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Fine-root biomass and soil properties in a semideciduous and a lower montane rain forest in Panama

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Abstract

The distribution of root biomass and physical and chemical properties of the soils were studied in a semideciduous and in a lower montane rain forest in Panama. Roots and soil samples were taken by means of soil cores (25 cm deep) and divided into five, 5-cm deep sections. Soils were wet-sieved to retrieve the roots that were classified in four diameter classes: very fine roots (<1 mm), fine roots (1–2 mm), medium roots (2–5 mm) and coarse roots (5–50 mm). Soil samples were analyzed for organic carbon, total nitrogen, available phosphorus, exchangeable bases, cation exchange capacity, pH, aluminium and exchangeable acidity. Total root biomass measured with the soil corer (roots <50 mm in diameter) was not different between the forests (9.45 t ha^{-1}), while biomass of very fine roots was larger in the mountains (2.00 t ha^{-1}) than in the lowlands (1.44 t ha^{-1}). The soils in the semideciduous forest were low in available phosphorus, while in the mountains, soils had low pH, high exchangeable aluminium and exchangeable acidity, and low concentration of exchangeable bases. Phosphorus was in high concentration only in the first 5 cm of the soil. In both forests, there was an exponential reduction of root biomass with increasing depth, and most of the variation in the vertical distribution of roots less than 2 mm in diameter was explained by the concentration of nitrogen in the soils. The results of this study support the hypothesis that a large root biomass in montane forests is related to nutrients in low concentration and diluted in organic soils with high CEC and low bulk density, and that fine root biomass in tropical forests in inversely related to calcium availability but not a phosphorus as has been suggested for other forests.

Introduction

Tropical rain forests are usually associated with soils of low pH, and low exchangeable cations, that are usually infertile for temperate type crops (Sanchez, 1976). Several mechanisms have been described for the enhanced efficiency of nutrient uptake (Jordan and Herrera, 1981), including retranslocation of nutrients before leaf shedding (Vitousek and Sanford, 1986), and roots growing vertically upward along the stems of trees (Sanford, 1987) and in the canopy (Stark and Spratt, 1977) to recover nutrients from rain and stemflow. The most important mechanism for nutrient cycling is located in the large root system close to the soil surface (Jenik, 1978; Klinge, 1973), with fine roots associated with mycorrhizal fungi. This association is very important for the recovery of nutrients from dead organic matter, by-passing the mineral phase of the soil (Stark, 1971b; Went and Stark, 1968). Although rootmats are found in some lowland rain forests

growing on nutrient poor soils (Klinge, 1973), root systems in lowland forests are usually less conspicuous than in montane forests, where an increase in the number of roots with increasing altitude have been interpreted as a result of nutrient shortage (Odum, 1970). Although high root biomass and high root/shoot biomass ratios are generally found in plants and communities growing in nutrient-poor habitats there is little information about what particular nutrients or soil conditions cause these large root systems.

Although most roots occur close to the soil surface, an exponential reduction of root biomass with depth has been observed in both tropical (Klinge, 1973; Odum, 1970; Stark, 1971b), and temperature forests (Gale and Grigal, 1987; Kimmins and Hawkes, 1978; McClaugherty et al., 1982; Persson, 1978, 1980, 1983; Safford and Bell, 1972; Vogt et al., 1981). The decline of root biomass with depth could be controlled by a) the inflow of nutrients returned to the soil via litter fall, canopy leachates and stemflow (Odum, 1970; Stark, 1971b), b) tropism for organic matter (Stark, 1971a), c) the successional status of the forest (Gale and Grigal, 1987; Grier et al., 1981; Vitousek and Reiners, 1975), d) increasing Al toxicity with increasing depth (Folster, 1986), or something else.

The objective of this paper was to investigate the distribution of root biomass, at the community level, in a semideciduous lowland forest and in a lower montane rain forest in Panama, and to determine whether there are any relationships between the vertical distribution of root biomass and the physical and chemical properties of the soil.

Material and methods

Study sites

The semideciduous lowland forest (Foster and Brokaw, 1982) is at an altitude of 60 m, and is located in the Gigante Peninsula, Barro Colorado National Monument (BCNM), Canal Zone (approx. 9° 07′ N, 80° 09′ W). Although this forest type has been described on Barro Colorado Island, BCI (see Leigh et al., 1982), there are no published descriptions of the structure of the forest in the study site at Gigante Peninsula. Because the Canal Zone has suffered different degrees of disturbance over the past decades, it is necessary to present a description of the forest structure so that appropriate comparisons can be made in future studies. The forest in the study site has a very uneven canopy, 10–30 m tall, with emergents 40 m tall. Most trees are of small girth, with 62% of the stems <20 cm dbh. In eight plots of 50 m by 50 m, the mean basal area for trees >10 cm in diameter was 24 $m^2 ha^{-1}$, similar to that found in a 60-year-old forest on BCI (Lang and Knight, 1983). There are approximately 476 stems ha^{-1} (>10 cm dbh), similar to the average density in 5 samples of 1-ha in young forest, and in 2 samples of 1 ha in old forest, also on BCI (Putz and Milton, 1982). Palms are abundant in the canopy, (*Astrocaryum standleyanum*) and also in the understory (*Oenocarpus panamanus* and *Socratea durissima*). Lianas are very abundant, some with thorns, and some with dbh >10 cm. There are also slender vines attached to trunks. The tree height, number of stems, basal area, lack of large trees and abundance of lianas, suggest that this is a young secondary forest. A list of the species of this forest type is in Croat (1978). Five kilometers north of the study site at Gigante (BCI laboratory clearing), the average annual temperature is 27°C and the average annual rainfall is 2567 mm. There is a dry season from early January to late April where monthly rainfall is less than pan-evaporation (Fig. 1). The soils at Gigante are oxisols (Anon., 1970), and are derived from a dense basalt flow which also occurs in the plateau of BCI (as shown in the maps of Woodring, 1957). According to a general survey of the Panamanian soils (fifty percent of the territory), oxisols occur in about 52% of the surveyed area. The only published information about the soils of BCNM are the N, P and S properties of surface soils (0–15 cm) of BCI, studied during July 1984 by Yavitt and Wieder (1988).

The lower montane rain forest is at an altitude of 1200 m and is located in the Cordillera Central, within the 'Fortuna' watershed in front of the Instituto de Recursos Hidraulicos y Electrificacion (IRHE) plant nursery (approx. 8° 43′ N, 82° 14′ W). Although there are some

