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Determinants of Leaf Litter Nutrient Cycling in a Tropical Rain Forest: Soil Fertility Versus Topography

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ABSTRACT

We investigated the influence of landscape-level variation in soil fertility and topographic position on leaf litter nutrient dynamics in a tropical rain forest in Costa Rica. We sampled across the three main edaphic conditions (ultisol slope, ultisol plateau, and inceptisol) to determine the effect of soil nutrients on leaf litter nutrient concentrations while controlling for topography, and to examine topographic effects while controlling for soil nutrients. Both leaf litter macronutrient [phosphorus (P), nitrogen (N), sulfur (S), calcium (Ca), potassium (K), magnesium (Mg)] and micronutrient concentrations were quantified throughout a 4-year period. Leaf litter [P], [N] and [K] varied significantly among soil types. The variation in [P], [N], and [K] was explained by soil fertility alone. Leaf litter [S], [Ca], and [Mg] did not vary among the three soil types. Macronutrient (P, K, Mg, S, Ca) concentrations in the leaf litter were much less variable than those of Fe and Al. Lower variability in essential plant nutrients suggests a great deal of plant control over the amount of nutrients resorbed before senescense. Leaf litter macronutrient concentrations varied significantly over the 4-year period, but the temporal variation did not differ among the three edaphic types as anticipated. Hence, although the magnitude of nutrient fluxes may be controlled by local factors such as soil fertility, temporal patterns are likely regulated by a common environmental variable such as precipitation or temperature.

Key words: cations; edaphic; leaf litter; nutrients; phosphorus; soil fertility; topography; tropical rain forest.

INTRODUCTION

On a global scale, patterns of nutrient cycling differ considerably among tropical sites with contrasting soil fertility (Vitousek and Sanford 1986). In general, an increase in soil fertility is positively associated with leaf litter quality, nutrient concentrations in live leaf tissue, decomposition rates, and nitrogen mineralization (Edwards 1982; Vitousek and Sanford 1986; Crews and others 1995; Vitousek 1988; Aerts and Chapin 2000). In addition, nutrient availability plays an important role in the ability of plants to withstand environmental stress. High nutrient levels contribute to maintaining osmotic pressure in leaves, enabling plants to withstand a higher degree of drought stress (Murphy and Lugo 1986). Therefore, soil fertility should affect both the magnitude and, depending on the degree of drought stress experienced, the temporal pattern of nutrient flow through leaf litterfall at the landscape scale.

Topography can also affect leaf litter nutrient cycling. Soil moisture and cation exchange capacity tend to be lower on steep slopes than on plateaus (Becker and others 1988; Silver and others 1994;

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Table 1. Characteristics of the Three Main Edaphic Types at La Selva Biological Station, Costa Rica: Inceptisol, Ultisol Plateau and Ultisol Slope

Soil type	Number[1] (stems/ha)	Leaf litter[2] mass (Mg/ha per year)	Eective cation[3] exchange capacity (ECEC)	PH[3]
Inceptisol	410	6.6	63	4.65
Ultisol plateau	510	7.2	62	4.43
Ultisol slope	593	6.5	47	4.66

[1] *Data are from Clark and Clark 2000.*
[2] *D.A. Clark, unpublished data.*
[3] *D.B. Clark, unpublished data.*

Laurance and others 1999). Steep slopes may also have lower clay content and thus lower concentrations of important nutrients such as nitrogen (N) or phosphorus (P) due to lower bonding of soil organic matter (Laurance and others 1999). Hence, we expected higher leaf litter nutrient concentrations in the flat versus sloped sites.

At our study site as many as 30% of tree species are distributed non-randomly with respect to soil type and topography. This non-random distribution suggests that small environmental gradients can affect the abundance and distribution of trees in tropical rain forests at the landscape scale (Clark and others 1998, 1999). Variation in tree species could influence the chemical composition of plant litter through differences in nutrient requirements (Palma and others 2000) or nutrient resorption (Scott and others 1993; Killingbeck 1996; Aerts and Chapin 2000) of the different species, and thus could produce spatial variation in leaf litter nutrient concentrations.

In this study we address three hypotheses about edaphic effects on litter nutrient dynamics: (1) Greater soil fertility leads to higher leaf litter nutrient concentrations; (2) Within a soil type, steep slopes have lower leaf litter nutrient concentrations than plateau sites, and (3) Variation in soil fertility and topography will influence the temporal pattern of leaf litter nutrient concentrations such that more fertile, non-sloped sites (inceptisols) will exhibit greater variation than the more nutrient stressed sites (ultisols).

