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Nutrient Dynamics of Soil Derived from Different Parent Material on Barro Colorado Island, Panama[1]

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ABSTRACT

I compared the concentrations of N, P, and S in both litter and mineral soil (0–15 cm depth) from three old-growth, tropical moist forests on Barro Colorado Island (BCI), Panama. Each site was on a different substrate (*i.e.,* parent material), but otherwise had similar climate, vegetation, and topography. There were no site differences in concentrations of N and S for either litter or soil. Concentrations of litter P and soil-extractable P were greater for the andesite (igneous rock) site than for two sites on different sedimentary rocks; however, concentrations of several other litter and soil P fractions did not differ among sites. Patterns in soil P fractions suggested advanced soil development to the point that parent material has little control of P dynamics. Litter samples from each site, leached in the laboratory, released similar amounts of N, P, and S to the soil, indicating no differences in rates of turnover in the litter and in fluxes from litter into the mineral soil among sites. I expected more site differences in soil nutrient dynamics given vastly different parent materials and soil types (*i.e.,* Oxisol vs. Alfisol) and very shallow soil on BCI that brings the parent material close to the plant root zone. Erosion and soil mixing may explain the uniformity in soil nutrient dynamics across the sites.

Key words: biogeochemistry; litter nutrients; nitrogen; phosphorus fractions; Panama; soil nutrients; sulfur; tropical moist forest.

In landscapes in which several types of rocks neighbor each other, different types of soil can develop from different parent materials (Jenny 1941). The effect of parent material is clearest when the other soil-forming factors (*i.e.*, climate, biota, topography, and age) are very similar across the landscape. In such cases, parent materials become the ultimate cause of variation in soil types, which in turn can control soil processes and soil nutrient dynamics (Jenny 1980, Binkley *et al.* 1995). Parent material control of soil processes, however, may be less intense in the humid tropics, for several reasons. For example, soils tend to be old and very deep. Plant ecology tends to be shaped more by light availability, disturbance regime, or by some complex interaction with animal species. Also, landscapes tend to have much topographic variation. Indeed, numerous studies have demonstrated relationships between soil processes and topography (Silver *et al.* 1994, Tiessen *et al.* 1994, Osher & Buol 1998), age (Crews *et al.* 1995), and climate (Austin & Vitousek 1998). Relatively few studies, however, have assessed parent material control of soil processes alone, without covariation in the other soil-forming factors (*cf.* Hamdan & Burnham 1996).

Barro Colorado Island (BCI), Republic of Panama, is well suited for studying potential parent material control of soil processes; at least three different Oligocene-aged parent materials come together, each with weathered soil supporting old-growth forest and exposed to very similar climate. Indeed, an earlier study by Yavitt and Wieder (1988) found some differences in concentrations of N, P, and S in soil derived from an igneous andesite flow versus a volcanic facies of a sedimentary rock formation on BCI. The andesite site, however, had an old-growth forest, whereas the sedimentary site had a much younger successional forest, and the differences in forest age could have compromised site differences in soil nutrient concentrations (*cf.* Ewel *et al.* 1991).

This study extended the analysis in several ways. First, I added a second, different sedimentary site, and I considered only sites with old-growth forest. I compared concentrations of N, P, and S in decomposing litter and in the top of the mineral soil because these three elements cycle rapidly through plant and soil microbial biomass (McGill & Cole 1981). I expected to find greater concentrations of nutrients in litter and soil of the more fertile sedimentary sites with less weathered Alfisol soils than in that of the andesite site with a more highly weathered Oxisol soil (Anonymous 1970). I also measured rates of nutrient release from litter and soil during incubations, which tend to show positive relationships with concentrations of soil

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and foliar nutrients, nutrient return to the soil in litter, and rates of litter decomposition (Vitousek 1982).

