

# Nitrogen, Phosphorus, and Sulfur Properties of Some Forest Soils on Barro Colorado Island, Panama<sup>1</sup>

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## ABSTRACT

Eight surface soils from lowland tropical moist forest on Barro Colorado Island, Panama, were evaluated for: (1)  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ ,  $\text{PO}_4^{3-}\text{-P}$ , and  $\text{SO}_4^{2-}\text{-S}$  concentrations in 10-mM  $\text{CaCl}_2$  extractions; (2) N, P, and S mineralization potentials in laboratory incubations; and (3) total N, P, and S concentrations. Concentrations of  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ , and  $\text{PO}_4^{3-}\text{-P}$  prior to incubation were similar among the soils despite significant differences in total C, N, and P concentrations. Initial concentrations of  $\text{SO}_4^{2-}\text{-S}$  generally were greater in basalt-derived soils than in sediment-derived soils, although a similar pattern in total S concentrations among these sites was not observed. The net mineralization potentials of the eight soil types had three characteristics in common: (1) most of the mineralized N was nitrified, and  $\text{NO}_3^-\text{-N}$  accumulated at an approximately linear rate over a 32-day incubation period; (2)  $\text{PO}_4^{3-}\text{-P}$  decreased between days 0 and 16, then increased more than ten times between days 16 and 32; and (3)  $\text{SO}_4^{2-}\text{-S}$  did not change over time. The striking consistency in the patterns of net mineralization among the eight soils was unexpected because of differences in the total element contents of the soils and in the parent materials, vegetation on the site, and history of disturbance to the vegetation.

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## RESUMEN

Se evaluaron ocho suelos de superficie de tierras bajas en selva tropical húmeda, sitios en la isla de Barro Colorado (Panamá), con respecto a: (1) concentraciones  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ ,  $\text{PO}_4^{3-}\text{-P}$  y  $\text{SO}_4^{2-}\text{-S}$  en extracciones 10-mM  $\text{CaCl}_2$ ; (2) potenciales de mineralización N, P y S en incubaciones de laboratorio; y (3) concentraciones totales N, P y S. Las concentraciones de  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$  y  $\text{PO}_4^{3-}\text{-P}$  anteriores a la incubación eran similares en todos los suelos, a pesar de las notables diferencias en cuanto a las concentraciones totales de C, N y P. Por lo general, las concentraciones iniciales de  $\text{SO}_4^{2-}\text{-S}$  eran mayores en los suelos basalto-derivados que en los sedimentario-derivados, si bien entre dichos suelos no se observó un patrón similar respecto al total de concentraciones S. Los potenciales de mineralización netos de los ocho tipos de suelo tenían en común lo siguiente: (1) la mayor parte del N mineralizado era nitrificado, y acumulación  $\text{NO}_3$  a una razón lineal aproximada sobre un periodo de incubación de 32 días; (2) el  $\text{PO}_4^{3-}\text{-P}$  decreció entre los días 0 y 16, para aumentar después en más de un orden de magnitud entre los días 16 y 32; y (3) el  $\text{SO}_4^{2-}\text{-S}$  no cambió en todo el periodo. La notable coherencia en los patrones de mineralización neta de los ocho suelos fue algo inesperado, dadas las diferencias en el contenido total de elementos, materiales generadores, vegetación de los lugares, e historial de los contratiempos sufridos por la vegetación.

NATURAL DISTURBANCES THAT CREATE "PATCHES" in a forest (*sensu* White & Pickett 1985) might result in a corresponding mosaic in the nutrient content of the soils associated with different forest patches. For example, treefall gaps are a prominent source of environmental heterogeneity in lowland tropical moist forest, and the amount of coarse woody litter on the soil surface in a gap is much greater than that in the surrounding undisturbed forest. Spycher *et al.* (1983) have shown that soil organic matter derived from woody litter has a much lower nutrient content, especially of N, than soil organic matter derived from leaf litter. In addition, rapid forest regeneration in treefall gaps results in higher demand for nutrients by

plant uptake than in mature forest, and plant uptake often is responsible for maintaining a low level of available nutrients in the soil (Aber *et al.* 1982). On a broader scale, the nutrient properties of a soil often are affected by the successional status of the forest (Lamb 1980, Robertson 1984, Werner 1984), as well as by the parent material (Jenny 1980).

On Barro Colorado Island, Panama, both young and old forest stands grow on soils derived from both basaltic and sedimentary parent materials, and treefall gaps in different stages of regeneration have been recorded (Lang & Knight 1983, Brokaw 1985). We have taken advantage of this diversity of conditions to examine variability in N, P, and S properties in surface soils. We emphasize N, P, and S because of the interrelationship among these nutrients in soil organic matter (McGill & Cole 1981).

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## STUDY SITES

BCI (9°09'N, 79°51'W) is a 15-km<sup>2</sup> island in Gatun Lake, Panama. Annual precipitation is 267 cm with a marked dry season from January to late March when monthly rainfall is usually less than 13 cm. The vegetation on BCI has been classified as tropical moist forest (Holdridge & Budowski 1956) with both deciduous and evergreen broadleaf tree species in the canopy. One-half of the island supports old-growth forest (>300 yr old); the other half has a successional forest developed on previous agricultural land that was abandoned in the early 1900s. Other features of the climate and vegetation are given in Knight (1975) and Leigh *et al.* (1982).

Basaltic bedrock, derived from an early Miocene age lava flow (Woodring 1958), forms a thick cap at high elevations near the center of the island. Sedimentary bedrock, composed of two different Oligocene age formations (Woodring 1958), occurs at low elevations along the flanks of the island. Thus the basalt is on a younger-aged surface than the sedimentary parent material. The basalt-derived soils are relatively nutrient-poor, whereas the sediment-derived soils are less weathered Alfisols. Three study sites, B1 through B3, were located on the basalt-derived soils; the remaining five sites, S1 through S5, were located on the sediment-derived soils.