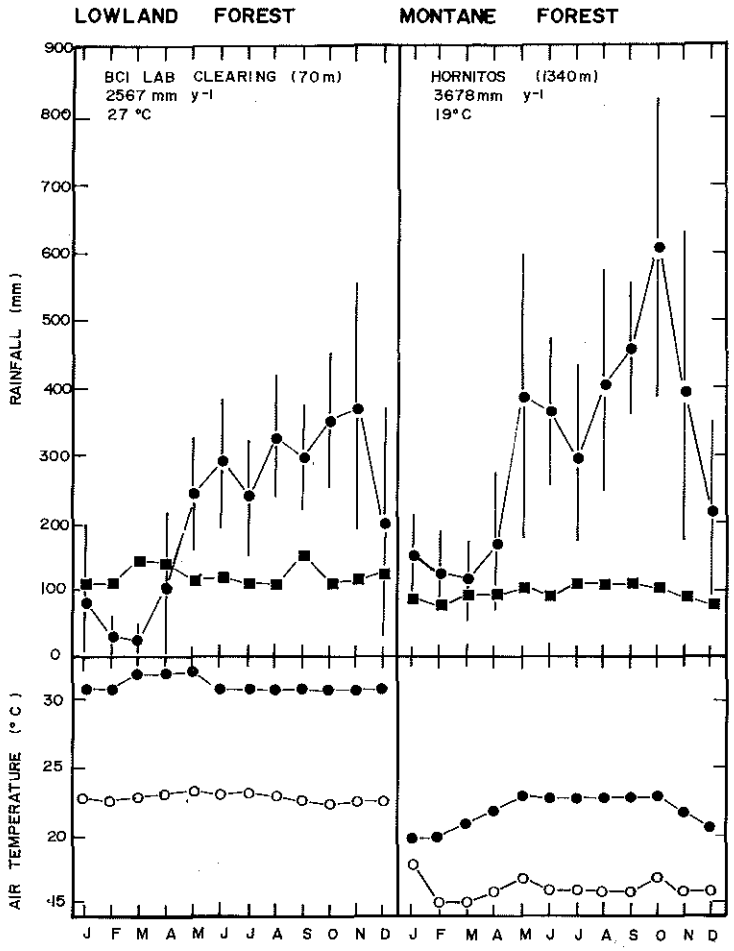

Fig. 1. Mean monthly rainfall (●), pan-evaporation (■), maximum (●) and minimum (○) air temperatures near the study sites in Panama (1972–1985). The vertical lines represent standard deviations. Data for the lowland forest from Smithsonian Tropical Research Institute (STRI) and for the montane forest, from the Instituto de Recursos Hidraulicos y Electrificación (IRHE), Panamá.

forestry investories of the area (F. Gonzales, personal communication), there are no published descriptions of the structure of this forest. The forest at Fortuna has a rather open canopy, 20–30 m tall, with emergents 40 m tall. Most trees are of small girth, with 64% of the stems <20 cm dbh and the largest tree 75 cm in diameter. In eight plots of 30 m by 30 m, the mean basal area for trees >10 cm in diameter was 30 m^2 ha^{-1}, similar to the well-developed montane rain forests in Venezuela (35.6–40.7 m^2 ha^{-1} in La Carbonera at 2300 m; Rollet, 1984), and in New Guinea (29.2 m^2 ha^{-1} in a montane forest at 1125 m; Paijmans, 1970), where trees are also tall (emergents of 40 m). Very few trees have buttresses, but vascular epiphytes are very frequent. Species of the genus Anthurium and Monstera are a very prominent feature of the forest. There are many vines and thin lianas attached to the trunks, but few bromeliads. Epiphytic bryophytes are present, but are not as abundant as the Araceae. Cyclanthaceae and Palmae are common in the understory, as are tree ferns. These physiognomic characteristics, except leaf-size classes (Microphylls, account for 43% of the leaves collected from the forest floor), and suggest that this forest is a lower montane rain forest *sensu strictii* (Grubb, 1977). A preliminary species list of this forest is in Mayo et al. (1977), and D'Arcy

(1987a,b). One kilometer north, and at the same altitude as the study site, the average annual temperature is 19°C, and the average annual rainfall is 3900 mm. There is seasonality in rainfall, but monthly pan evaporation is always lower than monthly rainfall (Fig. 1). The soils at Fortuna are Inceptisols (Anon., 1970) and are derived from thin layers of volcanic ash, andesites and basalts that can be found at depths of 30 cm to 35 cm on slopes, and at more than 100 cm on flat terrain. According to a general survey of the Panamanian soils, Inceptisols occur in about 44% of the surveyed area (Anon., 1970).

Sampling design and soil cores

In the lowland forest, 8 plots measuring 50 m by 50 m were marked along a north-south transect, with buffer zones of 50 m by 20 m between the plots. A 40-m by 40-m plot was marked within each plot and divided in 3 sectors. In the montane forest, the plots were 30 m by 30 m, with 30 m by 10 m buffer zones between them, and inner plots of 20 m by 20 m. For the determination of standing root biomass at different depths, three soil cores per plot (one from each of the three sectors) were collected monthly in both forests between February and October 1988. The mean annual values for root biomass presented here ($n = 108$ per forest) are from four of the plots in each forest (plots 2, 4, 6 and 7). The other plots were used in a fertilization experiment described elsewhere (Cavelier, 1989). For the estimation of soil physical and chemical properties, 12 soil cores per forest were collected in October 1988, with the same soil corer used to collect the root samples.

Standing root biomass was sampled by driving into the soil a sharp-edged steel corer with an internal diameter at the hardened cutting edge of 5.6 cm. The corer had an internal PVC pipe, 7.5 cm in diameter, divided longitudinally in two halves, so the samples could be removed easily. (Ford and Deans, 1977). The soil corer was placed on the forest floor without removing the litter, and pounded with a sledge hammer down to a depth of 25 cm. Each soil core was divided in the field into five sections of 5-cm depth each, placed in plastic bags, labelled and stored at 3°C until soil washing could take place (usually within 30 days). Every sample was wet-sieved to retrieve the roots. The samples were rinsed with tap water over a 500-μm sieve to loosen the soil and facilitate root sorting. During preliminary rinsing and sorting, a 200-μm sieve was placed under the 500-μm sieve to ensure that this sieve was fine enough to retain the finer roots. No root fragments were found on the 200-μm sieve, so it was not used during processing of the main set of samples. Roots (live + dead) were sorted by diameter using the following classes: Very Fine Roots, VFR = <1 mm; Fine Roots, FR = 1–2 mm; Medium Roots, MR = 2–5 mm; and Coarse Roots, CR = 5–50 mm. No attempt was made to categorize roots by species. After sorting, roots were dried at 60°C for 48 hours, weighed to the nearest 0.0001 g, and stored in plastic vials.

For soil chemical analysis, each soil core was divided in the field into five sections of 5-cm depth, and the samples from each depth were mixed to obtain one composite sample per plot, thus producing 4 samples per depth per forest. The composite samples were put into plastic bags, labelled and transported to the laboratory. Soils were air-dried before chemical analysis. For the determination of soil bulk density (g dry soil cm^{-3}), one soil core per plot per forest was collected with the same soil corer used to collect roots. Soil bulk density was estimated for 0–10 cm and 10–25 cm samples, collected in November 1988, dried at 80°C during 48 h, and weighed to the nearest 0.1 g.

Soil description and chemical analyses

A description of the soil profile of each forest was made following the method described in FAO (1977), and soil colours described using the Munsell soil colour chart (Appendix 1). In the lowland site, the pit was dug on relatively flat terrain which is common in the area. In the montane site, the pit was also dug on relatively flat terrain, but the soils in the area are not always as deep as the profile described here (soils are 25–30 cm deep on gentle slopes and a metre or more on flat terrain).

Soil samples were analyzed for organic carbon (%), total nitrogen (%) 'available' phosphorus (ppm), exchangeable calcium, magnesium,

potassium, sodium, aluminium and acidity (meq/100 g), cation exchange capacity (CEC), and pH. Percentage base saturation was calculated as the sum of exchangeable bases (Ca, Mg, Na and K) and expressed as percentage of CEC. Organic carbon was determined using acid potassium-dichromate (1 *N*) oxidation without heating, known as the 'Walkley-Black' procedure (Nelson and Sommers, 1982). Total nitrogen was determined using Kjeldahl digestion (Bremner and Mulvaney, 1982). Phosphorus was determined colorimetrically after extraction in ammonium-fluoride (1 *M*) hydrochloric acid (0.5 *M*), following Olsen and Sommers (1982). Exchangeable bases were determined by the ammonium acetate method, and exchangeable acidity by the Barium Chloride-Triethanolamine method (Thomas, 1982). Aluminium was determined colorimetrically after extraction in potassium chloride (1 N), as described in Barnhisel and Bertsch (1982). Cation exchange capacity was determined with ammonium acetate at pH 7.0 (Jackson, 1958). The pH was measured in a slurry of soil and water (1:1 mixture). Particle size analysis was carried out with the Pipette method (USDA, 1967). Soil characterization analyses were carried out in the Laboratorio de Suelos, Universidad de Panama. The guidelines in Landon (1984) and comparison with other similar forest soils in the tropics were used to evaluate soil chemical properties in the two study sites.