METHODS

Study Site

This study was conducted in old growth, tropical wet forest at La Selva Biological Station in Costa Rica (10°26′N, 84°00′W; Organization for Tropical Studies [OTS]; Holdridge 1947). The three dominant edaphic types in the upland old-growth forest are inceptisol terraces, flat terrain on ultisols, and slopes on ultisols. All of the soils are deep, well drained, clay-rich and acidic (pH 4–5) (Table 1; Sollins and others 1994; D.B. Clark, unpublished data). The effective cation exchange capacity ranges from 47 to 63 mmol/kg and is lowest on ultisol slopes (Table 1; D.B. Clark, unpublished data). The stocks of N, P, carbon (C), and potassium (K) in the soil vary significantly among soil types. Inceptisols have the highest concentrations of both P and K, whereas the ultisol plateaus have higher concentrations of C and N. The elements calcium (Ca), magnesium (Mg), iron (Fe), manganese (Mn), and aluminum (Al) do not vary significantly among the three soil types (D.B. Clark, unpublished data). The flora includes over 320 tree species, and the great majority of canopy trees are evergreen (Hartshorn and Hammel 1994). Stem density is highest on ultisol slopes (Table 1; Clark and Clark 2000).

Mean annual rainfall at La Selva is 4,400 mm (OTS, unpublished meteorological records). The driest period lasts from late January through April, with an average 60% less rainfall than during wet season months (180 vs. 440 mm/month). Biweekly rainfall varies from less than 25 mm to more than 350 mm, so the vegetation may experience brief periods of drought stress (OTS, unpublished meteorological records).

Leaf Collection and Nutrient Analysis

Eighteen 0.5 ha plots were established in 1996 (the CARBONO project; Clark and Clark 2000). The plot network was designed using the La Selva GIS system to provide six unbiased, replicated samples of the three dominant edaphic conditions in the upland landscape (inceptisol terrace, ultisol plateau, ultisol slope; compare Clark and Clark 2000; Figure 1). This design allows us to determine the effect of soil nutrients on leaf litter nutrient concentrations while controlling for topography, and to examine topographic effects on leaf litter nutrient concentrations while controlling for soil nutrients. Within each plot, fine litterfall (leaves,

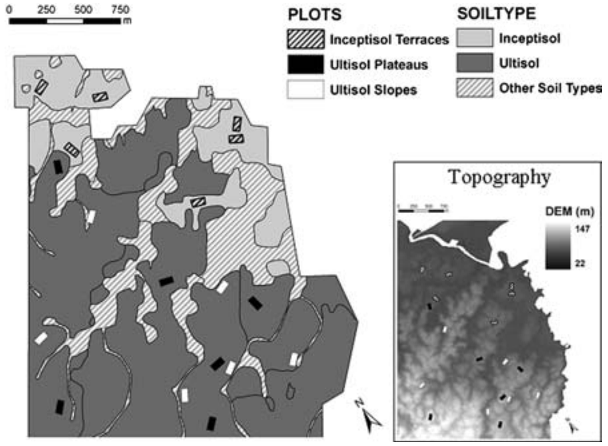

Figure 1. Location of the plots at La Selva Biological Station, Costa Rica shown in relation to both soil type and topography. The eighteen 0.5 ha plots were distributed across the three main edaphic site types: inceptisol terraces, ultisol hilltops, and ultisol slopes (Clark and Clark 2000; map prepared by M. Snyder).

reproductive material and twigs 1 cm in diameter) has been collected biweekly since September 1997. At each plot, nine 0.25 m^2 standing litterfall traps are paired with nine 0.25 m^2 ground traps for large items. Samples from the traps in each plot were combined, sorted by litter material, and oven-dried to constant mass (65°C). The dried leaf material was then run through a Wiley Mill to pass through a 1 mm mesh screen.

To determine [P] and [N] of the leaf litter, we used a modified Kjeldahl digestion on a Tecator 2000 Digestion System (Perstorp Analytical; Sweden). This method uses 30% hydrogen peroxide and concentrated sulfuric acid at 360°C to hydrolyze organic P and N to inorganic forms. We kept digested samples refrigerated until analyzing the matrix colorometrically on an Alpkem Flow Solution IV Autoanalyzer (OI Analytical, College Station, TX, USA) in accordance with the US EPA method for total P and N determination.

The remaining nutrients (Ca, Mg, K, Mn, Al, Fe, sodium (Na), sulfur (S), boron (B), copper (Cu), nickel (Ni), cobalt (Co), and zinc (Zn)) were analyzed at the Cornell Nutrient Analysis Laboratory (CNAL). Samples were digested in HNO_3/H_2O_2 on a block at 150°C. The samples were then re-dissolved in 50 ml of 10% nitric acid for analysis using Spectro CIROS CCDE Inductively Coupled Argon Emission Plasma Spectrometry (ICP).

We analyzed leaf litter nutrient data from all 18 sites for P and from 12 sites (4 ultisol slope, 4 ultisol plateau, and 4 inceptisol) for all other nutrients. Chemical analysis was conducted on samples taken every 4–5 months over a 4-year period (11 dates, yielding 198 samples for N and P and 132 samples for all other nutrients). Differences by soil type and topography were analyzed by repeated measures analysis of variance (RANOVA). When significant, the RANOVA was followed by the Tukey–Duncan post hoc test to determine where significant differences occurred. In addition, we used RANOVA to determine whether differences in temporal patterns occurred among elements.

