	K
Leaves	14.7 (0.5)	0.8 (0.02)	19.1 (0.5)	2.7 (0.1)	1.2 (0.2)
Stems	10.9 (0.5)	0.6 (0.04)	16.8 (0.6)	1.7 (0.1)	2.2 (0.4)
Reproductive	12.5 (0.5)	1.1 (0.1)	12.3 (0.6)	1.8 (0.1)	3.8 (0.3)
Miscellaneous	19.3 (0.5)	1.2 (0.04)	14.4 (0.3)	1.7 (0.1)	2.8 (0.2)

The mean nutrient pool (kg ha^{-1}) was: N, 159; P, 6.7; Ca, 213; Mg, 17; K, 16.

LITTER PRODUCTION.—Litter from the collectors that was clearly epiphytic in origin (the bryophyte category, equivalent to less than 3% of the total) was subtracted from total litter deposited in the collectors. Because we were unable to distinguish the origin of individual leaves between epiphytic and terrestrially rooted plants, we assumed that all of the leaves were terrestrial in origin so our estimates may be an overestimate of terrestrially rooted plant litterfall. The mean biomass of fine litterfall was $7.0 \text{ t ha}^{-1} \text{ y}^{-1}$ ($\text{SEM} = 0.03$).

There appeared to be seasonal distribution in litterfall. The time series analysis revealed that there was one primary peak at a low frequency which

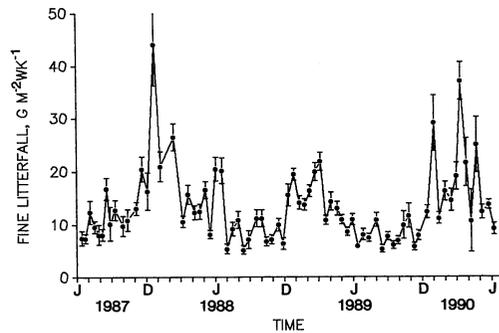


FIGURE 3. Biomass of fine litterfall during the study period. Bars represent one standard error of the mean.

closely matched the seasonal trend (Fig. 3). Litterfall was greatest in the misty-windy season; litterfall was 46 percent lower in the wet season ($9.3 \text{ g m}^{-2} \text{ wk}^{-1}$) than in the misty-windy season ($18.1 \text{ g m}^{-2} \text{ wk}^{-1}$). Litterfall was intermediate in the dry season ($14.4 \text{ g m}^{-2} \text{ wk}^{-1}$). The amounts of litterfall showed no striking differences among years.

The mean (\pm SEM) composition of fine litter was leaves, 68 percent (± 1.6); stems, 13 percent (± 1.2); reproductive parts, 10 percent (± 1.5); and miscellaneous, 9 percent (± 0.5). The composition of fine litter appeared to be fairly constant throughout the year (Fig. 4).

Nutrient concentrations of litterfall varied, but there did not appear to be any striking seasonal patterns. Generally, stems had the lowest nutrient content for all nutrients, leaves had the highest

TABLE 4. Mean nutrient concentrations (mg g^{-1}) (\pm SEM) of live foliage collected from trees between 24 April 1988 and 14 January 1989, pooled for all species and sampling intervals. Values represent means from 14 trees in six plant families. $N = 44$ sampling intervals overall, with three to six replicates per tree. P-values indicate the results of a one-way ANOVA testing the effects of season on nutrient concentration. See text for mean annual values.