MATERIALS AND METHODS

STUDY SITE.—Barro Colorado Island (9°9′N, 79°51′W) is a 15-km^2 former hilltop located in Gatun Lake, a freshwater reservoir formed by the construction of the Panama Canal in 1914. The vegetation on BCI is classified as a Tropical Moist Forest in the Holdridge System (Holdridge & Budowski 1956). I sampled from sites with old-growth forest (>450-years old); for details of the species present see Condit *et al.* (1995). Mean annual temperature is 26°C, and mean monthly temperature varies by just 1°C throughout the year. Annual rainfall averages 2600 mm with a dry season that usually begins in December and ends in April. Leaf litterfall peaks early in the dry season during December and January, remains high through April, and falls by 50 percent to low values through the wet season from May to November (Wright & Cornejo 1990). As a result, some plant species are leafless for part of the year.

Woodring (1958), and more recently, Johnsson and Stallard (1989) described the geology of BCI. The island is capped by an andesite flow, rather than basalt, as reported incorrectly in Woodring (1958) and repeated in Yavitt and Wieder (1988). Andesite is an igneous rock, which is the most abundant type of rock formed in volcanic island arcs. It is resistant and nonvesicular, with phenocrysts primarily of plagioclase set in a glassy matrix. This parent material on BCI has weathered into a clay-rich, Yellow-Brown Oxisol <50 cm thick.

The flanks of BCI have nearly flat-lying sedimentary rocks. One is the Caimito Formation, which has a marine facies and a non-marine volcanic facies. The marine facies is foraminiferal limestone with abundant volcanic debris. The volcanic facies is a volcanic glass-rich siltstone and sandstone. A sharp fault dissects BCI and separates the Caimito Formation from the Bohio Formation, which is a basaltic conglomerate (volcanic mudflow deposit) and clay-rich sandstone composed of basaltic material in a sandy matrix. Both the sedimentary parent materials have weathered into silty clay, Yellow-Brown Alfisol, mostly <30 cm thick.

Soil collection occurred in December, just after the end of the rainy period, along a 200-m-long transect line in each site. The transect on the andesite site extended from marker 12 to 14 along the AV Armour Trail. The transect on the limestone site (Caimito Formation, marine facies) was on Poacher's Peninsula. The transect on the conglomerate (Bohio Formation) extended from marker 13 to 15 on the Drayton Trail (map in Dietrich *et al.* 1982). Twelve sampling sites were established on the andesite site at *ca* 15-m intervals. Six sampling sites were established on each of the sedimentary sites, also at *ca* 15-m intervals.

At each sampling site, I established two small areas of 0.12 m^2 and collected all decomposing litter on the soil surface from within each sampling area. Both litter samples per sampling site were combined and placed in an individual bag. I then used a trowel to collect the mineral soil (0–15 cm deep) from each area. Both soil samples per site were combined, placed in a bag, and sieved by hand to remove rocks and large roots. I collected a 5-cm (diam) × 30-cm (depth) soil core per sampling site to estimate soil bulk density. All litter and soil samples were sent within 24 h of collection to a laboratory at West Virginia University (Morgantown, Virginia) for processing, which began immediately (*i.e.,* 3 d after collection). Each sample was separated into several subsamples to determine soil moisture, pH, concentrations of nutrients in litter, soil, and microbial biomass, and rates of nutrient release from litter during incubations.

LABORATORY ANALYSES.—Particle size distribution in the <2-mm fraction of the mineral soil was determined by the hydrometer method (Day 1965) after removing organic matter with H_2O_2. The pH of soil and litter was measured by electrode in a water matrix using a soil/water ratio of 1:4 and a litter/water ratio of 1:10, which settled for 30 min before the pH measurement. This value was an estimate of the pH of the sample in the field. I also measured pH on a separate subsample using the same ratios, but in a matrix of 1 mol/liter KCl. This value was an estimate of exchangeable acidity (Hendershot *et al.* 1993).

Concentrations of N and P in samples of litter and soil were determined on a digest using concentrated H_2SO_4, K_2SO_4, and HgO (Bremner & Mulvaney 1982). Concentrations of S in litter and in soil were determined using a LECO sulfur analyzer. I also estimated concentrations of extractable N, P, and S using standard soil-test assays. Inorganic N was extracted overnight (16 h) from 5 g of soil or litter using 20 ml of 2 mol/liter KCl. Inorganic P was extracted from 1 g of soil or litter in 7 ml of an acid fluoride solution for 3 min (Olsen & Sommers 1982). Inorganic S was extract-

ed overnight from 5 g of soil or litter using 50 ml of 16 mmol/liter NaH_2PO_4.