Site B1 was located in a stand of *Quararibea asterolepis* in the old-growth portion of the forest. Little decomposing wood was found on the forest floor, suggesting that the site had not been disturbed recently by a treefall gap. Site B2 was within the young forest dominated mainly by *Gustavia superba*. This forest is typical of most of the abandoned agricultural land on the island, and compared with site B1, its forest floor revealed much more decomposing wood. Site B3 was a swamp forest located in a wet depression. The surrounding forest was similar to that at site B2, but the surface soil was much darker, suggesting a high accumulation of organic matter in the surface soil. Another distinctive feature of site B3 was the abundance of the ground bromeliad *Aechmea magdalenae*.

Site S1 was a young forest analogous to site B2. Site S2 was a regeneration phase of an 8- to 10-yr-old treefall gap (G. E. Lang and D. H. Knight, pers. comm.) with much highly decomposed wood on the forest floor. Site S3 was a regeneration phase of a 2- to 3-yr-old treefall gap; wood in various stages of decay occurred on the forest floor. Both gaps were relatively small in size (<100 m<sup>2</sup>). Sites S4 and S5 were chosen to represent smaller-scale disturbances which could affect soil nutrient properties. Site S4 was situated directly beneath a log that was highly decomposed and flattened to the level of the forest floor. Site S5 was near the base of a *Scheelea zomensis* palm. The underlying mineral soil was covered with a buildup of partially decayed fronds, producing a localized area of high organic matter accumulation.

## METHODS

**SOIL SAMPLING AND HANDLING.**—Soil samples were taken during the wet season, July 1984, when the forest floor litter on BCI is minimal (Levings & Windsor 1982). At each study site, triplicate bulk soil samples of 250 g each were taken to a depth of 15 cm within a 10 × 10 m plot. The samples were stored in sealed plastic bags and transported to West Virginia University where all further analyses were done; processing of the samples was carried out within 48 hr of collection. The soils were evaluated for: (1) NH<sub>4</sub><sup>+</sup>-N, NO<sub>3</sub><sup>-</sup>-N, PO<sub>4</sub><sup>3-</sup>-P, and SO<sub>4</sub><sup>2-</sup>-S concentrations in 10-mM CaCl<sub>2</sub> extractions; (2) N, P, and S mineralization potentials; and (3) total N, P, and S concentrations. A CaCl<sub>2</sub> solution extracts mainly soluble ions, but not ions retained in the soil by adsorption onto soil minerals, thus providing an index of the chemical characteristics of the soil solution (Adams 1974). The mineralization potential is a measure of the net amount of nutrient that is mineralized to a plant-available form during a laboratory incubation and is an index of the nutrient-supplying power of a soil (Vitousek *et al.* 1983).

**LABORATORY PROCEDURES.**—Upon returning to the laboratory, one 5-g subsample from each of the 24 soil samples was extracted with 50 ml of 10-mM CaCl<sub>2</sub> by shaking the soil-extracting solution for 2 min, allowing to settle for 24 hr, and then decanting the supernatant. The solutions were retained for determination of initial concentrations of soluble ions. Five additional 5-g subsamples from each of the 24 soil samples were placed individually into 15-ml Styrofoam cups, capped, and incubated in the laboratory to determine the nutrient mineralization potential. The lid had a 5-mm hole punched in it to allow free gas exchange between the container headspace and the laboratory atmosphere. The cups were incubated in the dark under high-humidity conditions at 24°C. Gravimetric water contents of the soils were maintained at field-moist conditions during the course of incubation by periodically adding distilled water to replace the amount of water lost by evaporation. After 2, 4, 8, 16, and 32 days, one replicate incubation from each of the 24 soil samples was retrieved and destructively extracted with 50 ml of 10-mM CaCl<sub>2</sub>. The supernatants were analyzed for NH<sub>4</sub><sup>+</sup> colorimetrically by continuous flow analysis and for NO<sub>3</sub><sup>-</sup>, PO<sub>4</sub><sup>3-</sup>, and SO<sub>4</sub><sup>2-</sup> by ion chromatography.

A final subsample of the field-moist bulk soil was weighed, then dried to a constant mass at 105°C to estimate water content. The remaining portion of each soil was oven-dried at 70°C and ground with a mortar and pestle. Total C was determined on two replicates of each bulk sample using a Coleman C-H-O analyzer. Total N and P were determined on two different replicates by HgO-K<sub>2</sub>SO<sub>4</sub>-H<sub>2</sub>SO<sub>4</sub> digestion (modified Kjeldahl) with subsequent analysis of NH<sub>4</sub><sup>+</sup> and PO<sub>4</sub><sup>3-</sup> in the digest solutions

TABLE 1. Chemical characteristics of the soils from the eight sites. Calcium chloride extractable values are of samples prior to incubation. For each characteristic, mean values with the same letter superscript do not differ significantly.