Nutrient	Season			P
	Misty	Dry	Wet	
N	18.4 (1.2)	26.7 (3.4)	21.9 (2.7)	0.007
P	1.4 (0.2)	2.3 (0.5)	1.3 (0.7)	0.002
Ca	11.9 (2.3)	5.7 (1.3)	7.8 (0.6)	0.024
Mg	2.4 (0.3)	2.0 (0.1)	1.9 (0.1)	0.265
K	2.3 (0.5)	11.7 (1.1)	8.5 (0.8)	0.001

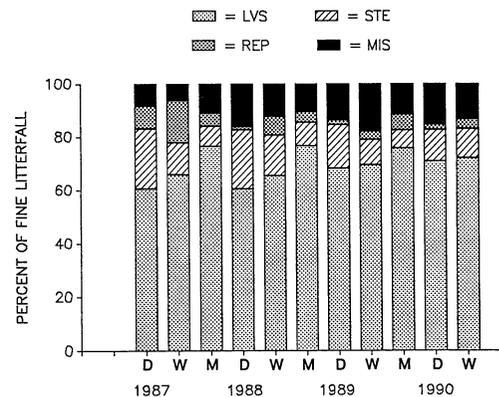


FIGURE 4. Composition of fine litterfall by season. LVS = leaves; STE = stems < 3 cm in diameter; REP = reproductive parts; MIS = miscellaneous litter.

TABLE 5. *Elemental concentration, nitrogen to phosphorus ratios, and nitrogen and phosphorus retranslocation^a of live foliage and leaf litter in tropical montane forests.*

Site	Elements (%)		N/P ratio	Retranslocation	
	N	P		N (%)	P (%)
Venezuela ^b					
live foliage	1.74	0.08	22		
leaf litter	1.2	0.06	20	31	25
Papua New Guinea ^c					
live foliage	1.32	0.09	15		
leaf litter	1.3	0.07	19	2	22
Colombia ^d					
live foliage	1.8	0.1	18		
leaf litter	1.1	0.06	18	38	40
This study					
live foliage	1.97	0.14	14		
leaf litter	1.47	0.08	18	25	42

^a Calculated as % retranslocation = (element concentration in live foliage - litterfall)/(concentration in live foliage).
^b Fassbender and Grimm 1981.
^c Grubb and Edwards 1982.
^d Veneklaas 1991.

concentrations of Ca and Mg, and miscellaneous and reproductive material were highest in N and P. There was no clear pattern for K.

Mean nutrient concentrations of litterfall (Table 3) were generally comparable to those in the forest floor standing litter (Table 2). The concentration of N in litterfall was slightly lower than in leaves and stems on the floor, probably due to microbial immobilization in the forest floor litter. The slightly lower concentrations of Mg in leaves and stems and of K in stems and miscellaneous material in the standing litter were probably caused by leaching of these materials after they had been deposited on the forest floor. The mean annual nutrient input (kg ha⁻¹ y⁻¹) for fine litter was: N, 93; P, 6; Ca, 115; Mg, 15; and K, 12.

LIVE FOLIAGE.—Mean concentrations (±SEM) of live foliage (mg g⁻¹) were: N, 19.7 (0.7); P, 1.4 (0.1); Ca, 8.5 (0.7); Mg, 2.0 (0.1); and K, 7.4 (0.7). The concentration of all elements except Mg was higher in live leaves than in the leaf component of litterfall (Table 4). There were striking seasonal differences in concentrations of all nutrients in live foliage except Mg. Nitrogen, P, and K concentrations were highest during the dry season; Ca concentrations were highest during the misty season (Table 4).

TABLE 6. *Fine litter production, nutrient transfer in litter, forest floor standing litter mass, annual decay constant (K_d), and biomass/element ratio of fine litter in tropical montane forests, based on steady state assumptions. * = not reported.*

	Litterfall (T ha ⁻¹ yr ⁻¹)		Nutrient transfer (kg ha ⁻¹ yr ⁻¹)					Forest floor standing crop (T ha ⁻¹)	Annual decay constant (K _d) ^a	Biomass/element ratio		Source
	N	P	N	Ca	Mg	K	N			P		
Costa Rica	7.0	6	93	115	15	12	10.1	0.69	75	1270	This study	
Venezuela	7.0	4	69	43	*	*	*	*	101	1750	Fassbender and Grimm 1981 Tanner 1977	
Jamaica												
Mor ridge	6.6	1.3	39	34	*	*	*	*	169	5076		
Mull ridge	5.5	1.5	94	50	*	*	*	*	112	3666		
wet slope	5.5	2.1	34	53	*	*	*	*	162	2620		
Puerto Rico	*	*	*	*	*	*	5.1	0.94	*	*	Wiegert and Murphey 1970	
Colombia	11.6	*	*	*	*	*	16.5	0.61	*	*	Jenny <i>et al.</i> 1949	
New Guinea	7.6	5	90	95	*	*	6.4	1.17	84	1520	Edwards 1982	