I further characterized P in soil and in litter using the sequential P fractionation described by Tiessen and Moir (1993), with some modifications. The method extracted P with differing degrees of availability held in a variety of inorganic and organic forms. A 0.5-g sample of soil or litter first was extracted by shaking for 16 h in a 50-ml centrifuge tube with 30 ml of distilled water and mesh bag containing 1 g of Dowex 1-X8 anion exchange resin. The resin bag was removed, and P adsorbed to the resin was extracted with 20 ml of 0.5 mol/liter HCl for 1 h; P in solution was analyzed colorimetrically. The soil suspension then was centrifuged at 7000 revolutions/min for 10 min and the water decanted through a Whatman 42 filter. Soil or litter on the filter was returned carefully to the centrifuge tube; the soil or litter was shaken for 16 h with 30 ml of 0.5 mol/liter $NaHCO_3$ (pH = 8.5). Following centrifugation, the liquid was decanted through a filter and analyzed for total and inorganic P. Soil or litter on the filter was returned to the centrifuge tube, and soil or litter was shaken for 16 h with 30 ml of 0.5 mol/liter NaOH. Following centrifugation, the liquid was decanted through a filter and analyzed for total and inorganic P. I did not perform the acid extractable fractions (Tiessen & Moir 1993). Total P was determined following digestion with H_2SO_4, K_2SO_4, and HgO; hence, organic P was the difference between total P and inorganic P in the extract.

For presentation, I grouped some of the different fractions into the following: (1) resin extractable inorganic P (Pi), which is plant available P; (2) inorganic P extracted with bicarbonate and NaOH is labile P, which consisted mostly of P associated with Fe and Al; (3) the sum of organic P (Po) extracted with bicarbonate and NaOH is alkali-extractable organic Po. The composition of this fractionation is still debated among soil scientists; and (4) the difference between total P and P in the resin, bicarbonate, and NaOH fractions is "resistant P." This fraction included Po protected by cellulose and P associated with soil Ca.

I also estimated the concentrations of N, P, and S in microbial biomass using a modification of the chloroform ($CHCl_3$) fumigation-extraction technique (Brookes *et al.* 1982, Strick & Nakas 1984, Brookes *et al.* 1985). A 50-g subsample of field-moist soil or litter was placed in a beaker, and the beakers were arranged in a glass desiccator lined with moist paper towels. A beaker of ethanol-free chloroform was placed among the samples, and the desiccator was evacuated and stored for 24 h at room temperature. The chloroform then was removed and separate subsamples of the soil or litter were extracted for N using 0.5 mol/liter K_2SO_4, P using 0.5 mol/liter $NaHCO_3$ at pH of 8.5, and S using 16 mmol/liter NaH_2PO_4. A second set of soil or litter samples were not fumigated with chloroform, but extracted, and the amount of element released from the fumigated soil minus the amount in extracted from the unfumigated soil was assumed to have come from lysed microbial cells.

Soil scientists often use conversion coefficients to change chloroform-labile nutrient concentrations to microbial biomass nutrient pools (*cf.* Brookes, Powlson *et al.* 1982, Brookes, Landman *et al.* 1985); however, conversion coefficients can vary from one soil type to another, and if misapplied can lead to spurious conclusions. For this reason, I report the data as chloroform-labile nutrient concentrations, without applying any assumed coefficient.

Nutrient release during incubation.—I used a variation of the techniques given by Stanford and Smith (1972) and Nadelhoffer (1990) to estimate rates of nutrient release from soil or litter during incubation in the laboratory. I placed a 20-g litter sample or a 40-g soil sample in a polypropylene Büchner funnel (70 mm diam) with a glass fiber filter and glass wool prefilters. The samples were incubated for 28 d at 25°C; at 3-d intervals, each sample was leached with four successive 24-ml aliquots of distilled, deionized water during a 1-h period. Then I applied 0.06 MPa to the funnels until no more leachate could be removed. Leachate volume was measured, and subsamples of the leachate were analyzed for NH_4, NO_3, PO_4, and SO_4 by ion chromatography. The cumulative amount of elements leached during the 28-d period provided an estimate of nutrient mineralization. After incubation, I measured concentrations of N, P, and S in the incubated litter and soil samples, using the methods described previously.