Statistical analysis

Regressions between mean root biomass at different depths and soil characteristics were calculated using STEP, a stepwise regression function in GENSTAT (Genstat, 1987). First, the correlation coefficients between all pairs of variables were calculated. Second, a model of the soil variable with the highest correlation coefficient with the biomass of a given diameter class was fitted using the FIT function. Third, this model was modified by three more soil variables with high correlation coefficients in the original matrix. The model was modified one term at a time. The residual sum of squares, the residual degrees of freedom and the percentage variance accounted for the addition of a new term (soil variable) were recorded, and the program reverted to the original model before trying the next run.

Results

Vertical distribution of root biomass

Total root biomass as measured with the soil corer (TRB = roots < 5 cm in diameter), was not significantly different between the montane (9.46 t ha^{-1}, SEM = 0.30) and the lowland rain forest (9.45 t ha^{-1}, SEM = 0.36). These values for 'total' root biomass are underestimations, since about 1 in each 10 points chosen for soil coring had to be abandoned because of large roots (usually more than 50 mm in diameter) being too big to be cut with the corer. When the soil corer was pounded down to 25 cm, it probably collected more than 90% of total biomass, because below 25 cm there were very few roots (Appendix 1). Total root biomass decreased with depth, but the distribution was not the same in both forests. In the montane forest, the TRB in the first 10 cm of the soil (5.92 t ha^{-1}) was higher than in the lowland (4.92 t ha^{-1}), while the opposite occurred between 15 and 25 cm (1.62 and 2.69 t ha^{-1} in the montane and lowland forest, respectively).

Biomass of very fine roots (VFR = <1 mm in diameter) decreased with depth in both forests (Fig. 2). In the first 15 cm of the soil, biomass of VFR was significantly higher ($p < 0.05$) in the montane than in the lowland forest. Similarly, in the first 10 cm of the soil, biomass of fine roots (VF = 1–2 mm) and medium roots (MR = 2–5 mm) was higher in the montane forest. The ratio of fine roots (1–2 mm) to very fine roots (<1 mm) was constant with depth, and was not significantly different between the forests (Fig. 3). In contrast, the ratio of coarse roots (5–50 mm) to roots 2–5 mm in diameter increased with depth, and was significantly higher for the lowland than for the montane forest (Fig. 3).

Soil chemical analysis

Soil nutrients varied with depth and between forests (Fig. 4). In the lowland forest, the concentration of elements in the soil decreased sig-

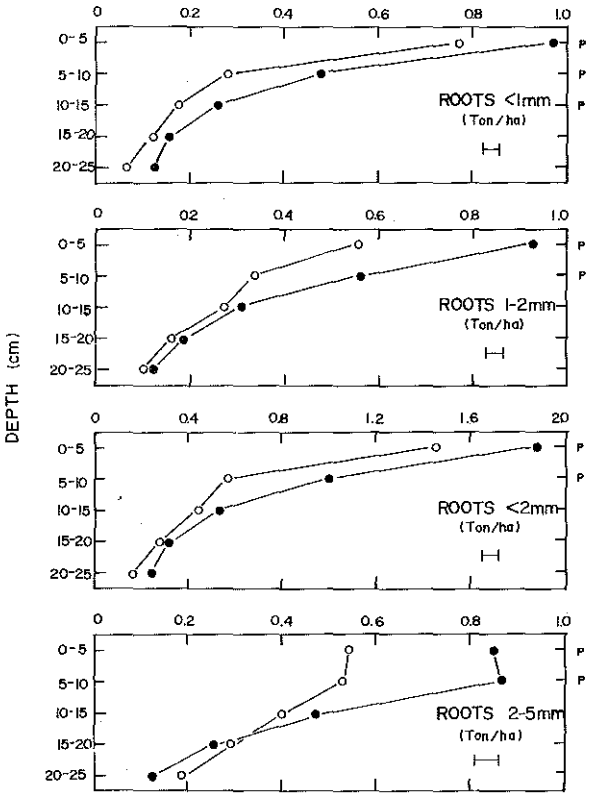

Fig. 2. Vertical distribution of roots of different diameter classes in the top 25 cm of the soil of the lowland (○) and montane (●) forest in Panama. The horizontal lines represent SEM when comparing depths between forests. The p's in the right margin represent significant differences in root biomass between forests ($p < 0.05$).

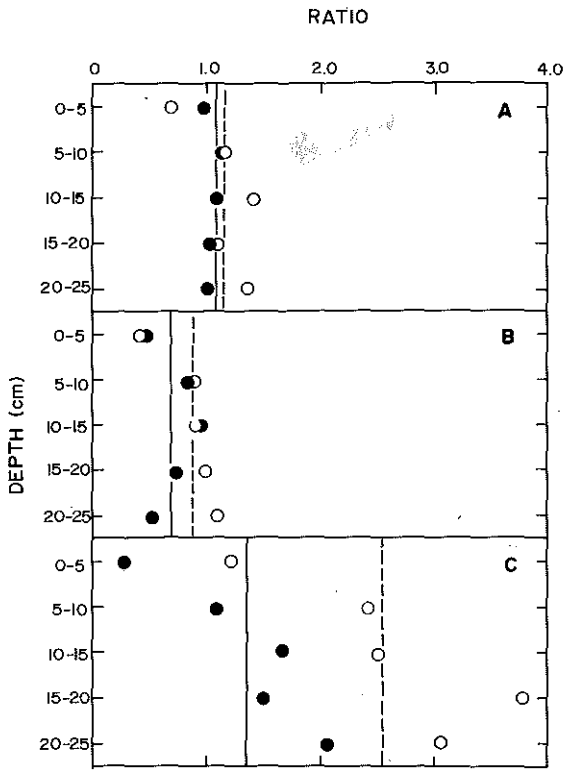

Fig. 3. Ratio of roots A) 1–2 mm: <1 mm in diameter, B) 2–5 mm: <2 mm in diameter, and C) <50 mm: <2 mm in diameter in the montane (●) and lowland (○) rain forests in Panama. The broken vertical lines represent the mean ratios for the lowland forest and the continuous vertical lines the mean ratios in the montane forest.

nificantly ($p < 0.05$) with depth, with the exception of P, Mg, and Al. When compared among forests, Ca and Mg were significantly higher in the soils of the lowland site, while N, P (0–5 cm) and Al were significantly higher in the montane site. Sodium was not significantly different between the two sites, and potassium was higher in the lowlands than in the mountains only between 10–15 cm and 20–25 cm.

The CEC in the soils of the lowland forest was significantly lower than in the montane forest only in the first 5 cm of the soils ($p < 0.05$). In contrast, percentage base saturation at all depths was significantly higher in the lowland forest (Fig. 4). Although CEC due to organic matter was not determined, it seems that the exchange properties reside mostly in the organic fraction of the soil; while CEC and organic carbon decrease with depth, the percentages of clay and silt increase (lowland forest), or remain constant (montane forest) throughout the profile (Table 1).

Physical properties of the soil

Soil bulk density was significantly different between the forests ($p < 0.01$). In the lowland forest, soil bulk density was 0.74 g cm^{-3} (SEM = 0.04) in the first 10 cm of the soil, and 0.73 g cm^{-3} (SEM = 0.05) between depths of 10 and 25 cm. In the montane forest, soil bulk density was 0.26 g cm^{-3} (SEM = 0.01) in the top 10 cm of the soil, and 0.49 g cm^{-3} (SEM = 0.01) in the next 15 cm.

