Plant and Soil **142**: 31–39, 1992.

PLSO 8888

Root biomass distribution in a moist tropical montane forest

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Received 19 September 1990. Revised November 1991

Key words: canopy, nutrient cycling, root biomass, tropical forest

Abstract

Root biomass was measured in the soil and canopy of a tropical montane forest in Costa Rica. Below-ground total root biomass in the soil of this forest ranged from 1600 g m^{-2} to 7200 g m^{-2} and biomass of fine roots (<2 mm diam.) ranged from 300 g m^{-2} to 1300 g m^{-2}, depending on slope position. A root mat was present on the forest floor which contained 50 to 70% of the below-ground fine root biomass. A similar estimate was obtained for fine root biomass in the forest floor ($H + A_1$ horizons) using both soil cores (10 cm diam. n = 15) and excavated soil pits (1 m^{-2}, n = 4). About 5% of the below-ground fine roots and 13% of the below-ground total root biomass resided in the B_2 horizon, which extended from 85 to 185 cm below the forest floor surface.

Root biomass on surfaces of inner branches and at branch junctions within the upper canopy of mature trees totaled 72 g m^{-2} forest floor area. Fine root biomass (<2 mm) in the canopy comprised about 45% of total canopy root biomass and about 5% of the below-ground fine root biomass. About 80% of canopy root biomass was found at branch junctions. The fine root density in canopy humus accumulated at these junctions was about 20% higher than that found in the forest floor humus layer, resulting in a potentially effective system for exploiting stemflow nutrient inputs. Root biomass in the canopy could be important in conserving nutrients mineralized from canopy humus, and those entering this forest in mist and rain.

Introduction

Knowledge of the structure and function of tropical rainforests is often limited by the lack of information on plant roots. The difficulty in excavating root samples at depth, coupled with the knowledge that many tropical forests occur on nutrient poor soils and tend to be shallow rooted (Jordan, 1985) has led to a preponderance of root studies concentrating on the upper 50 cm of soil (Gower, 1987; Jordan, 1985; Lawson et al., 1970; Raich, 1980; Singh and Singh, 1981) that is not always justified.

In some moist tropical forests, the canopy provides a second habitat for roots which could be potentially important in ecosystem functioning. Canopy roots can be derived from vascular epiphytes growing on tree branches, from the host trees themselves (Nadkarni, 1981) or from neighboring plants with roots that grow apogeotropically (Sanford, 1987). These roots are functional absorptive organs (Nadkarni and Primack, 1989; Sanford, 1987), so their presence increases the total nutrient absorption potential of many tropical forests. Nutrients may become available in the canopy either through microbial mineralization of canopy humus (Vance and Nadkarni, 1990), nitrogen fixation (Forman, 1975) or from the trapping of mist and rain inputs. Although canopy roots could be important in the cycling of

nutrients and carbon in some tropical forests, they have been largely ignored in ecosystem studies.

This paper is the first quantitative estimation of the root biomass held within the canopy of a tropical forest ecosystem. We report on the distribution and size class relationships of roots through the B horizon (to a depth of 85–185 cm) in the soil and in the canopy of a tropical montane forest in Costa Rica.

Methods

Site

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 September 1988. The study area was in a tropical lower montane wet forest (1550 m elevation) on the continental divide with wind and moisture derived from both the Caribbean and Pacific Oceans. The site is 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 approximately 150 trees ha^{-1} (>10 cm DBH). Because of high moisture (ca 2000 mm annual precipitation) and nutrient input from mist and rain, the trees in this forest have high densities of epiphytic plants with large accumulations of organic matter in the canopy. The understory is fairly open, with a poorly developed herbaceous layer. Many treefalls and gaps in various stages of recovery are evident. The soil is classified as a *Typic Dystrandept* (Table 1).

The epiphyte community of the Monteverde cloud forest is described by Nadkarni (1986). Unlike some other forests, tree species does not seem to be an important determinant of epiphyte biomass and organic matter accumulation on mature trees. Branch surfaces in the crown interior of nearly all mature trees support thick matters of epiphytes (bryophytes, herbs, woody shrubs, and hemi-epiphytes), and an interwoven root-humus mat up to 25 cm thick, with greatest accumulations on junctions of large branches. Outer branches and branch tips are partially to completely covered with mosses and other bryophytes, and small herbaceous plants with little or no accumulated humus. Relative to the forest floor, the upper tree canopy experiences more wind (Lawton, 1982), and more frequent wetting/drying cycles (Bohlman and Nadkarni, 1991).