Statistical analyses.—I used one-way ANOVAs to analyze differences in litter, soil, and ecosystem nutrient dynamics among sites. *Post hoc* mean comparisons were done with the Tukey-Kramer honestly significant difference (HSD) test.

RESULTS

Soil derived from the andesite parent material had lower bulk density and a slightly higher percentage

TABLE 1. *Soil characteristics (0- to 15-cm depth) interval of three forest ecosystems developed on different parent materials (Barro Colorado Island, Panama). Values are* $\bar{x}$ *with SD in parentheses for 12 samples from the andesite site and 6 samples from the other two sites. Differences among parent materials for all soil characteristics were not significant (P > 0.05 ANOVA).*

	Parent material		
	Andesite	Limestone	Conglomerate
Bulk density (g/cm^3)	0.85 (0.07)	0.94 (0.08)	1.03 (0.09)
Soil texture (%)			
Sand	20 (3)	25 (4)	25 (4)
Silt	38 (3)	35 (4)	36 (3)
Clay	42 (5)	40 (5)	39 (4)
Carbon (mg/ha)	70 (17)	68 (10)	63 (10)
Nitrogen (mg/ha)	5.5 (1.4)	4.9 (0.9)	5.4 (1.0)
Phosphorus (mg/ha)	0.9 (0.2)	0.9 (0.1)	0.9 (0.1)
Sulfur (mg/ha)	0.8 (0.1)	0.7 (0.1)	0.8 (0.1)

of clay-sized particles than soil derived from the two sedimentary parent materials (Table 1); however, total contents of C, N, P, and S in the top 15 cm of the mineral soil did not differ significantly among the three sites. Further, the pH of both litter and soil did not vary significantly among the three sites (Table 2). This included pH in water, which measures free acidity, as well as pH in KCl, which included acidity associated with exchange sites.

LITTER AND SOIL NUTRIENT CONCENTRATIONS.—Concentrations of total N, extractable NH_4, extractable NO_3, and chloroform-released N in both litter and soil did not differ significantly as a function of different parent material (Table 2). Chloroform-re-

TABLE 2. *Litter and soil (0- to 15-cm depth interval) characteristics of three forest ecosystems developed on different parent materials (Barro Colorado Island, Panama). Values are* $\bar{x}$ *with SD in parentheses for 12 samples from the andesite site and 6 samples from the other two sites. Same lowercase letters across parent material (done separately for litter and soil) indicate statistically similar means (one-way ANOVA).*

	Litter			Soil		
	Andesite	Limest.	Conglom.	Andesite	Limest.	Conglom.
pH (in H_2O)	6.49 a (0.03)	6.69 a (0.06)	6.53 a (0.05)	5.97 a (0.06)	5.97 a (0.07)	6.23 a (0.03)
pH (in KCl)	5.90 a (0.03)	5.68 a (0.02)	5.36 a (0.03)	4.88 a (0.03)	4.65 a (0.04)	4.65 a (0.04)
N (% dry mass)	1.45 a (0.35)	1.18 a (0.29)	1.23 a (0.46)	0.43 a (0.14)	0.34 a (0.06)	0.39 a (0.07)
NH_4 (mg N/kg)	196 a (85)	101 b (65)	179 a (96)	8.6 a (1.5)	11.8 a (6.1)	10.9 a (3.0)
NO_3 (mg N/kg)	8.0 a (5.1)	0.9 b (2.0)	3.0 b (4.3)	5.0 a (3.5)	2.6 b (2.9)	3.0 b (0.6)
$CHCl_3$-labile N (mg N/kg)	94 a (63)	109 a (110)	62 a (32)	110 a (43)	96 a (57)	117 a (84)
P (% dry mass)	0.075 a (0.010)	0.063 a, b (0.012)	0.056 b (0.010)	0.072 a (0.018)	0.067 a, b (0.010)	0.061 b (0.004)
PO_4 (mg P/kg)	33.4 a (19.1)	39.5 a (19.3)	49.7 a (47.7)	4.2 a (0.81)	3.1 b (0.35)	3.8 a, b (0.40)
$CHCl_3$-labile P	328 a (211)	268 a (131)	403 a (139)	8.0 a (5.0)	8.9 a (5.2)	7.3 a (3.0)
S (% dry mass)	0.12 b (0.05)	0.28 a (0.11)	0.17 b (0.04)	0.061 b (0.011)	0.083 a (0.021)	0.057 b (0.012)
SO_4 (mg S/kg)	19.6 a (17.7)	9.7 b (7.0)	27.6 a (37.4)	47.6 a (42.0)	20.6 b (18.5)	10.6 b (4.8)
$CHCl_3$-labile S (mg S/kg)	9.1 a (13.4)	6.2 a (4.1)	16.0 a (21.5)	3.3 b (1.7)	8.1 a (9.5)	4.4 b (1.8)