Total nutrient inputs (kg/ha per year) at each site for the sample years 1998–2001 were calculated by multiplying mean leaf litter nutrient concentration and leaf litter production for each plot and year (D.A. Clark, unpublished data). These figures were then averaged by edaphic type (for a given year). The yearly means for each type were then averaged to determine mean annual nutrient input for each of the elements. For the time period of interest (1998–2001), leaf litter mass did not vary significantly among soil types (Tables 1, 2; D.A. Clark, unpublished data).

We regressed mean leaf litter nutrient concentration on total soil nutrient stocks to 1 m depth in each plot (P, K, Mg, Mn, Fe, Al, Ca; D.B. Clark, unpublished data) to determine whether leaf litter nutrient concentrations are influenced by deep soil nutrient pools.

All regressions were conducted using SigmaPlot for Windows V7.1 (SPSS Inc., 2001) and RANOVAs were performed using SAS System for Windows V8 (SAS Institute Inc., 2001).

RESULTS

Macronutrients (P, N, K, S, Mg, Ca)

Leaf litter [P], [N], and [K] were significantly higher in the inceptisols than in both ultisol plateaus and ultisol slopes (Figure 2; RANOVA edaphic type effect, $F = 13.25$, $P = 0.0005$ (P); $F = 7.21$, $P = 0.01$ (N); $F = 4.63$, $P = 0.04$ (K); Tukey–Duncan). Within the ultisol soil type, topography (slope plots vs. plateau plots) did not significantly influence leaf litter [P], [N], or [K] (Figure 2). Mean leaf litter [P] for inceptisols was 0.84 mg/g, 0.66 mg/g for ultisol plateaus and 0.68 mg/g for ultisol slopes (Figure 2). These values are in the upper range of values reported for other tropical rain forests (Table 2). The N values (1.6–1.9%) are also on the high end of those reported for other tropical rainforests (Table 2). In contrast, mean leaf litter [K] was lower than the average tropical rain forest (2.1–3.3 mg/g vs. 3.8 mg/g), and also lower than the concentration reported by Gessel and others (1980) for the same forest (4.1 mg/g; Table 2).

Table 2. Mean Leaf Litter Mass and Nutrient Concentrations for Tropical Forests with above 1,500 mm Annual Precipitation