Site	C (%)	Total (mg/g dry soil)			CaCl <sub>2</sub> -extractable (μg/g dry soil)			
		N	P	S	NO <sub>3</sub> <sup>-</sup> -N	NH <sub>4</sub> <sup>+</sup> -N	PO <sub>4</sub> <sup>3-</sup> -P	SO <sub>4</sub> <sup>2-</sup> -S
B1	4.83 <sup>c</sup>	4.2 <sup>d</sup>	1.12 <sup>a,b</sup>	0.57 <sup>c</sup>	15.7 <sup>a</sup>	0.42 <sup>a</sup>	0.31 <sup>a</sup>	2.17 <sup>b</sup>
B2	4.82 <sup>c</sup>	5.1 <sup>b,c</sup>	1.15 <sup>a</sup>	0.74 <sup>b</sup>	17.3 <sup>a</sup>	0.70 <sup>a</sup>	0.31 <sup>a</sup>	3.79 <sup>a</sup>
B3	3.29 <sup>e</sup>	4.9 <sup>b,c</sup>	1.30 <sup>a</sup>	0.60 <sup>c</sup>	14.4 <sup>a</sup>	0.42 <sup>a</sup>	0.28 <sup>a</sup>	2.01 <sup>b</sup>
S1	2.50 <sup>f</sup>	4.1 <sup>d</sup>	0.72 <sup>c</sup>	0.49 <sup>d</sup>	13.1 <sup>a</sup>	0.42 <sup>a</sup>	0.27 <sup>a</sup>	1.39 <sup>b</sup>
S2	4.94 <sup>c</sup>	4.8 <sup>b,c,d</sup>	0.95 <sup>b</sup>	0.64 <sup>c</sup>	13.2 <sup>a</sup>	0.51 <sup>a</sup>	1.30 <sup>a</sup>	0.79 <sup>b</sup>
S3	4.30 <sup>d</sup>	4.5 <sup>c,d</sup>	0.66 <sup>c</sup>	0.57 <sup>c</sup>	13.4 <sup>a</sup>	4.11 <sup>a</sup>	0.27 <sup>a</sup>	1.60 <sup>b</sup>
S4	6.05 <sup>b</sup>	5.6 <sup>b</sup>	0.72 <sup>c</sup>	0.61 <sup>c</sup>	16.4 <sup>a</sup>	0.98 <sup>a</sup>	1.82 <sup>a</sup>	1.45 <sup>b</sup>
S5	6.84 <sup>a</sup>	7.5 <sup>a</sup>	1.12 <sup>a,b</sup>	0.83 <sup>a</sup>	8.3 <sup>a</sup>	5.70 <sup>a</sup>	0.36 <sup>a</sup>	4.17 <sup>a</sup>

by continuous flow analysis. Total S was determined using a LECO sulfur analyzer.

STATISTICAL ANALYSES.—The concentrations of extractable N, P, and S over time were statistically analyzed using linear regression techniques. First, for soluble inorganic nitrogen (SIN = NH<sub>4</sub><sup>+</sup>-N + NO<sub>3</sub><sup>-</sup>-N), NO<sub>3</sub><sup>-</sup>-N, PO<sub>4</sub><sup>3-</sup>-P, and SO<sub>4</sub><sup>2-</sup>-S concentrations, a test for homogeneity was performed among the eight sites in slopes of regression lines of concentration as a function of time (Sokal & Rohlf 1981). If this test indicated homogeneity of slopes among sites ( $P \geq 0.05$ ), then pairwise comparisons of intercept values among sites were performed using the  $t'$ -test for unplanned comparison of regression parameters (Sokal & Rohlf 1981). The latter test indicated differences among the sites in ion concentrations in the initial extractions prior to incubation. If the test for homogeneity of slopes indicated significant site differences ( $P < 0.05$ ), pairwise comparisons among slopes, then among intercepts, were performed using the  $t'$ -test. For total element concentrations, site differences were evaluated using analysis of variance and the least significant difference test.

## RESULTS

Surface soils from the eight sites varied significantly with regard to total C, N, P, and S concentrations (Table 1). Soil derived from the sedimentary parent material and supporting the young forest (S1) generally had the lowest total C, N, and S concentrations, whereas the soil collected from beneath the *Scheelea* palm (S5) had relatively high concentrations of all 4 elements. Soils from beneath the dead log (S4) and from beneath the *Scheelea* palm (S5), which were collected specifically because in the field they appeared to have a high organic matter content, had the highest total C concentrations. However, the black "organic" soil from the swamp forest (B3) had a low total C concentration. All of the soils derived from the basaltic parent material had higher total P concentrations than the

soils derived from sedimentary parent materials, except for comparable values for the *Scheelea* palm site (S5).

A stepwise discriminant analysis indicated that the eight sites could be separated on the basis of total C, N, and P, but not total S, concentrations in the soil (Fig. 1). The first canonical variable is negatively correlated with total N concentrations and is most effective in separating the 5 sediment-derived soils from each other. The three sites whose soils were derived from the basaltic parent material are clumped along this axis. The second canonical variable is negatively correlated with total P concentration in the soil, and is more effective in separating the basalt-derived from sediment-derived soils. It is important to note that the nutrient concentrations of the soils in the three replicate samples collected within the 10 × 10 m plot at each site were similar to each other, except for one of the replicate samples taken in the regenerated gap site (S2).

During the course of incubation, the concentration of SIN consistently increased over time (Fig. 2), with NO<sub>3</sub><sup>-</sup>-N accounting for about 85 percent of this increase. For both SIN and NO<sub>3</sub><sup>-</sup>-N concentrations, the slopes of change in concentration over time were not homogeneous among the eight sites (Table 2). Further analysis indicated that for both SIN and NO<sub>3</sub><sup>-</sup>-N, the estimated slope for one site, S5, was significantly different from the slopes for the other seven sites, which were statistically similar to each other. The estimated intercept values were statistically similar for all eight sites, indicating that SIN and NO<sub>3</sub><sup>-</sup>-N concentrations in the initial extractions were similar among the sites (Table 1).

Plots of changes in PO<sub>4</sub><sup>3-</sup>-P concentrations over time in soils from all eight sites indicated a gradual decline in PO<sub>4</sub><sup>3-</sup>-P concentration from days 0 to 16, followed by a sharp increase between days 16 and 32 (Fig. 2). Therefore, the data were divided into two time periods prior to statistical analysis (Table 2). From days 0 to 16, both the slopes and intercepts of the regression lines of PO<sub>4</sub><sup>3-</sup>-P over time were statistically similar among the eight sites.