leased N was a much larger pool of N in soil than extractable inorganic N, although chloroform-released N and NH_4 had comparable concentrations in litter.

Concentrations of P in some of the fractions in both litter and soil did differ significantly among sites (Table 2). For example, the andesite site had significantly greater concentrations of litter P and soil-extractable P, although concentrations of chloroform-released P in both litter and soil did not differ among the three sites. The distribution of litter P concentrations among fractions was: resistant P > labile Pi > alkali-extractable Po > available Pi; however, the conglomerate site (Bohio Formation) did have equal litter P concentrations in resistant alkali-extractable Po and labile fractions (Fig. 1). Resistant P in litter probably represented organic P protected by cellulose in leaf tissue. Resistant P accounted for nearly 80 percent of soil P in the two sedimentary sites, whereas the andesite site had significantly more alkali-extractable organic P. The resistant fraction in soil probably represented P bound to Ca.

Soil on BCI has very large concentrations of total S, especially in the limestone-derived soil (Table 2). Concentrations of extractable SO_4 and chloroform-released S in both litter and soil, however, did not differ among sites.

ELEMENT RELEASE FROM LITTER AND SOIL DURING INCUBATIONS.—The cumulative amount of inorganic N released from both litter and soil did not differ significantly among sites (Table 3). Therefore, across the three sites, inorganic N in litter leachate was *ca* 50 percent NH_4–N and 50 percent NO_3–N. In contrast, net nitrification predominated in the soil, and NO_3–N was 95 percent of the inorganic N in leachate from the soil. The litter also exhibited a very large increase in the concentration of chloroform-released N during the incubation (Table 4). Indeed, the increase was much larger than the associated decrease in the concentrations of extractable NH_4 and extractable NO_3, indicating a substantial rate of gross N mineralization and microbial N immobilization. The concentration of chloroform-released N in soil, however, decreased during the incubation (Table 4), and indeed, the decrease could account for nearly the entire inorganic N in leachate (Table 3), except in the andesite site.

A substantial amount of P was released from the three litter types during the incubation, but I essentially found no net release of P from soil (Table 3). Concentrations of litter P and soil P did not change during the incubation, but there was significant redistribution of P among fractions. For example, the concentration of alkali-extractable Po increased in both litter and soil; the concentrations of labile Pi in litter decreased; and concentrations of resistant P in soil decreased (Fig. 1). Furthermore, litter exhibited a very large decrease in chloroform-released P concentrations (Table 4), suggesting that microbial biomass supplied the P in leachate; however, soil microbial biomass immobilized P during the incubation.

The cumulative amount of S released from litter also was very large (Table 3) and much greater