In April 1987, a 2 ha study area, divided into 20 m × 20 m quadrats, was established within the 10 ha research area of the MVCFR. We marked and measured all trees >10 cm DBH in the study area; canopy height was 18–25 m; mean tree DBH was 65 cm. Within this area, we divided an intensive study subplot (60 m × 40 m) into 5 m × 5 m quadrats.

Below-ground root biomass determination

For determination of below-ground root biomass by horizon, four 1 m^2 soil pits were excavated within the intensive study subplot. All soil and roots were bagged and transported to the labora-

Table 1. Soil description

Horizon	Approximate Depth (cm)	pH(H_2O)	Color[a]	Texture	Structure	Bulk density ($g\,cm^{-3}$)
H/root mat	0–15	4.4	dark reddish brown 5 YR 3/3		weak to moderate crumb	0.046
A_1	15–20	4.7	dark brown 7.5 YR 3/4	loam	weak to moderate crumb	0.31
A_2/B_1	20–85	5.3	strong brown 7.5 YR 4/6	loam to sandy loam	weak crumb to moderate sub-angular blocky	0.50
B_2	85–180	5.5	strong brown 7.5 YR 4/6	clay loam	moderate sub-angular blocky	0.63

[a] determined using Munsell color chart.

tory where thorough measurements of both coarse and fine roots could be made. Two of the pits (pits 1 and 2) were on the non-sloping (below the slope) portion of the site and two (pits 3 and 4) were dug on the lower portion of a ca 15° slope. Soil horizons were designated as H, A_1 and A_2/B_1 and B_2. Measurements of root biomass in the B_2 horizon, which extended from about 85 to 180 cm deep, were made for soil from one of the pits.

Biomass of living roots only was measured. Roots which were structurally sound and contained white-colored, inner tissue were assumed to be living. To expedite processing, soil from each horizon was first coarsely sieved (<6.4 mm) and retained roots were collected and were washed over a 2 mm sieve with water. Washed roots were separated into <1, 1–2, 2–5 and >5 mm size classes, oven-dried (60°C until a constant weight was obtained), and weighed. Extended periods of drying were needed for very coarse roots before a constant weight was obtained; a drying time of 48 hr was sufficient for fine roots.

To determine the proportion of very fine roots (<1 mm) passing through the 6.4 mm sieve during processing, aliquots of coarsely sieved soil (10–20 replicates per pit, 20 g each) were washed through a 2 mm sieve with water and the proportion of roots lost per g dry weight of soil determined. Aliquots (2 replicates, 2 to 3 g each) of soil passing through the 2 mm sieve were then washed through a 50 mesh sieve with water to determine the proportion of roots not retained by the 2 mm sieve. Larger diameter roots (>1 mm) lost during sieving and washing were found to be negligible.

Total root loss (<1 mm only) due to sieving and washing was determined by multiplying the roots lost per g soil from each procedure by the total dry weight of soil for each horizon. Total root loss was then added to the root biomass obtained from the initial sieving and washing to calculate biomass of very fine roots (<1 mm) per soil horizon. The proportion of very fine roots lost through the 6.4 mm sieve but retained by the 2 mm sieve ranged from 28 to 76%, while the proportion lost through the 2 mm sieve ranged from 11 to 26%. Thus, fine root biomass would be considerably underestimated if 2 mm was the finest mesh size used without correcting for this loss. The proportion of the very fine root biomass (<1 mm) lost during washing of roots over the 2 mm sieve ranged from 1 to 5%.

To encompass horizontal variation in the upper horizons of the forest floor, we also sampled 15 randomly located points within the study area to a depth of 20 cm below the forest floor surface using a 10 cm diam. corer. This depth approximated the combined depth of the H and A_1 horizons and allowed a comparison of root biomass determined using the soil pit excavations. The core samples were processed using the same procedures as described for the pit samples.

Canopy root sampling and biomass determination

Organic matter residing in the canopy and derived mainly from epiphytic material (EM) in this forest is found in four major locations and forms: (1) Upper surfaces of branches; (2) branch and branch/trunk junctions; (3) trunks, and (4) understory plants. Nearly all organic matter and roots are found in the first two locations, so we concentrated on root biomass from EM at branch junctions and on branch surfaces of the inner crown of mature trees in this study. As a result, our ecosystem-level measures of canopy root biomass are underestimates as some root biomass and organic matter occurs on trunks and understory plants.