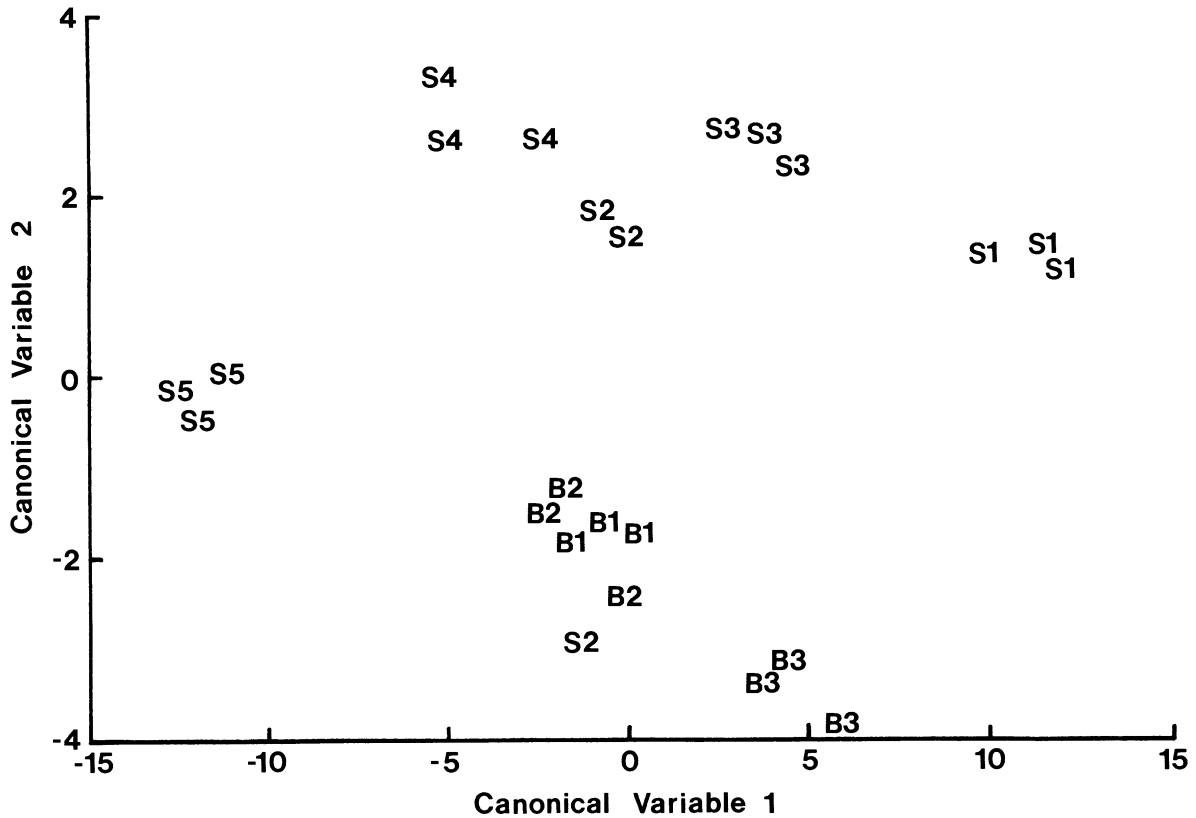


FIGURE 1. Separation of the eight sites by stepwise discriminant analysis. Equations for the canonical variables are:

$$\begin{aligned} \text{Canonical variable 1} &= 28.8 - 0.00096*N - 0.00463*P - 4.135*C \\ \text{Canonical variable 2} &= 6.27 + 0.00027*N - 0.00945*P + 0.312*C \end{aligned}$$

N and P are nitrogen and phosphorus concentrations in  $\mu\text{g/g}$  dry soil, and C is carbon concentration in percent. Canonical variable 1 is significantly negatively correlated with N and C, but not with P (correlation coefficients are  $-0.82$ ,  $-0.97$ , and  $-0.29$ , respectively). Canonical variable 2 is significantly negatively correlated with P, but not with either N or C (correlation coefficients are  $-0.99$ ,  $0.12$ , and  $0.004$ , respectively).

From days 16 to 32, the slopes of the regression lines were not statistically similar; sites B3, S2, and S4 had greater slopes than the values for the five other sites. Since the intercept values among the eight sites were similar for this second time period, the observed site differences in  $\text{PO}_4^{3-}\text{-P}$  concentrations occurred between days 16 and 32, the end of the incubation period.

As indicated by linear regression,  $\text{SO}_4^{2-}\text{-S}$  concentrations in the soils from all eight sites did not change during the course of incubation (Fig. 2), *i.e.*, slope values were not significantly different from zero (Table 2). Although the eight sites exhibited homogeneous slopes, the estimated intercept values were not homogeneous. In all eight sites then,  $\text{SO}_4^{2-}\text{-S}$  concentrations showed neither significant increase nor decrease over time; any differences in concentration manifested in the initial extractions (Table 1) were

maintained throughout the course of the incubation period.