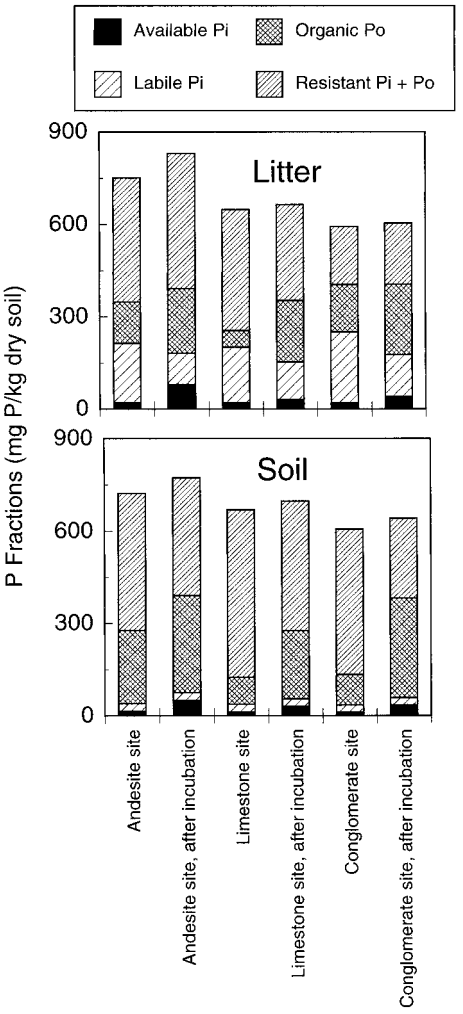

FIGURE 1. Cumulative mean concentrations of P fractions in litter and soil (0–15 cm depth) from three forest ecosystems developed on different parent materials.

TABLE 3. *Cumulative element release (top) and turnover in the total element pool (bottom) during 4-wk incubations of litter and soil (0–15 cm depth) from three forest ecosystems developed on different parent material (Barro Colorado Island Panama). Cumulative* N *release values are* NH_4–N + NO_3–N. *Values are* $\bar{x}$ *with SD in parentheses for 12 samples from the andesite site and 6 samples from the other two sites. Same lowercase letters across parent material (done separately for litter and soil) indicate statistically similar means (one-way ANOVA).*

	Litter			Soil		
	Andesite	Limest.	Conglom.	Andesite	Limest.	Conglom.
Cumulative release						
N (mg/kg)	217 a	170 a, b	153 b	41.5 a	36.4 a	37.5 a
	(157)	(83)	(75)	(12.9)	(16.6)	(4.4)
PO_4 (mg P/kg)	49 a	42 a	51 a	0.33 a	0.34 a	0.34 a
	(40)	(27)	(25)	(0.20)	(0.14)	(0.18)
SO_4 (mg S/kg)	441 a	425 a	358 a	10.6 a	10.3 a	8.3 a
	(114)	(86)	(160)	(4.8)	(4.6)	(2.6)
Turnover						
N (%)	1.5	1.2	1.2	1.0	1.1	1.0
PO_4 (%)	6.5	6.6	9.1	0.05	0.05	0.06
SO_4 (%)	36.1	15.2	21.0	1.7	1.2	1.4

than net change in concentrations of extractable S and chloroform-released S during the incubation (Table 4). The amount of S released from soil during the incubation (Table 3), however, can be explained by a net decrease in the concentration of extractable S or chloroform-released S during the incubation (Table 4).

DISCUSSION

Barro Colorado Island has clay-rich soil with low bulk density. Soil derived from the andesite parent material, having the lowest bulk density, contained slightly higher amounts of total C and total N than the other two soils. This negative relationship between bulk density and soil organic matter content has been shown in other studies of clay-rich tropical soil (*cf.* Raghubanshi 1992). The relationship can occur because soil with finer particles (*i.e.*, clays and silts) and high pore volume, which gives the soil lower bulk density, protects the soil organic matter.

Concentrations of N, P, and S in both litter and soil exhibited only few and relatively subtle differences among the three sites, despite the differences in parent materials. I expected more pronounced differences for two reasons. First, soil type differed greatly: the andesite-derived soil was an Oxisol, whereas both sedimentary sites developed into Alfisols; Oxisols are more developed, iron-rich, poor in base cations, and have almost no primary minerals remaining; Alfisols in the tropics are less developed, richer in base cations, and still can have primary minerals remaining. I expected soil N, P, and S concentrations to vary consistently with the differences in soil development (*cf.* Jenny 1980, Crews *et al.* 1995), but this was not true on BCI.