All trees over 10 cm DBH were stratified to an EM cover class, using a quartile index (1 = 0–25% cover, 2 = 25–50% cover, 3 = 50–75% cover, 4 = 75–100% cover). For a subsample of the trees, two individuals independently rated trees for cover class designation, and arrived at the same ratings. Epiphytic matter and associated roots were sampled on a random subset of trees with epiphyte cover of 3 or 4 of the two largest tree size classes (>45 cm DBH and >12 m in height). Overall, EM from 11 trees of eight genera were sampled (Table 2). These included species in seven genera which are among the six most common families of trees of this forest type (Lawton and Dryer, 1980). The sample trees were rigged and climbed with

Table 2. Tree taxon, diameter at breast height (DBH), and number of samples taken from trees for estimation of canopy root biomass

Tree taxon	DBH (cm)	Number of samples	
		Inner branch	Branch junctions
Beilschmeidia sp.	101.0	3	0
Beilschmeidia sp.	113.5	15	3
Ficus tuerckheimii	238.0	19	0
Ficus tuerckheimii	192.0	11	5
Ficus tuerckheimii	185.5	17	2
Beilschmeidia sp.	101.5	3	1
Guarea sp.	61.0	6	2
Ocotea tonduzii	60.0	3	1
Ocotea meziana	77.0	5	1
Pouteria sp.	70.1	20	2
Unknown	70.0	11	2
Total		111	19

mountain-climbing methods (Nadkarni, 1988; Perry, 1978).

Samples of EM and associated roots were collected from all accessible inner branches greater than 8 cm diameter (1 to 7 branches per tree) within a 5 m radius of the central trunk. All branches were located within the mid-crown (14–23 m above the forest floor). Three to six EM samples per branch (10–15 cm in length and, for three of the trees, one 75 cm sample per branch, 111 samples total) (Table 2) were collected by cutting through live and dead material around the circumference of the branch. Branch circumferences were recorded for each sample.

To measure EM and root biomass at branch junctions, two to four major branch-branch or branch-trunk intersections were selected from the upper crown of nine of the sample trees (19 junctions total) (Table 2). Branch junctions were chosen by taking a random subsample of branches used for the inner branch surface sampling described above. Surface litter was removed and cores (ca 10 cm × 15 cm × 30 cm) were cut into the pockets of humus and root material. The total volume of each branch junction was measured.

Each sample was bagged separately and roots were hand-sorted into the same size classes as used for below-ground roots. Fine root fragments were weighed separately and included in the biomass of the <1 mm size class. Roots were dried, sieved and sorted as described above.

To extrapolate canopy root biomass to a forest floor area basis, the number of branch junctions and length of branches that supported mats of crown humus (10 cm thick or greater) were visually estimated for 26 trees in the same size and epiphyte cover categories as the 11 sample trees. The crowns of all of these trees were visible from the trees we sampled for EM biomass estimations. From these counts, we calculated the mean surface area of inner branches and the number of branch junctions per tree. These estimates were multiplied by the biomass estimates of EM and roots on a branch-area and junction-volume basis to extrapolate to a whole-tree estimate of EM biomass. This estimate was multiplied by the mean density of trees in the same epiphyte cover and size class to estimate canopy root biomass of this EM type on a forest floor area basis. Values thus calculated underestimate total ecosystem EM, as EM also exists on trees with EM cover values of 1 and 2, on trunks and outer branches, and on understory vegetation which were not included in these calculations. Due to the lack of covariate information on branch dimensions and canopy root density, standard errors for canopy root biomass per area forest floor were not calculated.

Results and discussion

Below-ground root biomass

Total below-ground root biomass ranged from 1550 g m^{-2} on the sloping portion of the site to 7220 g m^{-2} on the non-sloping portion of the site (Fig. 1). This variation within our site spans the range of total root biomass reported for tropical montane forests (Edwards and Grubb, 1977; Jordan, 1985; Vitousek and Sanford, 1986) although estimates of total root biomass in other tropical forest types have been as high as 10,000 to 20,000 g m^{-2} (Jenik, 1971; Klinge, 1975; Klinge and Herrera, 1978). Fine root biomass (defined as roots with diameters <2 mm) ranged from 300 g m^{-2} on the slope to 1300 g m^{-2} on the non-sloping portion of the site (Fig. 1).