## DISCUSSION

We found little small-scale spatial variation in total C, N, P, and S concentrations among subsamples collected within a  $10 \times 10$  m plot at each site. Mueller-Harvey *et al.* (1985) also found that subsampling within a  $10 \times 10$  m plot in a tropical forest clearing in Nigeria accounted for little of the variation in C, N, P, and S concentrations. The apparent lack of variation in soil properties within each  $10 \times 10$  m plot certainly does not mean that small-scale variation is entirely absent in the eight soils. However, a more powerful analysis of spatial variation, such as geostatistics (Trangmar *et al.* 1985), is required to de-

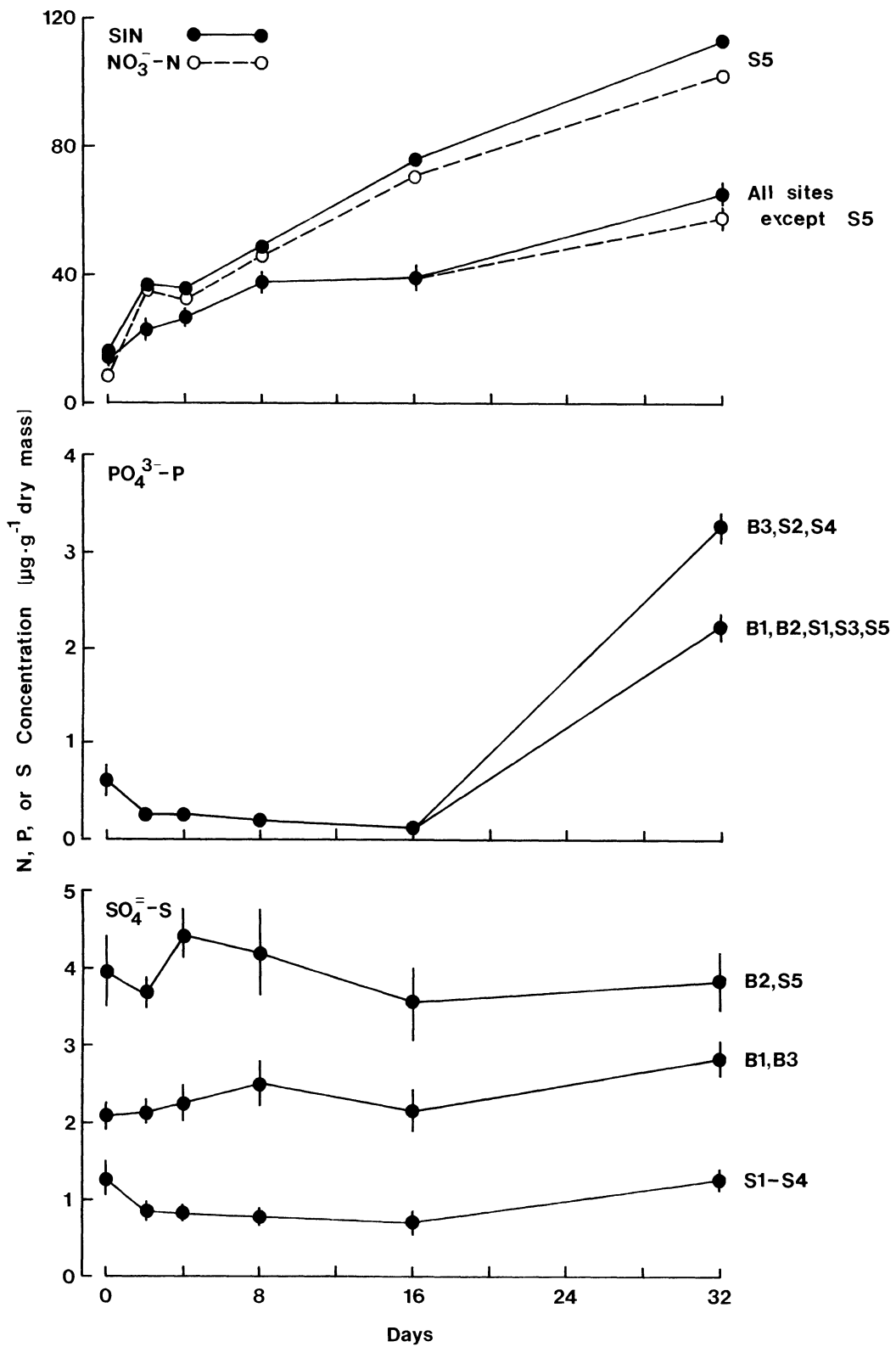


TABLE 2. Results of the statistical analyses performed on the data graphically presented in Figure 2. The P value for the homogeneity of slopes tests represents the probability of obtaining a higher F statistic; thus P values less than 0.05 indicate a lack of homogeneity of slopes among the eight sites. For the linear regression results, the P values also represent the probability of obtaining a greater F statistic, and the  $r^2$  values denote the proportion of the total variance explained by the linear regression model. For each inorganic characteristic, values with the same letter superscript do not differ significantly among the sites ( $P \leq 0.05$ ).

Inorganic characteristic	P value for homogeneity of slopes test	Sites	Linear regression results				
			Slope ( $\mu\text{g/g dry soil/day}$ )	Intercept ( $\mu\text{g/g dry soil}$ )	P value	$r^2$	N
SIN	<0.0001	S5	2.90 <sup>a</sup>	23.6 <sup>a</sup>	<0.0001	0.92	18
		B1-B3; S1-S4	1.40 <sup>b</sup>	20.2 <sup>a</sup>	<0.0001	0.71	126
NO <sub>3</sub> <sup>-</sup>	<0.0001	S5	2.66 <sup>a</sup>	21.7 <sup>a</sup>	<0.0001	0.86	18
		B1-B3; S1-S4	1.23 <sup>b</sup>	20.6 <sup>a</sup>	<0.0001	0.67	126
PO <sub>4</sub> <sup>3-</sup> ; days 0-16	0.08	All	-0.023	0.433	0.003	0.11	144
PO <sub>4</sub> <sup>3-</sup> ; days 16-32	<0.0001	B3, S2, S4	0.196 <sup>a</sup>	0.124 <sup>a</sup>	<0.0001	0.96	54
		B1, B2, S1, S3, S5	0.120 <sup>b</sup>	0.116 <sup>a</sup>	<0.0001	0.94	90
SO <sub>4</sub> <sup>2-</sup>	0.42	B2, S5	-0.0083 <sup>a</sup>	4.04 <sup>a</sup>	0.59	0.01	36
		B1, B3	0.0200 <sup>a</sup>	2.13 <sup>b</sup>	0.02	0.16	36
		S1-S4	0.0050 <sup>a</sup>	0.90 <sup>c</sup>	0.32	0.01	72

termine the scale of variation for each soil property and the soil-forming factor determining spatial change.