Place	Forest type	Precipitation (mm)	Production (trees/ha per year)		N (%)	Litter nutrient (mg/g)						Citation
			Total	Leaf		P	K	Ca	Mg	Na	S	
Columbia	Lower Montane	1,500	4.3	2.8	0.8	0.4	3.5	–	–	–	–	Veneklaas (1991)
Australia	Rain Forest	1,500	9.6	–	1.4	1.2	6.4	21.1	3.2	0.4	–	Brasell and others (1980)
Senegal	*Tectona* Plantation	1,590	–	5.3	–	0.8	7.0	17.5	3.5	–	–	Maheut and Dommergues (1960)
New Guinea	Lowland Rainforest	1,600	8.8	–	1.9	0.8	0.3	2.1	0.1	0.1	–	Enright (1979)*
Ghana	High Forest	1,630	10.5	7.0	1.9	0.7	6.5	19.6	4.3	–	–	Nye and Greenland (1960)
Congo	Plateau forest	1,700	12.4	–	1.8	0.6	3.9	8.5	4.3	–	–	Laudelot and Meyer (1954)
Ivory Coast	Rain Forest (Yapo I)	1,735	7.1	–	1.4	0.5	2.8	13.2	2.9	–	–	Bernhard-Reversat (1972)
Ivory Coast	Rain Forest (Yapo II)	1,735	6.2	–	1.4	0.5	4.9	13.6	3.2	–	–	Bernhard-Reversat (1972)
Trinidad	*Mom excelsa* Forest	1,800	–	6.9	0.9	0.4	1.6	9.1	2.2	–	–	Cornforth (1970)
India	Moist Deciduous	1,900	11.6	8.4	1.2	0.7	7.2	21.5	5.5	0.5	–	Swamy and Proctor (1994)
Brazil	Tierra Firme	1,900	7.3	5.6	1.5	0.3	2.0	2.5	2.0	0.7	–	Klinge and Rodriguez (1968a, b)*
Guatemala	Secondary Forest	2,000	10.0	–	1.4	0.7	2.4	21.2	3.5	–	–	Ewel (1976)
Guatemala	Mature Forest	2,000	9.0	–	1.9	0.6	2.2	9.8	7.1	–	–	Ewel (1976)
Malaysia	Dipterocarp Rain Forest	2,000	6.4	–	1.2	0.3	3.7	7.0	2.2	–	–	Lim(1978)*
Panama	Tropical Moist Forest	2,000	11.3	–	–	1.0	5.6	28.9	2.5	0.2	–	Golley and others (1975)
Ivory Coast	Rain Forest (plateau)	2,095	10.3	7.4	1.5	0.6	2.5	9.4	3.8	–	–	Bernhard (1970)
Ivory Coast	Rain Forest (valley)	2,095	9.0	6.8	1.6	1.1	7.0	11.6	3.7	–	–	Bernhard (1970)
Columbia	Lower Montane	2,115	7.0	4.6	1.1	0.7	8.9	–	–	–	–	Veneklaas (1991)
Panama	Premontane Wet Forest	2,500	10.5	–	–	1.6	5.0	14.7	2.3	0.3	–	Golley and others (1975)
Australia	Upland Rain forest	2,630	–	–	1.0	0.3	4.3	9.7	2.8	–	–	Herbohn and Congdon (1998)
Columbia	Humid Tropical Forest	3,000	6.6	–	1.3	0.4	2.3	10.8	1.6	–	–	Fölster and de las Solas (1976)
Venezuela	Tierra Firme	3,565	7.6	–	1.6	0.3	2.4	1.7	0.7	–	–	Cuevas and Medina (1986)
Venezuela	Tall Caatinga	3,565	4.0	–	0.7	0.5	2.1	7.7	3.1	–	–	Cuevas and Medina (1986)
Venezuela	Bana	3,565	2.1	–	0.6	0.2	4.7	7.4	2.5	–	–	Cuevas and Medina (1986)
India	Lowland Rain Forest	3,900	12.0	9.1	1.7	0.6	5.8	20.3	5.8	0.6	–	Swamy and Proctor (1994)
New Guinea	Lower Montane	4,000	6.4	–	1.3	0.7	3.9	12.5	2.7	–	–	Edwards (1982)
Puerto Rico	Lower Montane	4,200	4.8	–	–	–	0.4	8.3	2.1	–	–	Jordan and others (1972)
Costa Rica	Rain Forest	4,300	7.8	–	1.9	–	4.1	17.9	–	–	–	Gessel and others (1980)*
Costa Rica	Rain Forest (inceptisol)	4,300	–	6.6	1.9	0.9	3.3	8.0	2.0	0.5	1.8	This study
Costa Rica	Rain Forest (ultisol plateau)	4,300	–	7.2	1.6	0.7	2.0	8.3	2.3	0.6	1.7	This study
Costa Rica	Rain Forest (ultisol slope)	4,300	–	6.5	1.7	0.7	2.4	7.1	2.0	0.6	1.7	This study
India	Rain Forest	5,000	4.2	3.6	1.5	3.2	2.7	11.2	4.5	–	–	Rai and Proctor (1986)
India	Rain Forest	5,000	4.1	3.2	1.1	0.3	1.9	11.4	8.7	–	–	Rai and Proctor (1986)
India	Rain Forest	5,000	4.0	3.4	0.8	0.4	4.1	11.5	9.0	–	–	Rai and Proctor (1986)
India	Rain Forest	5,000	3.4	2.9	1.0	2.4	1.5	7.6	3.2	–	–	Rai and Proctor (1986)
Malaysia	Alluvial Forest	5,000	6.6	–	0.9	0.3	2.6	24.4	2.0	–	–	Proctor (1984)
Malaysia	Keranga	5,000	5.6	–	0.6	0.1	2.3	8.8	1.6	–	–	Proctor (1984)

Table 2. Continued

Place	Forest type	Precipitation (mm)	Production (trees/ha per year)		Litter nutrient (mg/g)							Citation
			Total	Leaf	N (%)	P	K	Ca	Mg	Na	S	
Malaysia	Dipterocarp Rain Forest	5,000	5.4	–	1.0	0.1	4.5	1.5	1.1	–	–	Proctor (1984)
Malaysia	Calcareous	5,000	7.3	–	1.2	0.4	1.6	31.8	3.3	–	–	Proctor (1984)
India	Lowland Rain Forest	6,400	13.3	9.0	1.5	0.6	6.6	13.8	3.9	0.9	–	Swamy and Proctor (1994)
India	Lower Montane	6,400	13.9	10.6	1.3	0.5	6.5	16.3	5.8	0.8	–	Swamy and Proctor (1994)
	Mean	–	7.7	6.1	1.3	0.7	3.8	12.5	3.3	0.5	1.7	

*Indicates studies where leaf litter was collected on the ground.

In contrast, the elements S, Ca, and Mg did not differ significantly among soil types. Leaf litter [Mg] and particularly [Ca] values were below the average for tropical rain forests (2.0–2.3 mg/g vs. 3.3 mg/g (Mg); 7.1–8.3 mg/g vs. 12.5 mg/g (Ca); Table 2). There were no S values reported for wet tropical forest to compare with these values.

Leaf litter [P] and [Ca] were positively related to total P and Ca stocks, respectively, in the top 1 m of the soil (Figure 3A: $R^2 = 0.628$, $P < 0.0001$; Figure 3B: $R^2 = 0.385$; $P = 0.031$). The relationship for Ca was driven by a single high value; it was not significant when the soil with a Ca stock above 700 Mg/ha was removed (Figure 3B). None of the other cations showed a significant relationship between leaf litter nutrient concentrations and their soil stocks. Although leaf litter N was not related to soil N stocks, leaf litter N was negatively related to soil C:N (Figure 4B: $R^2 = 0.39$; $P = 0.006$). Leaf litter P also declined as soil C:P increased (Figure 4A: $R^2 = 0.51$; $P = 0.0009$).