Second, the soil on BCI is relatively shallow; hence, the parent material is close to the soil surface. The Oxisol on BCI reaches a maximum thickness of 2 m deep in some places, but is commonly *ca* 50 cm thick (Dietrich *et al.* 1982). Well developed Oxisols in humid tropics can be several meters deep (Fox 1982); the Alfisols in the two sedimentary sites were mostly <50 cm deep (Johnsson & Stallard 1989). One reason for the shallow soil is that BCI has very rapid rates of soil erosion. Indeed, in the sedimentary sites, sediment transport rates can exceed mineral weathering rates, which brings relatively fresh parent material and primary minerals close to the soil surface (Johnsson & Stallard 1989).

Because of the high rates of erosion, soil mixing could have occurred among the sites and, in particular, may have added material from the andesite site that caps BCI to the lower-lying sedimentary sites. Several studies have found evidence of significant soil mixing on sloping landscapes. Most of the work has been done in semiarid landscapes (*cf.* Schimel *et al.* 1985), although the process has been studied in forested landscapes (Zak *et al.* 1991) and tropical forests (Raghubanshi 1992, Silver *et al.* 1994). The general belief is that finer soil particles move downslope, and in turn increase the content of organic matter and N and P in lower slope positions and in depressions relative to the slopes and ridgetops (Schimel *et al.* 1985). On BCI, however, we found a higher percentage of finer soil particles

TABLE 4. *Net change in litter and soil (0–15 cm depth) characteristics after 4-wk incubations of samples from three forest ecosystems developed on different parent materials (Barro Colorado Island, Panama). Negative values indicate that initial values (before incubation) were greater than final values (after incubation). Values are* $\bar{x}$ *with SD in parentheses for 12 samples from the andesite site and 6 samples from the other two sites. Same lowercase letters across parent material (done separately for litter and soil) indicate statistically similar means (one-way ANOVA).*

	Litter			Soil		
	Andesite	Limest.	Conglom.	Andesite	Limest.	Conglom.
NH_4 (mg N/kg)	−50 b	112 a	−34 b	5.2 a	4.6 a	1.5 b
	(106)	(116)	(88)	(1.8)	(5.8)	(4.0)
NO_3 (mg N/kg)	−7.0 b	0.1 a	−2.0 b	−5.0 b	−2.6 a	−3.0 a, b
	(3.1)	(1.0)	(4.2)	(3.4)	(2.5)	(3.6)
$CHCl_3$-labile N	122 a	130 a	180 a	−17 a	−25 a	−43 a
(mg N/kg)	(140)	(114)	(72)	(47)	(56)	(87)
PO_4 (mg P/kg)	3.1 a	−10.5 b	−16.8 b	−0.7 b	0.1 a	0.1 a
	(20.2)	(17.6)	(48.4)	(1.3)	(0.5)	(0.4)
$CHCl_3$-labile P	−116a	−133 a	−188 a	11.6 a	9.0 a, b	6.7 b
	(180)	(84)	(101)	(8.9)	(10.3)	(4.0)
SO_4 (mg S/kg)	−10.6 a	−5.1 a	−17.8 a	−1.0 a	1.2 a	−1.9 a
	(17.0)	(9.6)	(38.1)	(16.2)	(16.2)	(4.8)
$CHCl_3$-labile S	−1.6 a	1.7 a	−9.2 a	0.9 a	−2.6a	−0.4 a
(mg S/kg)	(13.1)	(2.0)	(22.0)	(2.5)	(4.6)	(2.8)

at the highest elevation in the andesite parent material, suggesting little soil mixing among our study sites. Nevertheless, the process of soil mixing in tropical forests deserves more attention.

It is reasonable that I did not find site differences in soil N and in rates of soil N transformations because igneous rock and most sedimentary rocks have extremely small amounts of N (Stevenson 1962). Therefore, weathering of different parent material did not add different amounts of N to the soil. Rather, the accumulation of N during soil development came from N deposited from the atmosphere and biological N-fixation. Parent material, however, can affect concentrations of soil N in other ways. For example, biological N-fixation requires trace metals such as Mo and Fe, and their availability in soil can vary with different mineral content. The predominant N-fixing plant species on BCI, (*Dipteryx panamensis*), however, has a wide-ranging distribution (Croat 1978), suggesting no difference in the availability of trace metals for N-fixation among the different parent materials.