Soil texture varied with depth (Table 1). In the lowland forest, the percentage of sand and

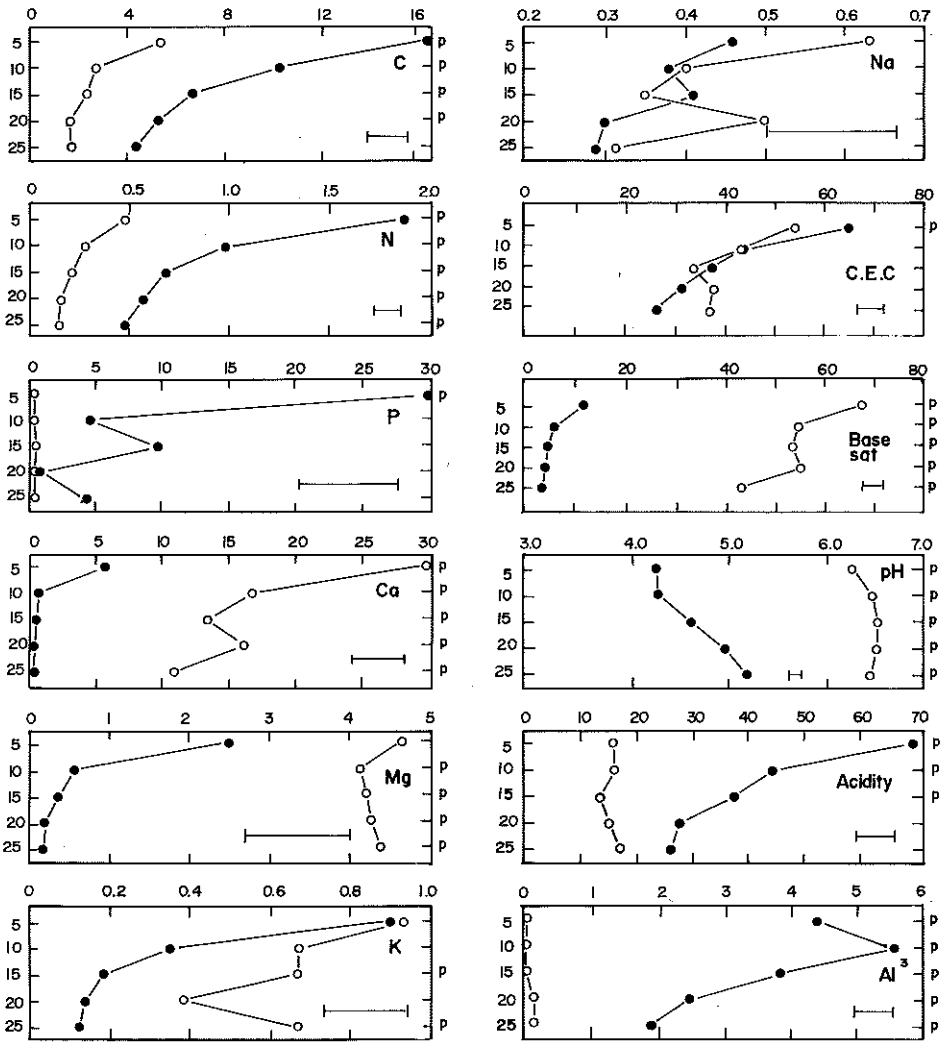

Fig. 4. Vertical distribution of organic carbon (C; %), total nitrogen (N; %) available phosphorus (P, ppm), calcium (Ca, meq/100 g), magnesium (Mg, meq/100 g), potassium (K, meq/100 g), sodium (Na, meq/100 g), cation exchange capacity (CEC, meq/100 g), percentage base saturation (%), pH, acidity (meq/100 g), and aluminium (Al, meq/100 g), in the top 25 cm of the soils (5-cm sections) in the lowland (○) and montane (●) forests. The horizontal lines represent SEM when comparing depths between forests. The p's in the right margin represent significant differences in root biomass between forests ($p < 0.05$).

silt decreased with depth, while the percentage of clay increased. In the montane forest, the first 5 cm of soil were primarily organic matter. In the next 20 cm, there was little variation in the amounts of sand, silt and clay, with large percentages of sand-size particles.

In the lowland forest, cracks were formed in the soils during the dry season, but they grew little after opening, and disappeared fast after the first showers (Fig. 5). During 10 months of coring, the water table was observed at 10 cm only in depressions or near streams. In contrast, the soils in the montane forests never cracked, and the water table was observed in the flattest plot between 16 and 21 cm, even during February, one of the drier months of the year.

Root biomass and soil nutrients

The distribution of roots was correlated with the concentration of some nutrients and properties in the soil profile. Considering only the mineral

Table 1. Soil texture in the lowland and montane forests. Analyses were made on composite soil samples of 4 primary samples collected in December 1988

Depth (cm)	Sand	Silt	Clay	Texture
	(%)			
Lowland				
00–05	49	20	31	Sandy clay loam
05–10	45	20	35	Clay loam
10–15	25	26	49	Clay
15–20	26	14	65	Clay
20–25	17	14	69	Clay
Montane				
00–5	—	—	—	Organic matter
05–10	77	17	7	Sandy loam
10–15	75	19	7	Sandy loam
15–20	70	24	7	Loam sandy
20–25	78	18	5	Sandy loam

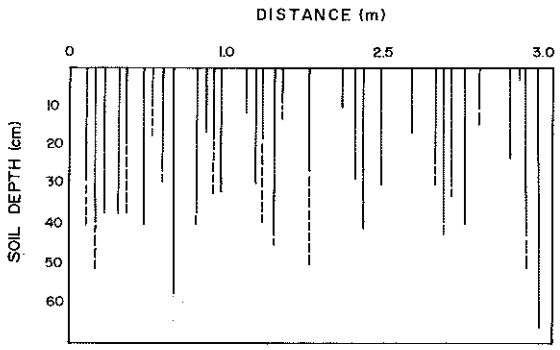

Fig. 5. Depth of cracks in the soils of the lowland rain forest along a 3 m transect during the dry season of 1988. The lengths of the lines represent the depths of the cracks measured on 13 February (——) and 15 March (– – –). The cracks were measured with a rod 1.5 mm in diameter.

nutrients, the vertical distribution of roots <1 mm and <2 mm in the lowland forest was significantly correlated ($p < 0.05$) with the concentrations of N, P and Ca as shown in the correlation coefficient matrix (Table 2). In the montane forest, the distribution of roots was correlated not only with N, P, and Ca, but also with Mg and K (Table 3). In both forests, C and CEC were also significantly correlated with the distribution of biomass of roots <1 mm and <2 mm in diameter. Because the percentage of carbon, a measure of organic matter, and CEC represent complex soil chemical properties and are positively correlated with the concentration of N, P and most exchangeable bases, these two characteristics were not used in the stepwise regression analysis (STEP).

The STEP analysis showed that in both forests, most of the variation in the vertical distribution of biomass of roots <1 mm and <2 mm was explained by the concentration of total nitrogen in the soil (Table 4). Furthermore, the addition of one more term (soil variable) to the regression had little effect on the percentage of variance explained by the model.

Discussion

Soil chemical properties

The soils in the lowland forest are characterized by moderate acidity (pH 5.5, and no exchangeable aluminium), and high CEC and percentage base saturation. Available P is in very low concentrations along the profile, and may be an important limiting factor for plant growth in this forest.