Fine root biomass in the H and A_1 horizons of the forest floor measured by 2 pit excavations on the non-sloping portion of the site (pits 1 and 2)

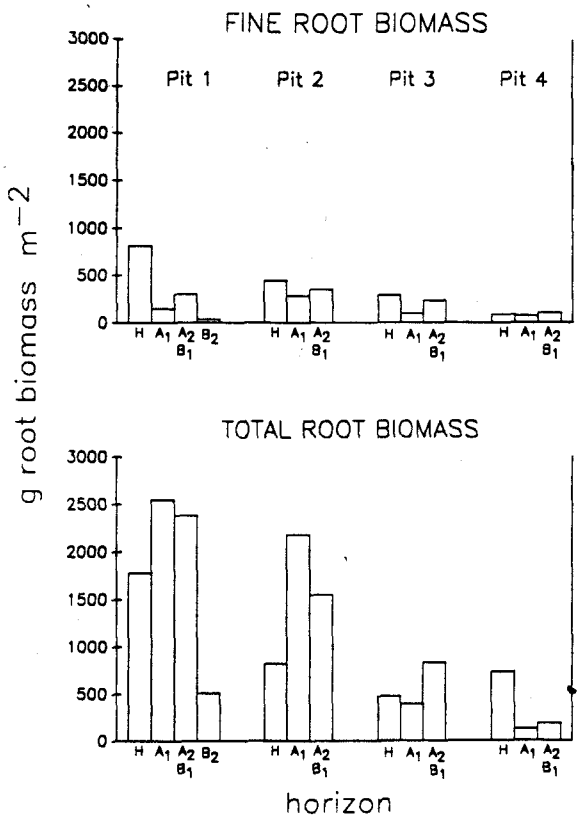

Fig. 1. Fine and total root biomass depth distribution for each soil pit.

was comparable to measurements made using soil cores: 840 g m^{-2} using pit excavations and 940 +/− 60, S.E. g m^{-2} using the cores. Fine root biomass comprised between and 20 and 40% of total below-ground root biomass (Fig. 1, Table 3). The proportion of total root biomass comprised of fine roots in tropical ecosystems varies widely, with reported ranges from 20 to 70% (Huttel, 1975; Klinge, 1975; Klinge and Herrera, 1978; Murphy and Lugo, 1986; Singh and Singh, 1981).

Despite the presence of a thick root mat in the highly organic H and A_1 horizons (ca 0–20 cm depth), greater than 30% of fine root biomass occurred below this depth (Fig. 1, Table 3). About 56% of total root biomass occurred in the H and A_1 horizons (ca 0–20 cm depth), greater than 30% of fine root biomass occurred below this depth (Fig. 1, Table 3). About 56% of total root biomass occurred in the H and A_1 horizons. Lawson et al. (1970) found that 80 to 85% of the total root biomass was in the upper 10 cm layer on upper and middle slopes of a tropical moist semi-deciduous forest catena, decreasing to 50% on the bottom slope. Other studies have shown 60 to 90% of total root biomass in the root mat/humus layer of tropical forests (Klinge, 1973; Klinge and Herrera, 1978; Stark and Spratt, 1977).

One of our soil pits was excavated to a depth of 180 cm, which was the bottom of the B_2 horizon. Although occurring below about 85 cm, the B_2 horizon contained about 40 g m^{-2} fine root biomass, which represents about 5% of the total below-ground fine root biomass (Table 3). Total root biomass in the B_2 horizon was about 13% of the below-ground total.

Table 3. Below-ground and canopy total and fine root biomass

	Soil horizons					Canopy				
	H	A_1	A_2B_1	B_2	Total	Inner branch surfaces		Branch junctions		Total
	(g roots m^{-2} forest floor[a])					(g m^{-2} branch)	(g m^{-2} forest floor)	(g dm^{-3} branch junctions[c])	(g m^{-2} forest floor)	(g m^{-2} forest floor)
Fine root biomass (<2 mm)	410 ± 150	150 ± 50	250 ± 50	40	850	105 ± 4	5	5.1 ± 0.8	26	31
Total root biomass	950 ± 280	1310 ± 610	1240 ± 470	510	4010	353 ± 50	16	10.9 ± 1.1	56	72

[a] mean ± S.E.; n = 4.
[b] mean ± S.E.; n = 111.
[c] mean ± S.E.; n = 19.