On a broad scale, total P concentration among the eight soils was associated to a greater extent with differences in parent material than forest structure. Generally, basaltic rocks have greater P concentrations than sedimentary rocks (Fortescue 1980), and in this case the difference was manifested in the surface soils, regardless of the vegetation growing on the site or the history of disturbance in that vegetation. In contrast, no clear patterns were discernible in the changes in C, N, and S concentrations among the sites. Any spatial patterns for these elements may have been obscured by the limited sample size.

Despite clear differences among the soils examined for total N concentrations, extractable SIN concentrations prior to incubation and N mineralization potentials differed little among the sites. Total N concentration of a soil often is a poor indicator of the SIN-supplying power because of the myriad of forms and ways in which N is stored in a soil. Sollins *et al.* (1984) showed that organic C and N in volcanic Costa Rican soils occurred mostly adsorbed on mineral surfaces or sequestered within organomineral microaggregates. Nitrogen stored in this manner is physically protected within the microaggregates, and therefore relatively inaccessible to microorganisms for mineralization;

in fact, <1.5 percent of the total N in the volcanic tropical soil was available for mineralization. The soils examined in this survey fit the same criteria as those examined by Sollins *et al.* (1984): low C:N ratios; a narrow range of C:N values across a wide range of organic C and total N concentrations (C:N range = 6.1-11.4 on the island); and the inability to mineralize much of the total N (range = 0.71-1.17% on the island).

Net NO<sub>3</sub><sup>-</sup>-N production accounted for virtually all of the mineralized N (Fig. 2). This observation indicates that NH<sub>4</sub><sup>+</sup> was rapidly oxidized to NO<sub>3</sub><sup>-</sup>, and therefore nitrification possibly was NH<sub>4</sub><sup>+</sup> limited. Robertson (1984) found that nitrification was NH<sub>4</sub><sup>+</sup> limited in lowland tropical wet forest soils in Costa Rica, based on NH<sub>4</sub><sup>+</sup> amendment experiments. The absence of a lag in nitrification also suggests that allelochemical inhibitors of nitrification were not present (*e.g.*, Robertson & Vitousek 1981, Christensen & MacAller 1985).

Net N mineralization rates for the forest soils ranged from 1.4 to 2.9  $\mu\text{g/g dry soil/day}$  (Table 2). Despite the fact that we measured only the mineralized N that was soluble, and not extractable as is more commonly measured, these values are within the range of net N mineralization rates for tropical forest soils reported by Robertson (1982) (*i.e.*, 0.1-6.0  $\mu\text{g/g dry soil/day}$ ). Net N

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FIGURE 2. Changes in CaCl<sub>2</sub>-extractable SIN, NO<sub>3</sub><sup>-</sup>-N, and PO<sub>4</sub><sup>3-</sup>-P concentrations in incubated soil samples over time. Since SIN and NO<sub>3</sub><sup>-</sup> accumulation in soil from site S5 was significantly different from soils from the other seven sites, site S5 is plotted separately. Values are means  $\pm$  one standard error, except for site S5 where the means of three observations are plotted without standard errors.

mineralization and net  $\text{NO}_3^-$ -N production rates for forest soils on Barro Colorado Island are similar to those for forest soils in Malaysia (Chandler 1985), whereas the rates for tropical forest soils in Costa Rica (Robertson 1984) and in Jamaica (Tanner 1977) are among the highest values reported.

The *Scheelea* palm site was interesting because it had the highest N mineralization potential of the soils examined. In addition, the area around *Scheelea* palms is characterized by a distinct lack of vegetation. This pattern is in striking contrast to the surrounding forest where rooted plant density is high. The establishment of vegetation beneath *Scheelea* palms may be inhibited chemically or perhaps physically by the buildup of a thick, fairly coarse and tough, layer of overlapping palm fronds. We found several forest sites where a *Scheelea* palm had died within the preceding 18 mo and noticed that the area previously beneath the palm canopy still had a low plant density.

As for N, the P and S mineralization potentials are net values in the sense that they represent the difference between gross mineralization and nutrient reimmobilization by heterotrophic microorganisms during the course of the incubation. N, P, and S mineralization potentials also are net values in a different sense. Since the mineralized form of each element is an ion (*i.e.*,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ ,  $\text{SO}_4^{2-}$ ), ion adsorption may remove a portion of each ion from solution, rendering it insoluble in the  $\text{CaCl}_2$  extraction (Black & Waring 1979, Nor 1981). Thus, estimates of the nutrient mineralization potential of the soil are a balance between gross mineralization and immobilization plus adsorption.