The soils in the montane forest are acid, have high CEC and low percentage base saturation. Fluoride-extractable P is high only in the top 5 cm of the soil. Because the pH is lower than 5.0 in the topsoil, solubility of Al^{+3} increases sharply, and thus results in high exchangeable acidity (Thomas and Hargrove, 1984). High acidity probably exacerbates the deficit of bases like Ca, K and Mg, which are in low concentration. The concentration of Mg in this forest is

Table 2. **Lowland forest.** Correlation matrix of all root and soil variables used in the stepwise regression analysis. Roots less than 1 mm in diameter (<1 mm), and 2 mm in diameter (<2 mm), concentration of nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na). Exchangeable acidity (Ac), cation exchange capacity (CEC), percentage base saturation (Bsa), exchangeable aluminium (Al), carbon (C), pH and carbon/nitrogen ratio (C:N). Correlation coefficients higher than 0.878 are significant at the 5% level, and those higher than 0.959 are significant at the 1% level

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	<1 mm	1.000														
2	<2 mm	0.998	1.000													
3	N	0.996	0.997	1.000												
4	P	0.965	0.938	0.951	1.000											
5	Ca	0.982	0.968	0.965	0.946	1.000										
6	Mg	0.402	0.314	0.362	0.619	0.419	1.000									
7	K	0.798	0.806	0.835	0.798	0.674	0.364	1.000								
8	Na	0.842	0.812	0.798	0.823	0.928	0.438	0.360	1.000							
9	Ac	−0.064	−0.120	−0.050	0.013	−0.049	0.431	0.091	−0.077	1.000						
10	CEC	0.940	0.920	0.937	0.906	0.951	0.459	0.718	0.844	0.244	1.000					
11	Bsa	0.889	0.898	0.866	0.796	0.929	0.139	0.475	0.913	−0.356	0.796	1.000				
12	Al	−0.585	−0.661	−0.633	−0.415	−0.479	0.397	−0.655	0.217	0.490	−0.397	−0.576	1.000			
13	C	0.996	0.993	0.999	0.962	0.963	0.403	0.846	0.794	−0.021	0.941	0.849	−0.606	1.000		
14	pH	−0.798	−0.797	−0.827	−0.717	−0.769	−0.248	−0.753	−0.576	−0.422	−0.913	−0.583	0.475	−0.828	1.000	
15	C:N	0.588	0.540	0.601	0.719	0.507	0.784	0.804	0.297	0.521	0.636	0.167	−0.078	0.637	−0.631	1.000

Table 3. **Montane forest.** Correlation matrix of root and soil variables used in the stepwise regression analysis. Roots less than 1 mm in diameter (<1 mm), and 2 mm in diameter (<2 mm), concentration of nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na). Exchangeable acidity (Ac), cation exchange capacity (CEC), percentage base saturation (Bsa), exchangeable aluminium (Al), carbon (C), pH and carbon/nitrogen ratio (C:N). Correlation coefficients higher than 0.878 are significant at the 5% level, and those higher than 0.959 are significant at the 1% level

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	<1 mm	1.000														
2	<2 mm	0.998	1.000													
3	N	0.998	0.993	1.000												
4	P	0.912	0.890	0.931	1.000											
5	Ca	0.940	0.918	0.959	0.975	1.000										
6	Mg	0.960	0.948	0.980	0.970	0.996	1.000									
7	K	0.980	0.966	0.990	0.962	0.989	0.998	1.000								
8	Na	0.842	0.851	0.833	0.806	0.732	0.769	0.784	1.000							
9	Ac	0.985	0.989	0.978	0.893	0.892	0.925	0.944	0.917	1.000						
10	CEC	0.994	0.992	0.994	0.921	0.937	0.963	0.974	0.883	0.990	1.000					
11	Bsa	0.995	0.987	0.999	0.942	0.970	0.987	0.995	0.817	0.969	0.989	1.000				
12	Al	0.628	0.674	0.582	0.330	0.330	0.408	0.462	0.727	0.713	0.632	0.546	1.000			
13	C	0.998	1.000	0.992	0.892	0.917	0.947	0.965	0.859	0.992	0.993	0.986	0.0677	1.000		
14	pH	−0.682	−0.694	−0.661	−0.411	−0.563	−0.595	−0.631	−0.262	−0.602	−0.610	−0.658	−0.521	−0.685	1.000	
15	C:N	−0.541	−0.491	−0.590	−0.719	−0.781	−0.731	−0.686	−0.243	−0.426	−0.542	−0.620	0.289	−0.485	0.268	1.000

Table 4. Equations of the multiple regression analysis between root biomass (Y) and the concentration of different nutrients in the soil profile (0–25) cm). Total nitrogen (N), calcium (Ca) and magnesium (Mg). Regressions were calculated using STEP, a stepwise regression function in Genstat 5 (1987). The correlation coefficients between all pairs of variables were calculated, and a model with the soil variable having the highest correlation coefficient with the biomass of a given diameter class was fitted. Then, the model was modified with one more term. There is only equation for roots <2 mm in diameter in the lowland forest because the second term did not increase the variance explained

Root diameter (mm)	Equation	Variance explained (%)
Lowland		
<1	$Y = -0.0656 + 0.5386\ (N)$	99.0
	$Y = -0.0738 + 0.3859\ (N) + 0.002699\ (Ca)$	99.7
<2	$Y = -0.0809 + 0.8709\ (N)$	99.2
Montane		
<1	$Y = -0.0402 + 0.1537\ (N)$	99.5
	$Y = -0.0617 + 0,1993\ (N) - 0.02644\ (Mg)$	100.0
<2	$Y = -0.0667 + 0.2964\ (N)$	98.0
	$Y = -0.1495 + 0.4721\ (N) - 0.10193\ (Mg)$	99.1

lower than in the relatively rich soils of the mountains of New Guinea (5.0–13.8 meq/100 g; Edwards, 1982), and in the relatively poor soils in the mountains of Jamaica (1.7–15.8; Tanner, 1977), and may be an important limiting factor for plant growth. The value for total bases in the montane forest (9.5 meq/100 g dry soil) is lower than in the rich soil of the mountains of N. Guinea (20.0–69.3 meq/100 g drysoil, n = 4) as reported by Edwards (1982), and lower than in the mor ridge (129 meq/100 g dry soil) and wet slope forests (21.6 meq/100 g dry soil) in the blue mountains of Jamaica, but similar to the mull ridge and gap forest in the same mountain range (Tanner, 1977).

In summary, plant growth may be limited by phosphorus in the lowlands, and by acidity and low concentration of exchangeable bases in the mountains. In the montane site, phosphorus is in high concentration in the first 5 cm of the soil only, and may be a limiting factor in deeper horizons of the soil.

Soil chemical properties and the distribution of root biomass

The results of the stepwise regression analysis should be taken with caution because they are based on correlations and not on experiments, and the analysis should have been made with independent variables (Sokal and Rohlf, 1981) which was not always the case. The results of the STEP analysis showed that total nitrogen can explain most of the variation in root biomass in both forests. Nevertheless, the concentration of other nutrients such as P and Ca in the lowlands, and P, Ca, Mg, and K in the mountains is significantly correlated with root biomass. These nutrients could be, from the biological point of view, as important as N in explaining the reduction in root biomass with increasing depth. In contrast to the results of the present study, no correlation was found between root distribution and the concentration of individual cations in an Amazonian forest on oxisols (Stark and Spratt, 1977). Some manipulation experiments are needed to establish the relative importance of individual nutrients for the distribution of roots, and to test the hypothesis that the reduction in the number of roots is controlled by the inflow of nutrients from above (Odum, 1970).

Large amounts of fine roots on the soil-surface have been observed in other montane forests, for instance in Puerto Rico (Gill, 1969, Lyford, 1969), where the atmosphere is close to saturation (Odum, 1970), but not in the elfin cloud forest of Serrania de Macuira, Colombia, where there is a daily wetting and drying of the soil-surface (Cavelier and Peñuela, 1990). Odum (1970) suggested that the existence of superficial root systems in montane forests may be the result of higher oxygen availability at the soil surface, or the 'selective reward of mineral recycling wherever there are mineral problems'.

Superficial root systems in the montane site seem to be the response to both, anaerobic conditions in the soil (water table at 20 to 25 cm), and higher nutrient concentrations near the surface. Large numbers of roots (free of soil) were observed above the ground throughout the year, while in the lowland forest, this was observed only during the beginning of the rainy season, probably as a response to water and nutrient pulses (Cavelier, 1989). This suggests that roots in the montane forest may absorb more nutrients directly from litter fall, throughfall and stemflow without nutrients entering the soil solution, than in the lowlands.

