

The Effect of Phosphorus Availability on Decomposition Dynamics in a Seasonal Lowland Amazonian Forest

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ABSTRACT

Once the weathering of parent material ceases to supply significant inputs of phosphorus (P), vegetation depends largely on the decomposition of litter and soil organic matter and the associated mineralization of organic P forms to provide an adequate supply of this essential nutrient. At the same time, the decomposition of litter is often characterized by the immobilization of nutrients, suggesting that nutrient availability is a limiting factor for this process. Immobilization temporally decouples nutrient mineralization from decomposition and may play an important role in nutrient retention in low-nutrient ecosystems. In this study, we used a common substrate to study the effects of native soil P availability as well as artificially elevated P availability on litter decomposition rates in a lowland Amazonian rain forest on highly weathered soils. Although both available and total soil P pools varied almost three fold across treatments, there was no significant difference in decomposition rates among treatments.

Decomposition was rapid in all treatments, with approximately 50% of the mass lost over the 11-month study period. Carbon (C) and nitrogen (N) remaining and C:N ratios were the most effective predictors of amount of mass remaining at each time point in all treatments. Fertilized treatments showed significant amounts of P immobilization ($P < 0.001$). By the final collection point, the remaining litter contained a quantity equivalent to two-thirds of the initial P and N, even though only half of the original mass remained. In these soils, immobilization of nutrients in the microbial biomass, late in the decomposition process, effectively prevents the loss of essential nutrients through leaching or occlusion in the mineral soil.

Key words: litter; soil nutrients; fertilization; tropical forest; phosphorus; decomposition; Amazonian rain forest.

INTRODUCTION

Over two-thirds of the Neotropics, and one-third of the humid tropics worldwide, is characterized by

highly weathered soils, such that low phosphorus (P) levels are considered the principal limitation to net primary productivity (Walker and Syers 1976; Vitousek and Sanford 1986). Once the weathering of parent material ceases to provide a significant input of nutrients, the recycling of nutrients through biological processes becomes an essential mechanism to maintain productivity levels (Tiessen

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and others 1994). Although the importance of decomposition as a key step in the biological cycling of nutrients in nutrient-limited systems is widely recognized, the role of soil nutrient availability as a control on decomposition has been debated for several decades (Swift and others 1979; Fog 1988; Enriquez and others 1993).

Decomposition is primarily driven by microbial activity and has thus far been best predicted by precipitation, temperature (Berg and others 1993; Aerts 1997; Schuur 2001), and litter quality (Enriquez and others 1993; Aerts 1997; Hobbie and Vitousek 2000). The carbon–nitrogen (C:N) ratio of initial tissue is one of the best and most commonly measured indices of litter quality (Heal and others 1997). Carbon-to-nutrient ratios in litter are generally much larger than the same ratios in the microbial biomass. As a result, the immobilization of nutrients is common during the initial stages of decomposition. This suggests that nutrient availability, both in the litter itself and the surrounding environment, may be a limiting factor (Swift and others 1979; Staaf and Berg 1981). However, the effect of soil nutrient levels on decomposition is not straightforward. Some fertilization studies have shown positive effects on the rate of litter decomposition (Gil and Lavender 1983; Prescott and others 1992; Hobbie and Vitousek 2000), whereas others have found a negative (O'Connell 1994; Prescott 1995) or no effect (Pastor and others 1987). Most studies have focused on the effect of N fertilization in temperate systems. In highly weathered Hawaiian soils, P fertilization was found to increase both initial rates of P immobilization and overall decomposition rates (Ostertag and Hobbie 1999; Hobbie and Vitousek 2000). Fertilization with P was also found to increase microbial respiration rates in highly weathered soils in Costa Rica (Cleveland and others 2002). Soil nutrient availability and litter nutrient content tend to be strongly and positively correlated, making it difficult to separate the effects of soil nutrient availability from those of litter chemistry.

In this study, we tested the hypothesis that litter decomposition in highly weathered soils is limited by soil P availability. To avoid the confounding issue of soil nutrient effects on litter quality, we used single-species litter from a native species produced in a nearby plantation as a common substrate. We looked at the effect of differences in soil P availability by decomposing litter in two distinct but adjacent soils with significantly different soil P pools and by comparing rates of decomposition in control and P-fertilized plots on each soil type.