The fact that  $\text{CaCl}_2$ -extractable  $\text{PO}_4^{3-}$ -P accumulated in the soils during the course of incubation is remarkable given the paradigm that aluminum and iron oxides in Alfisols and Oxisols have a high affinity for  $\text{PO}_4^{3-}$ -P and can bind it nearly irreversibly (Borggaard 1983, Iniguez & Val 1984). However, it seems unlikely that all of the  $\text{PO}_4^{3-}$ -P adsorption sites became occupied during the first 16 days of the incubation period so that the increase in soluble ions between days 16 and 32 resulted from the loss of adsorption capacity. Two plausible hypotheses could account for the net increase in soluble  $\text{PO}_4^{3-}$ -P during the later stages of the incubation period. First, the pH of the soils could have changed during the course of the incubations so that in the later stages the mineralized  $\text{PO}_4^{3-}$ -P remained in the soil solution. The second hypothesis involves the action of extracellular phosphatase enzymes that are responsible for mineralization; immobilization during the first part of the incubation period could have lowered the solution  $\text{PO}_4^{3-}$ -P concentrations enough so that extracellular phosphatase activity was no longer suppressed by the endproduct (*cf.* Harrison 1979), leading to subsequent net mineralization.

Without further data on pH and enzyme activity, it is impossible to determine which mechanism is responsible for the observed  $\text{PO}_4^{3-}$ -P accumulation during incubation. Regardless of the mechanism, however, forest soils on Barro Colorado Island appear to have a net positive P-supplying power. Although Vitousek (1984) has suggested that P availability is low enough in most Oxisols to limit forest productivity, Barro Colorado forest had the highest P return in litterfall and the lowest ratio of dry mass of litter to P (*i.e.*, most inefficient P economy) of the forests considered by Vitousek. Taken together, these results suggest a relatively high P availability here compared with other lowland tropical forest soils.

Net S mineralization was not observed in our forest soils. This observation cannot be attributed to the lack of S in the soils, because total S concentrations in these soils are extremely high, especially compared with other tropical soils (Neptune *et al.* 1975, Sanchez 1976). In fact, the mean S concentration we observed (640  $\mu\text{g/g}$  dry soil) is similar to that in temperate grassland soils (Rehm & Caldwell 1968, Bailey 1985). Previous studies have tried to relate S mineralization to the C and N contents of the soil. Barrow (1960) argued that net S mineralization should occur in soils with C:S ratios of less than 200:1 and net S immobilization should occur in soils with C:S ratios of greater than 400:1. Others (*e.g.*, Walker 1957, White 1959) have argued that N and S should be mineralized in the same ratio as they occur in soil organic matter. Bailey (1985) suggested that soils with N:S ratios of less than 8.7:1 should have a high potential to mineralize S. None of these propositions are supported by the results of this study. The C:S ratios of all Barro Colorado soils are 100:1 or less, the N:S ratios are about 8.1:1, and despite a net N mineralization and no net S mineralization.

The lack of net S mineralization could be an artifact of  $\text{CaCl}_2$  extraction. However, Nor (1981) found significant accumulation of  $\text{SO}_4^{2-}$  in 0.1-M  $\text{LiCl}_2$  extractions during incubation of several forest soils from Malaysia. A plausible explanation to account for the lack of net S mineralization in Barro Colorado soils is that much of the mineralized  $\text{SO}_4^{2-}$  is rapidly reimmobilized (in <1 day) into a nonextractable, organic matter fraction (Strickland & Fitzgerald 1984). This mechanism is temperature dependent, microbially mediated, and important in soils with relatively high organic matter contents. A combination of reimmobilization and physical adsorption probably contributes to the low S-supplying capacity of the forest soils on Barro Colorado Island.

Simultaneous measurement of net N, P, and S mineralization in lowland tropical forest soils on Barro Colorado Island indicates that SIN and  $\text{PO}_4^{3-}$ -P, but not  $\text{SO}_4^{2-}$ , accumulate during laboratory incubation studies. The results showed a striking consistency in the patterns of N, P, and S mineralization potentials across the forest,

despite clear differences in the total element contents of the soils and in parent materials, vegetation, and history of the disturbance to the vegetation.