Comparisons with other tropical forests

Comparing root biomass among forests is difficult because of differences in measuring techniques, soil-depth classes and root-diameter classes (Table 5). The biomass of small roots (<6 mm in diameter) in the lowland site is lower than in other semideciduous forests in Ghana (Lawson et al., 1970) and Mexico (Kellman, 1990) and is probably low because the soils are relatively rich, with the exception of phosphorus which is very low. It is important to note that biomass of small roots in young-successional forests reaches the volume of that in old-successional or mature forests in a few years (probably faster than above-ground biomass), as shown by the data from Costa Rica (Berish, 1982; Raich, 1980). The biomass of small roots in the montane site is higher than that in lowland rain forests of Costa Rica (Berish, 1982; Gower, 1987; Raich, 1980), but lower than that in the Tierra Firme, Caatinga and Bana forests of the Rio Negro River (Sanford, 1985), and in latosols and spodosols in Central Amazonia (Klinge, 1973; Stark and Spratt). This is because root-mats above the soil occur in some Amazonian forest and not in the montane forest. If the biomass of small roots in the montane forest (2500 m) of New Guinea (4.0 t ha^{-1} for roots <6 mm in diameter) is significantly lower than in the montane forest of Fortuna (6.6 t ha^{-1} for roots <5 mm), it is probably the result of richer soils in New Guinea, which have a higher pH (5.7–6.3) and exchangeable bases (Edwards and Grubb, 1982) than the montane site of Panama.

While the total biomass of fine-roots is higher in the montane than in the lowland forest, the concentrations and total amounts of bases (particularly Ca and Mg) are higher in the lowlands. These results support the hypothesis that total fine root biomass in tropical forests is inversely related to calcium availability, but not to phosphorus (Gower, 1987). The concentration and total amount of available P (concentration x soil bulk density) are higher in the mountains probably because the soils are derived from volcanic ash.

The observation that large fine-root biomasses occur in soils with an accumulation of organic matter (Stark, 1971a; St. John, 1983), is probably related to plants' need for root systems with large surface areas that absorb nutrients diluted in a soil of low bulk density, high CEC and low percentage base saturation. It is important to note that in the montane site, most of the fine-roots are associated with the layers of soil that have the highest concentrations of nutrients and also the highest acidity. Surface roots experience acidities at which aluminium and manganese are usually soluble, and may have toxic effects on plant tissues (Small, 1972). These two elements may be left in the soil or taken up by the plants and concentrated in leaf tissues (Gauch, 1952; Webb, 1954). Thus, roots in the montane forest have to compromise between potential soil toxicity and the need to absorb the nutrients that are in low supply.

The results of this study suggest that the vertical distribution of root biomass in tropical forests is controlled mainly by the concentration of N in the soil, and that large root systems in montane forests are a response to nutrients in low concentration and diluted in organic soils with high CEC and low bulk density.

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Table 5. Biomass ($t\ ha^{-1}$) of roots of different diameter classes in selected tropical forests

Forests	Depth (cm)	Root diameter class (mm)					References
		<1	1–2	<2	<5	<6	
LOWLAND AND RAIN FORESTS							
Mature forests							
Venezuela (Tierra Firme = TF)	30	10.3	3.5	13.8	20.4	—	Sanford (1985) (a)
Venezuela (TF/Caatinga transit.)	30	35.4	4.1	39.5	46.2	—	Sanford (1985)
Venezuela (Oxisols)	34	—	—	—	—	28.3	Stark and Spratt (1977) (b)
Brazil (Latosol)	27	3.1	2.2	5.3	—	9.3	Klinge (1973) (c)
Brazil (Podzol)	29	3.4	1.5	4.9	—	9.2	Klinge (1973)
Venezuela (Caatinga)	30	12.8	5.1	17.9	27.1	—	Sanford (1985)
Venezuela (Caatinga Ya-I)	40	—	—	—	—	44.4	Klinge and Herrera (1978) (d)
Venezuela (Caatinga Ya-II)	40	—	—	—	—	58.6	Klinge and Herrera (1978)
Venezuela (Caatinga Cu-III)	40	—	—	—	—	25.3	Klinge and Herrera (1978)
Venezuela (Caatinga Cu-IV)	40	—	—	—	—	67.9	Klinge and Herrera (1978)
Venezuela (Caatinga Cu-VII)	40	—	—	—	—	123.4	Klinge and Herrera (1978)
Venezuela (Caatinga Cu-X)	40	—	—	—	—	53.0	Klinge and Herrera (1978)
Venezuela (Caatinga/Bana transit)	30	11.0	4.7	15.7	23.7	—	Sanford (1985)
Venezuela (Bana)	30	11.4	3.3	14.7	22.9	—	Sanford (1985)
Costa Rica (Evergreen-Terrace)	30	0.2	0.3	0.5	1.1	—	Gower (1987) (e)
Costa Rica (Evergreen-Upland)	30	0.5	0.6	1.1	1.6	—	Gower (1987)
Costa Rica (Premontane wet forest)	30	—	—	2.4	—	—	Raich (1980) (f)
Ivory Coast (Banco P.)	30	—	—	12.6	15.9	—	Huttel (1975)
Ivory Coast (Banco T.)	30	—	—	11.0	16.8		Huttel (1975)
Ivory Coast (Yapo)	30	—	—	12.4	18.4		Huttel (1975)
Secondary forests							
Costa Rica, Succession (1 year)	25	0.3	0.3	0.6	0.7	—	Berish (1982) (g)
Costa Rica, Succession (1 year)	30	—	—	2.5	—	—	Raich (1980)
C Rica Enriched Succession (6 years)	—	—	—	1.8	—	—	Berish and Ewel (1988) (h)
Costa Rica, Succesion (8 years)	25	1.2	1.0	2.2	3.9	—	Berish (1982)
Costa Rica, Succesion (70 years)	25	1.7	1.1	2.8	4.4	—	Berish (1982)
SEMIDECIDUOUS FORESTS							
Panama	25	1.4	1.4	2.8	4.7	—	This study
Ghana (Upper slope)	30	—	—	3.8	5.6	—	Lawson et al. (1970) (i)
Ghana (Middle slope)	30	—	—	10.2	12.4	—	Lawson et al. (1970)
Ghana (Bottom slope)	30	—	—	3.4	4.8	—	Lawson et al. (1970)
Mexico (Recent sand)	40	—	—	3.5	—	—	Kellmann (1990) (j)
Mexico (Weathered sand)	40	—	—	4.8	—	—	Kellman (1990)
MONTANE FORESTS							
Panama (1200 m)	25	2.0	2.0	4.0	6.6	—	This study
New Guinea (2500 m)	25	—	—	—	—	4.0	Edwards and Grubb (1977) (k)
Tanzania (1500 m)	30	—	—	—	8.5	—	Lundgren (1978) (l)

(a) Soil cores 8 cm in diameter. The values include surface roots. (n = 3–5).
(b) Soil blocks 50 cm by 50 cm. The values include roots in mat and sand horizons. (n = 18.)
(c) Soil blocks 50 cm by 50 cm. The values include L and F layers of the soil (2 cm deep). (n = ?).
(d) Soil quadrats, 0.25 m^2 (n = 1–2). The value includes roots from the root mass (Ao + Al horizons = 4–12.5 cm) and dark-grey sand (5–21 cm).
(e) Soil cores, 7 cm in diameter (n = 6).
(f) Soil blocks 10 cm by 10 cm. (n = 3–10).
(g) Soil blocks (n = 6) for the 1-year-old-succession vegetation, and soil cores (n4.2 cm in diameter) for the other two forests (n = 33).
(h) Soil cores 4.3 cm in diameter. The value (obtained from the graph) represents the mean of seven sampling times between 1980 and 1984. Each sample was a composite of 5 cores).
(i) Soil block, 25 cm by 25 cm. (n = 1?). All values were read from the graph.
(j) Soil cores, 6 cm in diameter. (n = 6).
(k) Soil quadrants, 10 m by 5 m. (n = 2).
(l) Soil cores (3.25 cm^3).