Total estimated annual nutrient inputs of P and K via leaf litterfall varied among the three edaphic conditions in parallel with their leaf litter concentrations (Table 3; Figure 2). Inputs of both P and K were significantly higher in the inceptisols than in the ultisols [RANOVA edaphic type effect, $df = 2$, $F = 4.05$, $P = 0.0393$ (P); $df = 2$, $F = 5.84$, $P = 0.0237$ (K)]. Mean annual nutrient inputs of N, Mg, and S did not differ significantly among the three soil types; however, their inputs differed in a pattern similar to that of their nutrient concentrations (RANOVA edaphic type effect, n.s.; Figure 2; Table 3).

Although the magnitude of leaf litter nutrient concentrations differed significantly among the three edaphic conditions, the temporal patterns of leaf litter P, N, K, Mg, Ca, and S cycling were not significantly related to either soil fertility or topography (time × edaphic type effect, $P > 0.05$, n.s.; RANOVA). In contrast, the temporal patterns of all elements differed significantly from one another with the exception of the three cations (K, Mg, and Ca) (RANOVA time × element category effect, $F = 1.70$, $P < 0.0001$; Figure 5). The temporal patterns were most distinct in late 1999 and early 2000. Cation concentrations increased while N and P concentrations decreased during this period (Figure 5).

Micronutrients (B, Na, Mn, Mo, Al, Ni, Co, Cu, Fe)

Of the micronutrients examined, the leaf litter concentrations of only B and Cu differed signifi-

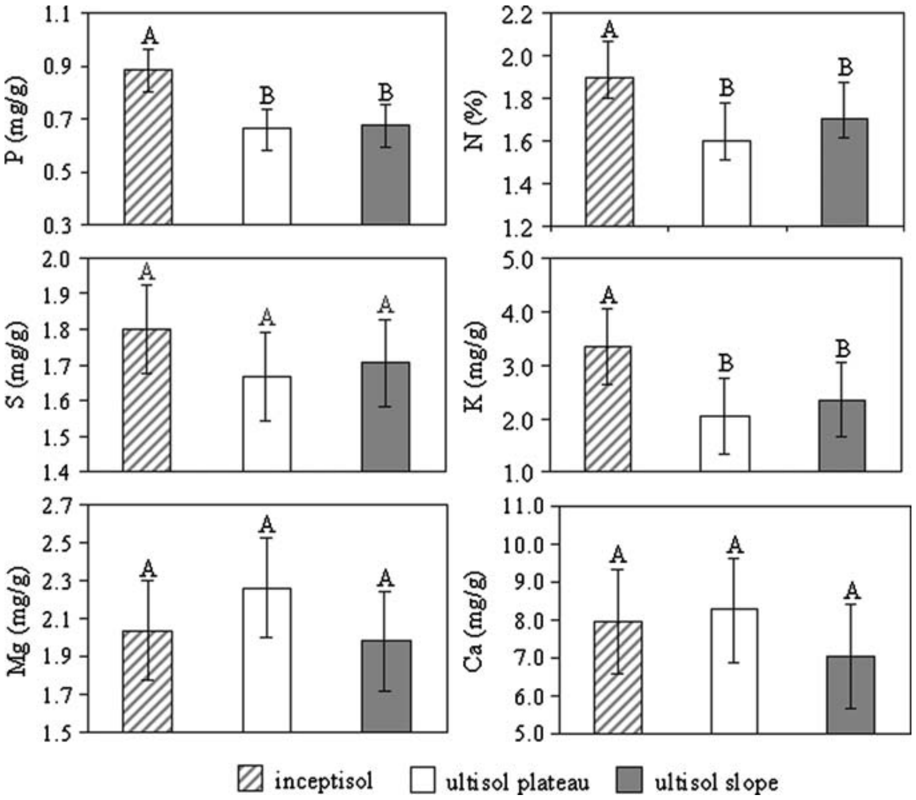

Figure 2. Average leaf litter macronutrient concentrations by edaphic type ± confidence interval. The *different letters* represent significant differences among edaphic types. Confidence intervals are presented in conformity with use of RANOVA.