Canopy root biomass

The total biomass of roots in the canopy was estimated to be 72 g m^{-2} of forest floor area, which is about 2% of the total below-ground root biomass (Table 3). We calculate the biomass of fine roots (<2 mm) in the canopy to be 31 g m^{-2} forest floor area, or about 45% of the total canopy root biomass. Thus, the proportion of total canopy root biomass comprised of fine roots is larger than found in any of the below-ground horizons.

Canopy fine root biomass was distributed in two distinct spatial microhabitats. These two habitats were considered separately due to the different techniques required for their study and to their potential difference in ecological significance. One habitat was within humus mats, which were about 10 cm thick on average and occurred along inner branch surfaces (beginning about 1 m from the central trunk). On inner branch surfaces, total root biomass averaged 350 g m^{-2} branch (Table 3). About 30% of the total root biomass on branch surfaces was comprised of fine root biomass. The total weight of roots on inner branches, expressed per unit branch surface, was about 37% of the roots in the H horizon of the forest floor, expressed per unit forest floor area.

The second habitat observed for canopy roots was within deeper humus pockets at branch junctions. Although branch junctions represent considerably less surface area than inner branch surfaces, they hold about 80% of the total canopy root biomass. Per unit forest floor area, branch junctions contain three times more total root biomass and five times more fine root biomass than inner branch surfaces (Table 3). Fine roots comprised ca 45% of total root biomass at branch junctions.

Below-ground and canopy root density

The density of roots in a particular environment relates to their absorption capacity and potential for conserving nutrients (Jordan, 1985). As might be expected, below-ground root densities decreased with depth from the forest floor H and A_1 horizons to the lower mineral soil (Table 4). The very high total root density in the A_1 horizon was due to the inclusion of a few very large roots in our samples. The number of soil pits used for sampling was probably inadequate for very coarse roots due to their highly variable distribution. Fine root density at branch junctions was about 20% higher than found in the forest floor (Table 4). Root density on inner branch surfaces, however, was lower than found in the forest floor.

Table 4. Root density (mg root cm^{-3} soil[a]) of canopy epiphytic material (EM) and soil horizons

Sample	Fine roots (<2 mm)	Total roots
EM		
Inner branches	1.7 ± 1.2	5.6 ± 0.8
Branch junctions	5.1 ± 0.8	10.0 ± 1.1
Soil horizons		
H	3.8 ± 0.9	9.9 ± 2.1
A_1	4.4 ± 1.0	44.6 ± 27.0
A_2/B_1	0.6 ± 0.0	2.9 ± 0.9
B_2	0.1[b]	1.7[b]

[a] mean ± S.E., n = 111 for inner branches, n = 19 for branch junctions, n = 4 for soil horizons.
[b] determined for one pit only.

Root size distribution

For roots below 5 mm diam. (i.e., from the <1 mm, 1–2 mm, and 2–5 mm size classes), the <1 mm size class comprised the highest proportion of biomass in both canopy and below-ground environments, often three times the biomass as roots in either of the other two size classes (Table 5). The highest percentage of fine roots (<2 mm) occurred in branch junctions. Roots less than 1 or 2 mm in diameter commonly comprise a considerable proportion of the root biomass in tropical soils (Gower, 1987; Klinge, 1973; Stark and Spratt, 1977; Srivastava et al., 1986).

The distribution of fine roots reflects the distribution of available nutrients within an ecosystem (Jordan, 1985; Vitousek and Sanford, 1986). The productivity of tropical montane forests may be limited by the availability of nutrients (Grubb, 1977; Vitousek and Sanford, 1986). Atmospheric deposition probably provides the ultimate source of nutrients which could be potentially exploited by canopy roots, as only very

Table 5. Root size distribution (g root biomass per unit area[a,b,c,d]) in canopy epiphytic material (EM) and soil horizons