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References

Anon 1970 Final Report on the Catastro Rural de Tierras y Aguas de Panama. Vol. I and II. Republica de Panama, Comision de Reforma Agraria. The Jacobs Company.

Barnhisel R and Bertsch P M 1982 Aluminium. *In* Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties. Second Edition. Ed. A L Page. pp 275–300. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI.

Berish C W and Ewel J J 1988 Root development and complex tropical successional ecosystems. Plant and Soil 106, 73–84.

Berish C W 1982 Root biomass and surface area in three successional tropical forests. Can. J. For. Res. 12, 699–704.

Bremner J M and Mulvaney C S 1982 Nitrogen-Total. *In* Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties. Second Edition. Ed. A L Page. pp 595–624. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI.

Cavelier J 1989 Root biomass production and the effect of fertilization in two tropical rain forests. Ph.D. thesis. University of Cambridge, UK. 116 p.

Cavelier J and Penuela M C 1990 Soil respiration in the cloud forest and dry deciduous forest of Serrania de Macuira, Colombia. Biotropica 22, 346–352.

Croat T B 1978 Flora of Barro Colorado Island. Stanford University Press, Stanford, CA.

D'Arcy W G 1987a Flora of Panama Part I: The Introduction and Check List. Missouri Botanical Garden, St. Louis, MO. 328 p.

D'Arcy W G 1987b Flora of Panama Part II: Index. Missouri Botanical Garden, St. Louis, MO. 672 p.

Edwards P J and Grubb P J 1977 Studies of mineral cycling in a montane rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. J. Ecol. 65, 943–969.

Edwards P J 1982 Studies of mineral cycling in a montane rain forest in New Guinea. V. Rates of cycling in throughfall and litter fall. J. Ecol. 70, 807–827.

Edwards P J and Grubb P J 1982 Studies of mineral cycling in a montane rain forest in New Guinea. II. Soil characteristics and the division of mineral elements between the vegetation and soil. J. Ecol. 70, 649–666.

FAO 1977 Guidelines for Soil Profile Description. Second edition. FAO, Rome, Italy.

Folster H 1986 Forest-savanna dynamics and desertification processes in the Gran Sabana. Interciencia 11, 311–316.

Ford E D and Deans J D 1977 Growth of a *Sitka spruce* plantation: Spatial distribution and seasonal fluctuations of lengths, weights and carbohydrate concentrations of fine roots. Plant and Soil 47, 463–485.

Foster R B and Brokaw N V L 1982 Structure and history of the vegetation of Barro Colorado Island. *In* The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. Eds. E G Leigh Jr, A S Rand and D M Windsor. pp 67–82. Smithsonian Institution Press, Washington, DC.

Gale M R and Grigal D F 1987 Vertical distribution of northern tree species in relation to successional status. Can. J. For. Res. 17, 829–834.

Gauch H G 1972 Inorganic Plant Nutrition. Dowen, Hutchinson and Ross, Inc. PA.

Genstat 1987 Genstat 5: Reference Manual. The Genstat 5 Committee of the Statistics Department Rothamsted Experimetal Station. Oxford Science Publications, Clarendon Press, Oxford. 749 p.

Gill A M 1969 The ecology of an elfin forest in Puerto Rico 5: Aerial roots. J. Arnold Arbor., Harv. Univ. 50, 197–209.

Gower S T 1987 Relations between mineral nutrient availability and fine root biomass in two Costa Rican wet forests: A hypothesis. Biotropica 19, 171–175.

Grier C C, Vogt K A, Keyes M R and Edmonds R L 1981 Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystem of the Washington Cascades. Can. J. For. Res. 11, 155–167.

Grubb P J 1977 Control of forest growth and distribution on wet tropical mountains: Special reference to mineral nutrition. Ann. Rev. Ecol. Syst. 8, 83–107.

Huttel C 1975 Root distribution and biomass in three Ivory Coast rain forest plots. *In* Tropical Ecological Systems. Ecological Studies II. Eds. F B Golley and E Medina. pp 213–130. Springer-Verlag, New York.

Jackson M L 1958 Soil Chemical Analysis. Constable and Co. Ltd, London. 498 p.

Jenik J 1978 Roots and root systems of tropical trees: Morphologic and ecologic aspects. *In* Tropical Trees as Living Systems. Eds. P Tomlinson and M Zimmerman. pp 323–349. Cambridge University Press, UK.

Jordan C F and Herrera R 1981 Tropical rain forests: Are nutrients really critical? Am. Nat. 117, 167–180.

Kellman M 1990 Root proliferation in recent and weathered sandy soils from Veracruz, Mexico. J. Trop. Ecol. 6, 355–370.

Kimmins J P and Hawkes B C 1978 Distribution and chemistry of fine roots in a White Spruce-subalpine fir stand in British Columbia: Implication for management. Can. J. For. Res. 8, 265–279.

Klinge H and Herrera R 1978 Biomass studies in Amazon

caatinga forest in southern Venezuela. I. Standing crop of composite root mass in selected stands. Trop. Ecol. 19, 93–110.

Klinge H 1973 Root mass estimation in lowland tropical rain forest of Central Amazonia Brazil. I. Fine root masses of a pale yellow latosol and a giant humus podzol. Trop. Ecol. 14, 29–38.

Landon J R (Ed) 1984 Booker Tropical Soil Manual. Longman Inc., New York. 450 p.

Lang G E and Knight D H 1983 Tree growth mortality recruitment and canopy gap formation during a 10-year period in a tropical forest. Ecology 64, 1075–1080.

Lawson G W, Armstrong-Mensah K O and Hall J B 1970 A catena in tropical moist semideciduous forest near Kade Ghana. J. Ecol. 58, 371–398.

Leigh E G Jr, Rand A S, and Windsor D M (Eds) 1982 The Ecology of a Tropical Forest, Seasonal Rhythms and Long-term Changes. Smithsonian Institution Press, Washington, DC. 468 p.

Lundgren B 1978 Soil conditions and nutrient cycling under natural and plantation forests in Tanzanian highlands. Department of Forest Soils, Swedish University of Agricultural Sciences, Reports in Forest Ecology and Forest Soils 31, 1–261.

Lyford W H 1969 The ecology of an elfin forest in Puerto Rico. 7. Soil root and earthworm relationships. J. Arnold Arbor., Harv. Univ. 50, 210–224.

Mayo E, Correa M, Escobar N and Dressler R 1977 Vegetacion terrestre. *In* Evaluación Ambiental y Efectos del Proyecto Hidroelectrico Fortuna. Ed. Adames A J. pp 161–216. Revista Loteria Nos. 254–6.

McClaugherty C, Aber J D and Melillo J M 1982 The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 65, 1481–1490.

Nelson D W and Sommers L E 1982 Total carbon, organic carbon, and organic matter. *In* Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties. Second Edition. Ed. A L Page. pp 539–580. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI.

Odum H T 1970 Rain forest structure and mineral-cycling homeostasis. *In* A Tropical Rain Forest. Eds. H T Odum and R F Pigeon. pp H3-52. U.S. Atom. Energ. Comm., Springfield, VA.

Olsen S R and Sommers S R 1982 Phosphorus. *In* Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties. Second Edition. Ed. A L Page. pp 403–430. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI.

Paijmans K 1970 An analysis of four tropical rain forest sites in New Guinea. J. Ecol. 58, 77–101.

Persson H A 1978 Root dynamics in a young Scots pine stand in central Sweden. Oikos 30, 508–519.