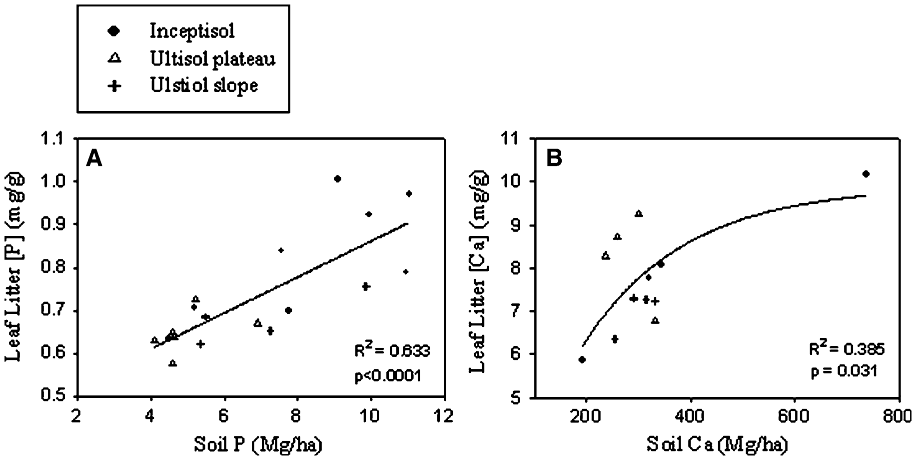

Figure 3. Regressions of leaf litter [P] and [Ca] concentrations (mg/g dry mass) versus total soil nutrient stocks to 1 m depth in four plots per edaphic type.

cantly among edaphic types (RANOVA edaphic type effect; $F = 5.19$, $P = 0.0317$ (B), $F = 5.89$, $P = 0.0232$ (Cu)). Both B and Cu concentrations were significantly higher in ultisol plateaus than in both inceptisols and ultisol slopes (Table 4, Tukey–Duncan). The elements Cu, B, Zn, Ni, and Na varied significantly with time (RANOVA time effect; $F = 7.61$, $P < 0.0001$ (Cu); $F = 5.19$, $P = 0.0317$ (B), $F = 2.24$, $P = 0.0218$ (Zn), $F = 6.13$, $P < 0.0001$ (Ni); $F = 37.17$, $P \leq 0.0001$ (Na)).

The concentration of elements Al, B, Mo, Fe, and Pb were lower than values found in other tropical forests (Table 2). Co, Ni, and Mn showed higher concentrations, and the remaining micronutrients (Na, Cu) had values similar to those in other tropical forests (Table 4). Leaf litter [Mn] was strongly related to total soil Mn stocks (Mg/ha) to 1 m (Figure 6; $R^2 = 0.831$, $P < 0.0001$). Neither Fe nor Al in litter was significantly related to soil stocks. There were no soils data for the remaining

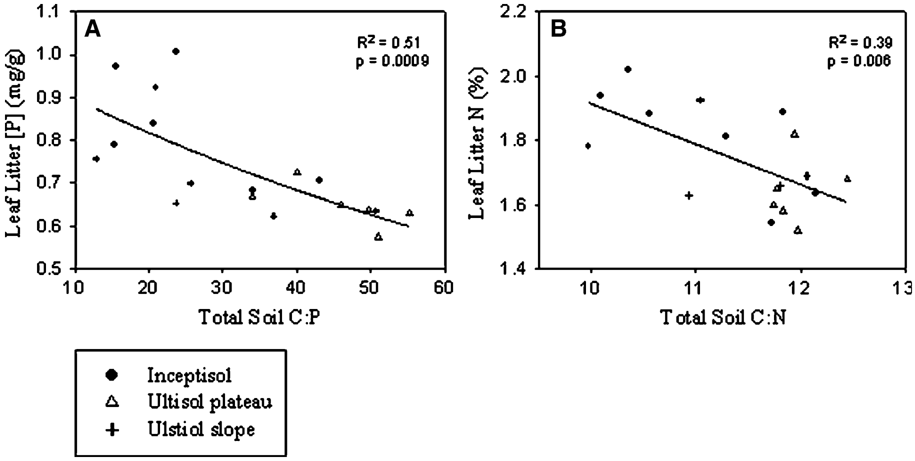

Figure 4. Regressions of leaf litter [N] and [P] concentrations (mg/g dry mass) versus total soil carbon:nutrient stocks to 1 m depth.

Table 3. Mean Estimated Nutrient Inputs (kg/ha per year) in Leaf Litterfall by Edaphic Type at La Selva, Costa Rica

	Mean annual nutrient input (kg/ha/y)		
Element	Inceptisol	Ultisol Plateau	Ultisol Slope
N	A	A	A
	133	126	114
P	A	B	B
	6	5	4
K	A	B	B
	23	15	15
Ca	A	A	A
	56	65	46
Mg	A	A	A
	14	18	13
S	A	A	A
	13	13	11
Na	A	A	A
	4	4	4

Letters indicate significant differences among soil types.

micronutrients. Neither topography nor soil type influenced the temporal pattern of leaf litter concentrations for any of the micronutrients (RANOVA time × edaphic type effect, $P < 0.05$, n.s.).

Regardless of soil type, leaf litter concentrations of the macronutrients varied less over the 4-year period of study than those of the micronutrients. The coefficient of variation (CV) ranged from 12–38% for the macronutrients, whereas nutrients such as Fe and Al varied as much as 354 and 250%, respectively (Table 5). Interestingly, the variation in Cu was similar in scale to that of the macronutrients (12–23%). The CV of element concentrations in leaf litter did not differ significantly among the three edaphic types.