Sample	Size class (mm)			
	<1	1–2	2–5	>5
EM				
Inner branches[c]	110 ± 10(31.3)	30 ± 4(8.6)	80 ± 30(22.9)	130 ± 40(37.2)
Branch junctions[d]	6.7 ± 1.3(48.3)	1.0 ± 0.5(7.2)	2.5 ± 0.8(18.4)	3.6 ± 1.7(26.1)
Soil horizons				
H	300 ± 210(31.2)	110 ± 90(11.5)	110 ± 90(11.5)	440 ± 310(45.8)
A_1	130 ± 80(9.9)	20 ± 10(1.5)	40 ± 20(3.1)	1120 ± 1140(85.5)
A_2/B_1	190 ± 90(15.3)	60 ± 20(4.8)	90 ± 50(7.2)	900 ± 820(72.6)
B_2^e	90(15.5)	17(2.9)	23(4.0)	450(77.6)

[a] mean ± S.E., n = 111 for EM inner branches, n = 11 for EM branch junctions, n = 4 for soil horizons.
[b] percent of root biomass in all size classes in parentheses.
[c] for EM (inner branch surfaces), biomass expressed as g m^{-2} branch area.
[d] for EM (branch junctions), biomass expressed as g dm^{-3} branch junction.
[e] biomass determined for one pit only.

small amounts of nutrients within the canopy are derived from intercepted host tree litterfall (Nadkarni and Matelson, 1991). It is likely that the interception of mist, which is a frequency occurrence at our study site, provides a major nutrient flux to the canopy. Nutrients are also trapped on leaf and branch surfaces through dry deposition and are leached from leaves during precipitation events. The nutrients associated with this throughfall were found to be similar to the nutrient return in litterfall in one montane forest in New Guinea (Edwards, 1977). Throughfall nutrient concentrations in this forest have been found to be comparable to those in other tropical cloud forests (Clark and Nadkarni, 1990; Vitousek and Sanford, 1986). Comparisons of NO_3^- and NH_4^+ concentrations in bulk deposition versus throughfall suggest that the canopy is a significant sink for NO_3^- (ca 85% of total wet deposition) during the transition between dry and wet seasons (April–July, 1989) and a significant sink for NH_4^+ (40% of total wet deposition) during the latter part of the dry season (Clark and Nadkarni, 1990).

Due to the large proportion of canopy roots which reside at branch junctions, the trapping of nutrients contained in stemflow could be of particular significance. Stemflow was found to contribute up to 5% of the total water borne nutrient input to a Puerto Rican montane rain forest (Clements and Colon, 1975) and up to 20% in forests containing large proportions of smooth-barked tree species (Parker, 1983). Further work on nutrient fluxes in the canopy is needed to differentiate the relative roles of various canopy components in altering nutrient concentrations and forms entering the system via precipitation.

The turnover of canopy organic matter also provides nutrients which could be exploited by host tree and epiphytic root systems on branch surfaces and junctions. Nutrients associated with accumulated organic matter in tropical cloud forest canopies can be considerable, equivalent to 45% of the above ground foliage in one neotropical elfin forest (Nadkarni, 1984). At our study site, rates of microbial mineralization of N per g canopy humus was found to be similar to that occurring in forest floor humus (Vance and Nadkarni, 1990). It is therefore not surprising to find high densities of canopy fine roots exploiting these varied sources of nutrients.

Conclusions

We provide data on the below-ground and canopy root biomass in a moist tropical montane forest. The substantial biomass of fine roots at lower soil depths found in this study suggests a potential mode of nutrients conservation which has not been widely documented. Although the biomass of canopy roots is small relative to that

found below-ground, they appear to occupy an important niche in this forest due to their access to potentially large fluxes of nutrients passing through the canopy in mist and rain and mineralized from canopy humus. High concentrations of roots at branch junctions could be particularly effective in exploiting nutrients in stemflow. Canopy roots could thus act as an important nutrient conserving mechanism in the montane rain forest ecosystem by trapping a portion of these nutrient inputs before they reach the forest floor.

Acknowledgements

We thank Teri Matelson for technical support in the canopy and on the ground, Marco Tulio Arguedas and Guillermo Vargas for help in root washing and sorting, Kent Schwaegerle for statistical advice and Jim Crisp and Jack Longino for valuable discussion. We also thank the Tropical Science Center and the Monteverde Cloud Forest Reserve for access to the reserve and coordination of site activities. This work was sponsored by the National Science Foundation (BSR 86-14935 and 90-18006), the Whitehall Foundation and the University of California Academic Senate. Early stages of this research were conducted while the authors were based at the University of California-Santa Barbara.

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