MATERIALS AND METHODS

Study Site

The study was conducted in the Tapajós National Forest, which is located 80 km south of Santarém, Pará, Brazil (2°64'S and 54°59'W). The forest is a mature closed-canopy evergreen tropical lowland forest (Parrotta and others 1995). The 60,000-ha forest was established in 1974 and is currently managed by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA), with the joint aims of conservation and management for sustainable timber extraction (Parrotta and others 1995). The region has a mean annual temperature of 25°C and receives approximately 2,000 mm of rain per year, with a dry season lasting from August through November (Parrotta and others 1995; Hernandez-Filho and others 1993).

This site is particularly well suited for testing the effects of soil P availability on decomposition due to the variation in soil texture and available P pools found there. The soils at the site can be broadly classified into sands (Ultisols) and clays (Oxisols), with intermediate sandy and clay loams occurring at the contacts (Silver and others 2000). In the Brazilian system, the clays are classified as dystrophic yellow argisols and dystrophic yellow latosols, respectively (R. Cosme de Oliveira, Jr. personal communication). Both soils are characterized by low pH and low nutrient cation availability. The clay soils have higher levels of soil C, N, and P in the surface layer (0–10-cm depth); the sand soils have greater-fine and coarse-root biomass (Silver and others 2000).

Experimental Design

Six experimental blocks (100 × 12 m) were established, three in clays and three in sands, in April 1999, and each was divided into five plots (20 × 12 m). The first, third, and fifth plots were used as treatment plots; the second and fourth plots acted as buffer zones to prevent potential contamination. One treatment plot in each block was randomly selected to receive 67 kg P ha⁻¹ y⁻¹ as super triple phosphate granules (3 Ca(H₂PO₄)₂·H₂O), which approximately doubled the total soil P pool to a depth of 10 cm. One-third of the fertilizer was applied in May 1999, and applications were repeated every 4 months thereafter.

To assess decomposition, leaves of marupá (*Simaruba amara* (Aubl.)) were collected from an 18-year-old plantation managed by Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) in Belterra, Pará, approximately 40 km north of the study site.

Marupá was chosen because it is a native species found in the Tapajós National Forest. The plantations were established on abandoned pastures with highly weathered soils similar to the clay soils at the study site. Litterfall was collected weekly in 1-m² traps 0.5 m above the ground. The marupá leaves were separated from the rest of the collection, dried at 50°C for 72 h, and pooled.

We constructed 20 × 20 cm litterbags from fiberglass window screening (openings approximately 1 mm²) and filled each bag with 5 g of air-dried litter ($n = 720$). The bags were strung together with nylon fishing line, into groups of five, with 20 cm between each bag. Four strings of litterbags (one string for each harvest) were placed in each replicate location three replicates per plot). All litterbags were installed in the field on 2, March 2000. Litterbags were collected 3, 6, 9, and 11 months after installation. All collections were done at least 1 month after the most recent fertilization.

Three soil samples (to 10-cm depth) were collected from each treatment plot in April 2000 to determine initial soil nutrient content. In addition, three forest floor samples were taken from each treatment plot using a 15 × 15 cm template (inside dimensions). Forest floor soil includes all of the dead plant material plus all recently humified, but still identifiable, organic material above the soil surface.

Laboratory Methods

Litterbags were air-dried in a drying room for 2–5 days immediately after collection. The litter was then removed from the bag; cleaned of visible roots, frass, and fungi; oven-dried at 50°C for 48 h; and weighed. Subsamples of all tissue (litter, initial decomposition samples that were never placed in the field, and forest floor) were dried to 65°C to develop dry-weight conversions. Ground 0.5-g subsamples were then ashed in a muffle furnace at 550°C for 4 h to determine inorganic content. All data are reported on an ash-free, 65°C dry-weight basis.

Total tissue C, N, and P was measured for all forest floor and initial litter samples and a subset of the decomposition samples collected from the field (three bags from each string of five collected, $n = 432$). Ground samples were analyzed for total C and N on a CE Instruments NC2500 Soil Elemental Analyzer (CE Instruments, Lakewood, NJ, USA) at the University of California, Berkeley, using acetanilide (10.36% N and 71.09% C) as a reference standard. Samples were analyzed in duplicate. Rejection criterion was set at more than 10% variance between duplicates. Total P was determined on a Thermo Jarrell Ash axial IRIS ICP-AES (Thermo Elemental, Franklin, MA, USA) at the University of California,

Berkeley, after a H₂O₂ predigest and modified Kjeldhal digest of ground plant tissue (J. Tilley personal communication). NIST Apple leaves were used as a reference standard with a 98% (± 2) recovery.