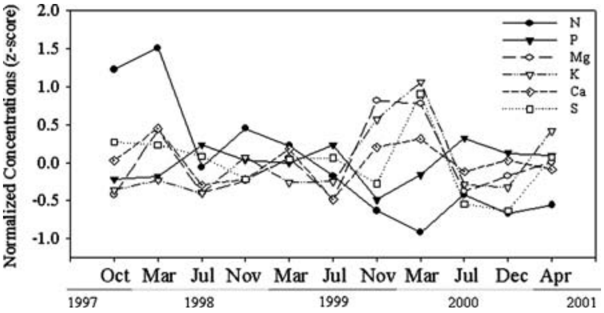

Figure 5. Seasonal patterns of leaf litter macronutrient concentrations over the 4-year study period. The dry season is generally late January through April. Data were normalized (mean = 0, SD ± 1) to illustrate differences among elements.

Discussion

Three of the major leaf litter macronutrients (P, N, K) varied significantly among the three dominant edaphic types in the upland old growth forest at La Selva. As expected, leaf litter [P], [N], and [K] were highest in the more fertile inceptisols. For P, variation in leaf litter nutrient concentrations was positively related to total soil nutrient stocks to 1 m depth suggesting that plants exploit a deeper nutrient pool for P (Figure 3A). The negative relationship between leaf litter N, P and their respective soil nutrient:carbon ratios suggests that as the carbon-nutrient ratio increases, the availability of these nutrients decreases, leading to lower nutrient concentrations in the litter. That leaf litter K was not related to soil K stocks to 1 m suggests that the vegetation may be exploiting a shallower available nutrient pool for this nutrient or that K is not as limiting as N and P. Neither soil fertility nor topography significantly influenced leaf litter [S], [Mg], and [Ca], most likely, because soil levels do not vary significantly among the three edaphic

Table 4. Mean Leaf Litter Micronutrient Concentrations by Edaphic Type for La Selva, Costa Rica (this study) and for Eastern Panama (Golley and others 1975)

	La Selva, Costa Rica			Eastern Panama			
Element	Inceptisol	Ultisol plateau	Ultisol slope	Premontane	Riverine	Mangrove	Tropical Moist
Al	479	828	778	2,000	–	–	1,740
B	15	19	15	25	–	–	26
Co	860	505	2,077	39	91	0.07	54
Cu	11	11	10	13	5	4	13
Fe	243	229	288	1,079	1,069	1	755
Mn	665	530	655	369	127	0.08	269
Mo	0.20	0.33	0.33	11	–	–	8
Ni	869	970	920	–	–	–	26
Pb	0.06	0.01	0.02	36	68	0.05	43
Zn	26	21	29	39	12	0.01	39

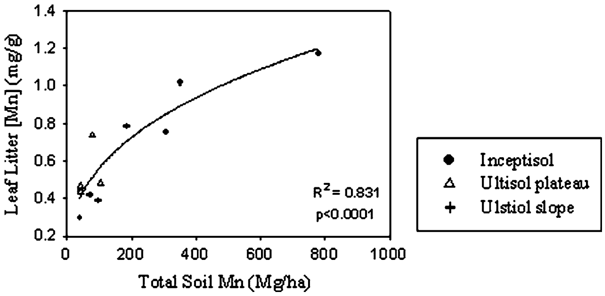

Figure 6. Regressions of leaf litter [Mn] versus total soil Mn stocks to 1 m depth in each of the 12 sampled plots.

types (D.B. Clark, unpublished data). Alternatively, uptake may be limited by more than one environmental factor (that is, a combination of nutrients) or by a factor that does not vary systematically with soil fertility. Further research is necessary to test these hypotheses.

As expected, mean annual nutrient inputs varied among the three soil types in the same manner as leaf litter nutrient concentrations (Table 3; Figure 2). Leaf litter P and K inputs were significantly higher on inceptisols than on ultisols. Although leaf litter N inputs were not significantly higher, these values also tended to be greater on inceptisols than on the ultisols (Table 3). Hence, mean annual leaf litter inputs of N, P, and K are likely driven by soil nutrient status rather than topography. In contrast, mean annual Ca, Mg, and S inputs, although not significant, were on average lower on the sloped plots than on the plateaus. This trend towards lower Ca, Mg, and S inputs on sloped sites may be due to the lower cation exchange capacity at these sites (Table 1).

In summary, neither the higher soil nutrient status nor the higher leaf litter concentrations/inputs of N, P, and K led to greater leaf litter production on inceptisols than ultisols (Table 1; D.A. Clark, unpublished data). Therefore, forests located on ultisols have higher overall nutrient use efficiency than those on inceptisols (that is, more organic matter produced per unit nutrient; compare Vitousek 1982). Although Ca, Mg, and S inputs tended to be lower on sloped sites than on plateaus, topographic position did not significantly influence leaf litter nutrient cycling at La Selva.