^a K_d = annual litterfall/forest floor standing crop (Olson 1963).

Retranslocation of N and P was calculated, following Veneklaas (1991), by dividing the difference between elemental concentrations of live foliage and litterfall by the concentration of that element in live foliage. The percent retranslocation of N and P was calculated as 25 percent and 42 percent, respectively, which is comparable to other montane forests (Tanner 1980a) (Table 5).

DISCUSSION

In this study, the values for the mass and nutrient concentrations in the forest floor standing litter and litterfall are within the ranges reported for other wet tropical montane and lower montane forests (Table 6). The litter input we report ($7.0 \text{ t ha}^{-1} \text{ y}^{-1}$) may be an overestimate of litterfall material derived from terrestrially rooted plants. Some of that litter is derived from the abundant epiphyte community which ultimately may derive at least a portion of its nutrients from atmospheric sources (Nadkarni & Matelson 1991, 1992). Further measurements to separate epiphyte from tree leaves in the collectors is needed to quantify that overestimate.

In contrast to other montane forest sites (*e.g.*, Edwards 1982), the forest floor litter mass and composition in Monteverde did not show seasonality. As with other tropical forests (Vitousek & Sanford 1986), however, there were seasonal differences in the rates of litterfall, with the greatest amounts of fine litter falling during the misty-windy season. The relationship of litterfall to weather patterns, which has been documented for other montane forests (Tanner 1980b), awaits quantified meteorological data, especially the input of mist and windspeed. Litterfall pulses appeared to coincide with strong bouts of wind during the dry and the misty seasons. Unfortunately, there are no quantitative wind data from our research area at this time.

The amounts of N, P, Ca, and K transferred in litter to the forest floor at Monteverde are high compared to those reported from other tropical montane forests (Table 6). In Monteverde, the large quantity of nutrient return in litterfall (despite moderate retranslocation rates) is caused by comparatively high concentrations of nutrients (except Mg) in the live tree foliage (Fassbender & Grimm 1981,

Grubb & Edwards 1982, Tanner 1985). The foliar nutrient levels we found in Monteverde fall more closely within the range reported for forests growing on alfisols and other moderately fertile tropical sites (Vitousek & Sanford 1986).

Why might trees in this forest support foliage with high nutrient concentrations? One reason is that large amounts of nutrients come into the system via interception of precipitation, especially in the form of wind-blown mist. Collection of this precipitation may be facilitated by the interceptive capacity of the abundant epiphytes in this forest (Nadkarni 1986a, b). Other montane and lowland forests may not receive as much direct atmospheric input of precipitation in this form (Vitousek and Sanford 1986). Secondly, the soils upon which the forest grows may be relatively fertile, in at least some macronutrients, as they are of recent volcanic origin. Mineralization rates of N and P in the field on the forest floor are fairly high (Vance & Nadkarni 1990).

Nitrogen and P availability in our study area, as indicated by high foliar concentrations and only moderate retranslocation, appears comparable or even higher than in other tropical montane forests (Table 6). Nutrient use efficiency (calculated as biomass/nutrient return) is low relative to other tropical forest and other montane forests (Table 6). The Monteverde forest may be less limited by nutrients than are the other cloud forests. Cloud forests as a vegetation type are diverse with respect to their nutrient cycling regimes. Until the amounts of nutrient input from such sources as mist can be quantified, the reasons for these differences will be difficult to ascertain.

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