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## LITERATURE CITED

- ABER, J. D., J. M. MELILLO, AND C. A. FEDERER. 1982. Predicting the effects of rotation length, harvest intensity, and fertilization on fiber yield from northern hardwood forests in New England. *For. Sci.* 28: 31-45.
- ADAMS, F. 1974. Soil solution. *In* E. W. Carson (Ed.). *The plant root and its environment*, pp. 441-481. University Press of Virginia, Charlottesville.
- BAILEY, L. D. 1985. The sulfur status of eastern Canadian prairie soils: the relationship of sulfur, nitrogen, and organic carbon. *Can. J. Soil Sci.* 65: 179-186.
- BARROW, N. J. 1960. Stimulated decomposition of soil organic matter during the decomposition of added organic materials. *Aust. J. Agric. Res.* 11: 331-338.
- BLACK, A. S., AND S. A. WARING. 1979. Adsorption of nitrate, chloride and sulphate by some highly weathered soils from south-east Queensland. *Aust. J. Soil Res.* 17: 271-282.
- BORGGARD, O. K. 1983. The influence of iron oxides on phosphate adsorption by soil. *J. Soil Sci.* 34: 333-341.
- BROKAW, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66: 682-687.
- CHANDLER, G. 1985. Mineralization and nitrification in three Malaysian forest soils. *Soil Biol. Biochem.* 17: 347-353.
- CHRISTENSEN, N. L., AND T. MACALLER. 1985. Soil mineral nitrogen transformations during succession in the piedmont of North Carolina. *Soil Biol. Biochem.* 17: 675-681.
- FORTESCUE, J. A. C. 1980. *Environmental geochemistry*. Springer-Verlag, New York.
- HARRISON, A. F. 1979. Variation in four phosphorus properties in woodland soils. *Soil Biol. Biochem.* 11: 393-403.
- HOLDRIDGE, L. R., AND G. BUDOWSKI. 1956. Report on an ecological survey of the Republic of Panama. *Caribb. For.* 17: 92-110.
- INIGUEZ, J., AND R. M. VAL. 1984. Evaluation of phosphorus adsorption by an allophanic soil. *Geoderma* 33: 119-134.
- JENNY, H. 1980. *The soil resource: origin and behavior*. Springer-Verlag, New York.
- KNIGHT, D. H. 1975. A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. *Ecol. Monogr.* 45: 259-284.
- LAMB, D. 1980. Soil nitrogen mineralization in a secondary rain forest succession. *Oecologia* 47: 257-263.
- LANG, G. E., AND D. H. KNIGHT. 1983. Tree growth, mortality, recruitment, and canopy gap formation during a 10-year period in a tropical moist forest. *Ecology* 64: 1075-1080.
- LEIGH, E. G., JR., A. S. RAND, AND D. M. WINDSOR (Eds.). 1982. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C.
- LEVINGS, S. C., AND D. M. WINDSOR. 1982. Seasonal and annual variation in litter arthropod populations. *In* E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest*, pp. 355-387. Smithsonian Institution Press, Washington, D.C.
- MCGILL, W. B., AND C. V. COLE. 1981. Comparative aspects of cycling of organic C, N, S, and P through soil organic matter. *Geoderma* 26: 267-286.
- MUELLER-HARVEY, I., A. S. R. JUO, AND A. WILD. 1985. Soil organic C, N, S, and P after forest clearance in Nigeria: mineralization rates and spatial variability. *J. Soil Sci.* 36: 585-591.
- NEPTUNE, A. M. L., M. A. TABATABAI, AND J. J. HANWAY. 1975. Sulfur fractions and carbon-nitrogen-phosphorus-sulfur relationships in some Brazilian and Iowa soils. *Soil Sci. Soc. Am. Proc.* 39: 51-55.
- NOR, Y. M. 1981. Sulfur mineralization and adsorption in soils. *Plant Soil* 60: 451-459.
- REHM, G. W., AND A. C. CALDWELL. 1968. Sulfur supplying capacity of soils and the relationship to soil type. *Soil Sci.* 105: 355-361.
- ROBERTSON, G. P. 1982. Nitrification in forest ecosystems. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 296: 445-457.
- . 1984. Nitrification and nitrogen mineralization in a lowland rain forest succession in Costa Rica, Central America. *Oecologia* 61: 99-104.
- , AND P. M. VITOUSEK. 1981. Nitrification in primary and secondary succession. *Ecology* 62: 376-386.
- SANCHEZ, P. A. 1976. *Properties and management of soils in the tropics*. Wiley, New York.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry*, 2nd edition. W. H. Freeman, San Francisco.
- SOLLINS, P., G. SPYCHER, AND C. A. GLASSMAN. 1984. Net nitrogen mineralization from light- and heavy-fraction forest soil organic matter. *Soil Biol. Biochem.* 16: 34-37.
- SPYCHER, G., P. SOLLINS, AND S. L. ROSE. 1983. Carbon and nitrogen in the light fraction of a forest soil: vertical distribution and seasonal patterns. *Soil Sci.* 135: 79-87.
- STRICKLAND, T. C., AND J. W. FITZGERALD. 1984. Formation and mineralization of organic sulfur in forest soils. *Biogeochemistry* 1: 79-95.
- TANNER, E. V. J. 1977. Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *J. Ecol.* 65: 883-918.



- TRANGMAR, B. B., R. S. YOST, AND G. UEHARA. 1985. Application of geostatistics to spatial studies of soil properties. *Adv. Agron.* 38: 45-94.
- VITOUSEK, P. M. 1984. Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65: 285-298.
- , K. VAN CLEVE, N. BALAKRISHNAN, AND D. MUELLER-DOMBOIS. 1983. Soil development and nitrogen turnover in montane rain forest soils on Hawaii. *Biotropica* 15: 268-274.
- WALKER, T. W. 1957. The sulfur cycle in grassland soils. *J. Br. Grassl. Soc.* 12: 10-18.
- WERNER, P. 1984. Changes in soil properties during tropical wet forest succession in Costa Rica. *Biotropica* 16: 43-50.
- WHITE, J. G. 1959. Mineralization of nitrogen and sulfur in sulfur deficient soils. *N. Z. J. Agric. Res.* 2: 255-258.
- WHITE, P. S., AND S. T. A. PICKETT. 1985. Natural disturbances and patch dynamics: an introduction. *In* S. T. A. Pickett and P. S. White (Eds.). *The ecology of natural disturbances and patch dynamics*, pp. 3-13. Academic Press, Orlando, Florida.
- WOODRING, W. P. 1958. Geology of Barro Colorado Island, Canal Zone. *Smithsonian Miscellaneous Collection* 135, Number 3.

## International Symposium on the Biological Diversity of México

The Instituto de Biología of the Universidad Nacional Autónoma de México announces an International Symposium on the Biological Diversity of Mexico, to be held in Mexico from 3rd to 7th of October, 1988. Diversity in México is the fourth highest on the globe after Brazil, Indonesia and Colombia with many generic and species endemisms. The purpose of this meeting is to bring scholars from various disciplines to: evaluate the state of knowledge of biological diversity of Mexico (biological richness, origin, maintenance and interactions), to identify priorities and perspectives for the study of such phenomena, and to provide a forum for exchange of ideas, experiences and future collaboration. Topics in the symposium will include the geological and paleoclimatic history of Mexico as well as recent interpretations of floral and faunal diversity of the country. The invited presentations will be published in book form in English and Spanish. Contributed posters and round table discussions will appear separately in UNAM publications. Those interested in further details are invited to write to Biological Diversity, Apartado Postal 70-233, Universidad Nacional Autónoma de México, Delegación Coyoacán, México D. F. 04510, México. T. P. Ramamoorthy and Robert Bye are corresponding secretaries for the Organizing Committee.