Overall, there is a large degree of variation in leaf litter nutrient concentrations among tropical rain forests (CV: 30% N, 78% P, 69% K, 76% Ca, 75% Mg; Table 2). For La Selva, leaf litter [N] and [P] are above average in comparison to other tropical rainforests, whereas cation concentrations are below average (Table 2). However, these concentrations fall well within the range of values reported for other tropical rain forests (Table 2); thus, findings from this study are likely relevant for a broad range of tropical forests. The large variation in leaf litter nutrient concentrations among tropical rain forests is not explained by mean annual rainfall, latitude or region (regressions not shown). Results from this study suggest that a large degree of variation in leaf litter nutrient concentrations both within and among tropical rain forests is related to soil nutrient status.

In addition to influencing the magnitude of nutrient concentrations in the leaf litter, we also proposed that soil type would influence the temporal pattern of leaf litter nutrient cycling. We expected ultisols to show less temporal variability in leaf litter nutrient concentrations than inceptisols (that is, tighter nutrient cycling), based on the assumption that vegetation on ultisols operates under greater nutrient stress. Leaf litter [P] and

Table 5. Coefficient of Variation and the Range of Leaf Litter Nutrient Concentrations of both Macro and Micronutrients at La Selva, Costa Rica

	Coefficient of variation [range]		
Element	**Inceptisol**	**Ultisol Plateau**	**Ultisol Slope**
S	11 (1.37–2.23)	15 (1.17–2.51)	12 (1.37–2.27)
P	18 (0.56–1.42)	15 (0.45–0.96)	14 (0.46–0.97)
Cu	23 (0.01–0.025)	12 (0.008–0.014)	13 (0.007–0.013)
Mg	18 (1.40–2.85)	23 (1.22–4.91)	16 (1.4–2.62)
Ca	23 (5.03–12.25)	20 (3.58–14.90)	14 (4.74–9.76)
N	24 (1.26–3.45)	23 (0.98–2.57)	27 (0.87–3.65)
K	37 (1.45–7.55)	38 (4.60–7.77)	29 (1.55–4.09)
B	46 (0.008–0.051)	47 (0.01–0.07)	30 (0.01–0.03)
Zn	39 (0.015–0.059)	48 (0.01–0.075)	46 (0.015–0.065)
Mn	57 (0.21–1.73)	33 (0.27–1.16)	47 (0.26–1.22)
Cr	56 (0.0003–0.005)	72 (0.0002–0.008)	46 (0.0004–0.005)
Na	65 (0.23–2.20)	68 (0.05–1.91)	61 (0.25–1.52)
Al	251 (0.12–17.59)	107 (0.18–6.82)	68 (0.14–2.19)
V	209 (0–0.049)	211 (0.00–0.035)	98 (0.0004–0.009)
Fe	287 (0.06–13.61)	354 (0.08–15.64)	107 (0.08–1.32)

[Ca] did vary more in the inceptisols than in the ultisols overall; however, this trend did not hold for the other macronutrients (Table 2). Despite links between soil type and leaf litter nutrient cycling, the temporal pattern of leaf litter nutrient concentrations did not differ significantly among the three edaphic types for any of the nutrients analyzed. Although local factors such as topography (hydrological regime, erosion, weathering, gap formation) and soil fertility may be influencing the magnitude of nutrient fluxes, the temporal pattern is likely regulated by a common environmental factor such as precipitation or temperature. The significant difference in temporal patterns among the different elements suggests that there are seasonal demands for some elements over others. This is especially true for N and P versus the cations (Figure 5). Cations in senescing leaves are more susceptible to leeching during periods of high precipitation than N or P, whereas P in senescing leaves may increase during wet season months due to an associated increase in soil nutrient availability and uptake (Wood and others 2005).

The micronutrients Cu, B, Zn, Ni, and Na, which are somewhat mobile in leaf tissue (Salisbury and Ross 1992), varied significantly with time. Variation in the concentration of these nutrients in the leaf litter may be caused by temporal patterns of either nutrient leeching or nutrient resorption. The similarity between the CV of Cu and that of the more limiting macronutrients is the evidence of more plant control over this nutrient. As we observed for the cations (Wood and others 2005), rainfall may be leeching other micronutrients from the leaf surface; however, B is the only one for which we found a negative relationship with precipitation (Regression; $R^2 = 0.554$, $P = 0.0397$; T.E. Wood and D. Lawrence, unpublished data). Hence, it is more likely that variation in the micronutrients is the result of inconsistencies in availability or due to plant control (that is, nutrient resorption or nutrient uptake).

CONCLUSIONS

Leaf litter nutrient concentrations varied significantly among soil types for N, P, and K. For these nutrients, the difference was explained by soil fertility rather than topography. In contrast, [S], [Ca], and [Mg] were not influenced by soil type. Over the 4-year sample period, leaf litter P, S, K, Ca, Mg, B, and Cu concentrations varied significantly with time. The pattern, however, did not differ among the three soil types as anticipated. This similarity in pattern suggests that forest patches on different soil types within the landscape are responding to common environmental cues. The major nutrients N, P, K, Mg, S, and Ca were much less variable than non-limiting nutrients such as Fe and Al, suggesting that there is a large degree of plant control over the amount of soluble nutrients that are resorbed before leaf senescence.

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