Persson H A 1980 Spatial distribution of fine-root growth mortality and decomposition in a young Scots pine stand in Central Sweden. Oikos 34, 77–87.

Perrson H A 1983 The distribution and productivity of fine roots in boreal forests. Plant and Soil 71, 87–101.

Putz F E and Milton K 1982 Tree mortality rates on Barro Colorado Island. *In* The Ecology of a Tropical Forest Seasonal Rhythms and Long-term Changes. Eds. E G Leigh Jr., A S Rand and D M Windsor. pp 95–100. Smithsonian Institution Press, Washington, DC.

Raich J A 1980 Fine roots regrow rapidly after forest felling. Biotropica 12, 231–232.

Rollet B 1984 Études sur un forêt d'altitude des Andes Venezueliennes. Bois For. Trop. 205, 3–23.

Safford L O and Bell S 1972 Biomass of fine roots in a White Spruce plantation. Can. J. For. Res. 2, 169–172.

Sanchez P A 1976 Properties and Management of Soils in the Tropics. Wiley, 618 p.

Sanford R L Jr 1985 Root Ecology and Successional Amazon Forests. Ph. D. thesis. University of California, Berkeley. 135 p.

Sanford R L Jr 1987 Apogeotropic roots in an Amazonian rain forest. Science 235, 1062–1064.

Small E 1972. Ecological significance of four critical elements in plants of raised sphagnum peat bogs. Ecology 53, 498–502.

Sokal R R and Rohlf F J 1981. Biometry. Second Edition. W. H. Freeman, San Francisco. 859 p.

St. John T V 1983 Response of tree roots to decomposing organic matter in two lowland Amazonian rain forest. Can. J. For. Res. 13, 346–349.

Stark N 1971a Nutrient cycling. I. Nutrient distribution in some Amazonian soils. Trop. Ecol. 12, 24–50.

Stark N 1971b Nutrient cycling pathways and litter fungi. BioScience 22, 355–360.

Stark N and Spratt M 1977 Root biomass and nutrient storage in rain forest oxisols near San Carlos de Rio Negro. Trop. Ecol. 18, 1–9.

Tanner E V T 1977 Four montane rain forests of Jamaica: Quantitative characterization of the floristics, the soils and the foliar mineral levels and a discussion of the interrelations. J. Ecol. 65, 883–918.

Thomas G W 1982 Exchangeable cations. *In* Methods of Soil Analysis. Part 2: Chemical and Microbiological Properties. Second Edition. Ed. A L Page. pp 159–166. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI.

Thomas G W and Hargrove W L 1984 The chemistry of soil acidity. *In* Soil Acidity and Liming. Second Edition. Ed. F. Adams. pp 3–56. American Society of Agronomy Inc., Crop Science Society of America, Inc., Soil Science Society of America Inc., Madison, WI.

United States Department of Agriculture (USDA) 1967 Soil Survey Laboratory Methods and Procedures for Collecting Soil Samples. Washington, DC. 50 p.

Vitousek P M and Sanford R L Jr 1986 Nutrient cycling in moist tropical forests. Annu Rev. Ecol. Syst. 17, 137–167.

Vitousek P M and Reiners W A 1975 Ecosystem succession and nutrient retention: a hypothesis. BioScience 25, 376–381.

Vogt K A, Edmonds R L and Grier C C 1981 Seasonal changes in biomass and vertical distribution of mycorrhizal and fibrous-textured conifer fine roots in 23- and 180-year-old subalpine *Abies amabilis* stands. Can. J. For. Res. 11, 223–229.

Webb L B 1954 Aluminium accumulation in the Australian-New Guinea flora. Aust. J. Bot. 2, 176–196.

Went F W and Stark N 1968 Mycorrhiza. BioScience 18, 1035–1039.

Woodring W P 1957 Geology and paleontology of Canal Zone and adjoining parts of Panama. Geological Survey Professional paper 306-A. United States Geological Survey, Washington, DC.

Yavitt J B and Wieder R K 1988. Nitrogen, phosphorus and sulphur properties of some forest soils on Barro Colorado Islands, Panama. Biotropica 20, 2–10.

Appendix 1.

Description of an oxisol in the semideciduous lowland forest at Gigante Peninsula (80 cm), Barro Colorado Natural Monument, Panama.

A_{00}	0–3 cm	Litter layer (L) continuous, fragmentation layer (F) very thin.
A_1	0–8 cm	Dark reddish (5YR 4/2) when dry, dark reddish brown (5YR 3/2) when wet; sandy clay loam; strong subangular blocks, coarse to medium; slightly sticky and plastic when wet, firm when moist, hard when dry; many medium to large cracks during the dry season; abundant roots, very fine to coarse; clear wavy boundary; pH (H_2O) = 6.3.
A_2	8–25 cm	Reddish brown (5YR 4/3) when dry, dark reddish brown (5YR 3/3) when wet; clay loam; strong subangular blocks, medium to fine; sticky and plastic when wet, friable when moist, hard when dry; many medium to large cracks during the dry season; abundant very fine to coarse roots; clear wavy boundary; pH (H_2O) = 6.5.
A_3	25–40 cm	Reddish brown (5YR 4/4) when dry, dark reddish brown (5YR 3/4) when wet; clayey; moderate subangular blocks medium to fine; sticky and very plastic when wet, friable when moist, hard when dry; fine cracks during the dry season; few very-fine to fine roots; clear, wavy boundary; pH (H_2O) = 6.6.
B	40–100 cm	Yellowish red (5YR 5/6) when dry, yellowish red (5YR 4/6) when wet; clayey; weak subangular blocks fine to very fine; slightly sticky and slightly plastic when wet, very friable when moist, hard when dry; few very-fine to fine-roots; pH (H_2O) = 6.5.

Description of an inceptisol in the lower montane rain forest (1200 m) in Fortuna watershed in Panama.

A_{00}	0–2 cm	Litter layer (L) continuous, fragmentation layer (F) very thin.
A_1	0–5 cm	Dark reddish brown (5YR 2.5/2), when dry and very dark brown (10YR 2/2) when wet; weak granules medium to fine; slightly sticky and plastic when wet, very friable when moist, slightly hard when dry; abundant very fine to coarse roots; abrupt, smooth boundary; pH(H_2O) = 4.3.
A_2	5–13 cm	Reddish black (10R 2.5/1) when dry and black (5YR 2.5/1) when wet; sandy loam; weak subangular blocks medium to fine; sticky and plastic to very plastic when wet, friable when moist, hard dry; abundant very-fine to coarse roots; clear smooth boundary; pH (H_2O) = 4.4.
AB_g	13–24 cm	Brown dark brown (10YR 4/3) when dry and very dark greyish brown (10YR 3/2) when wet; common, fine, distinct, diffuse, yellowish and reddish mottles; sandy loam; weak subangular blocks medium to fine; sticky and plastic when wet, firm when moist, slightly hard when dry; very few very-fine to coarse roots; gradual smooth boundary; pH (H_2O) = 4.6.
B_{g1}	24–40 cm	Light yellowish brown (10YR6/4) when dry and yellowish brown (10YR 5/4) when wet; common, fine, faint, diffuse, reddish mottles; loamy sand; weak subangular blocks medium to fine; sticky and plastic when wet, firm when moist, very hard when dry; very few very-fine to coarse roots; diffuse smooth boundary, pH (H_2O) = 5.0.
B_{g2}	40–74 cm	Pale brown (10YR 6/3) when dry and brown (10YR 5/3) when wet; common, fine, faint, diffuse, reddish mottles; sandy loam; weak subangular blocks coarse to medium; sticky and plastic when wet, firm when moist, slightly hard when dry; very few very-fine to coarse roots; clear smooth boundary; pH (H_2O) = 5.2.
C	80+ cm	Saprolite, material very weathered.