The andesite site had greater concentrations of litter P and soil-extractable P. One reason is that clay minerals in the andesite on BCI have about two times more P (*i.e.,* 0.25 percent by weight P_2O_5; Stallard 1995 cited in Leigh 1996) than minerals in the Caimito Formation (0.13 percent by weight P_2O_5; Johnsson & Stallard 1989). Soil P from all three sites, however, was mainly in the resistant Pi+Po and alkali-extractable organic P fractions. This distribution among fractions is typical of highly weathered soil in which all of the primary minerals from the parent material have been altered to the extent that labile Pi from primary minerals no longer exists (Walker & Syers 1976). Therefore, I conclude that parent material exerts little control on the availability of P, at least in the top part of the mineral soil across BCI.

The cumulative amount of elements leached from litter or soil during incubation in the laboratory is a useful measurement for several reasons. For example, the sum of leached nutrients is an index of plant nutrient availability. Since there was no uptake of nutrients by plants during the incubation, the assumption was that nutrients in leachate were released by microorganisms during their decomposition of organic matter, in amounts in excess of their metabolic needs. Further, the ratio of elements leached during the incubation divided by the total content of the element in the litter or soil is an index of element turnover. For example, higher ratios indicate that the element is in a relatively labile form in the litter or soil.

The turnover of N was essentially the same in all of the incubations using either litter or soil, with 1.0 to 1.5 percent of the total N leached as NH_4 and NO_3 during the incubation. For P, however, the turnover in litter ranged from 6.5 percent on the andesite and limestone sites to 9.1 percent on the conglomerate site, in contrast to the P turnover in soil of only 0.055 percent. This finding suggests there is: (1) much more labile P in litter than in soil; and (2) much more labile P than labile N in litter. Phosphorus in organic matter is mostly in an ester bond (McGill & Cole 1981), unlike N bonded to C, and thus different mechanisms carry out N turnover and P turnover. Therefore, litter-decomposing microorganisms could produce more enzymes to mineralize P than microorganisms in the soil; however, it is also important to note that not all of the P released into the soil during the incubation was leached. Rather, PO_4 released can be sorbed very rapidly to Fe, Al, and Ca in soil minerals before leaching, or before uptake by plants can occur (Walbridge *et al.* 1991). These sorption sites were much less abundant in litter.

Nevertheless, litter on BCI released a remarkable amount of P. For example, Nadelhoffer *et al.* (1991) reported P release of only 0.1 to 4.0 mg P/kg of organic matter from organic surface soil in Arctic ecosystems during 13-wk incubations. Their interpretation of the finding was that microorganisms in the organic soil immobilized much of the P. In contrast, I did not find evidence for the immobilization of P in litter. Rather, microbial biomass in the litter layer seemed to turn over quickly and supply the P. Further, the ratio of N to P leached during incubations of the litter was a very narrow value of 4:1, compared to typical ratios of >10:1 for soil organic matter (Stevenson & Elliott 1989).

Barro Colorado Island also has very S-rich soil. It is not clear whether the S comes from the weathering of primary minerals, with a high content of pyrite, or from atmospheric deposition. In soils on uplifted marine terraces in coastal Oregon, Bockheim and Langley-Turnbaugh (1997) found that most of the plant-available S was atmospheric deposition from the oceanic air. Nevertheless, the turnover of S in litter on BCI was truly astounding, with 15 to 36 percent of the total being released. Further, this came from net S mineralization rather than from microbial biomass or exchange sites. Results from an earlier study by Yavitt and Wieder (1988) suggested no net soil S mineralization on BCI, and we had speculated that the soil might have S-limitation of plant growth. The conclusion,

however, came from studies that used a relatively weak CaCl extraction to remove mineralized S. In this study, I used a stronger PO_4 extraction to leach the soil. Moreover, the ratio of N to S leached during incubations of litter and soil was typical of soil with a large S supply (White 1959, Bailey 1985).

Overall, the results of this study suggest almost no variation in concentrations of N, P, and S among litter and soil across three very different parent materials on BCI. This does not mean that the sites support the exact same rates of nutrient cycling. Rather, it is important to consider the results as a function of scale; differences in parent material are not the ultimate control of variation in soil nutrient cycling on BCI.

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