Soil samples were passed through a 2-mm sieve before analyses. A subsample was finely ground on a rolling mill and analyzed for total C and N on a CE Instruments NC2500 Soil Analyzer using an atropine reference standard (4.84% N and 70.56% C) and the same quality control methods as for the litter tissue. Total soil P pools were determined using the modified Kjeldhal digestion as described for litter. Digest solutions were analyzed for P on a DCP-AES at the International Institute for Tropical Forestry–USDA Forest Service Analytical Laboratory in Río Piedras, Puerto Rico. NIST San Joaquin standard soil was used as a reference standard, and recovery of P in the standard averaged 78% (± 1.3). The low rate of recovery can be mainly attributed to a difference in methods, because the NIST values are determined with an HF digest whereas total P in this study was determined using an H₂SO₄ digest. Available P was determined for each soil sample using the initial steps of the modified Hedley sequential extraction method (Tiessen and Moir 1993). Air-dried 0.5-g soil samples were extracted first with an anion exchange resin-impregnated membrane in water, then with 0.5 M NaHCO₃, and finally with 0.1 M NaOH (Tiessen and Moir 1993). The NaHCO₃ and NaOH solutions were then digested with H₂SO₄ and ammonium persulfate, and total P concentrations were determined on a Lachat QuickChem 8000 Automated Ion Analyzer (Lachat Instruments Division, Zellweger Analytics, Milwaukee, WI, USA).

Much work has been done to relate the P pools as defined by chemical extractants to biological uptake (Cross and Schlesinger 1995). The resin- and NaHCO₃-extractable fractions are generally agreed to be readily available to the biota, and the P that is only released with sulfuric acid digestion is generally considered recalcitrant and unavailable on time scales of less than centuries (Cross and Schlesinger 1995). The intermediary extractions are thought to be in equilibrium with the more available pools and to replenish those that are depleted by uptake. Some of the organic components of the intermediate pools may also contribute to biotic uptake directly through mineralization. We chose to include the NaOH-extractable fraction in our definition of available P at this site as because previous work had shown that this fraction was the most sensitive to both fertilization and seasonal patterns in soil moisture, suggesting that it is very biologically active (M. E. McGroddy and others unpublished).

Table 1. Initial Carbon and Nutrient Pools for Soils and Forest Floor

	Soil					Forest floor			
	Available P (kg ha ⁻¹)	Total P (kg ha ⁻¹)	Total C (Mg ha ⁻¹)	C:P	C:N	Total P (kg ha ⁻¹)	Total C (Mg ha ⁻¹)	C:P	C:N
Clay	23.4 (2.5) ^A	113.2 ^A (4.8)	25 ^A (3)	221 (30)	12 (0.3)	2.1 (0.2)	2.5 (0.2)	1190 (218)	24 (1)
Clay PO ₄	44.3 (3.6) ^B	142.4 ^B (8.6)	27 ^A (2)	190 (23)	12 (0.1)	5.7 (2.3)	2.7 (0.7)	474 (154)	21 (1)
Sand	14.9 (2.5) ^C	54.7 ^C (8.7)	13 ^B (1)	238 (19)	13 (0.2)	3.0 (0.4)	2.6 (0.3)	867 (112)	20 (1)
Sand PO ₄	20.6 (1.9) ^{AC}	59.5 ^C (7.3)	15 ^B (1)	252 (12)	15 (0.0)	6.2 (1.7)	3.3 (0.6)	532 (126)	26 (2)

P, phosphorus; C, carbon; N, nitrogen

Samples were collected from clay and sand soils fertilized with super-triple phosphate (Clay PO₄; S and PO₄) and controls from both soils.

Values are given as mean (± SE).

Statistically significant differences (at a 95% confidence level) between values within a column are indicated with letters.

Statistical Methods

Decomposition rates (*k*) for each treatment were calculated by regression analyses. Both linear and exponential models were tested, and the most appropriate equations based on *r*² values were determined (Wieder and Lang 1982). Decomposition rates were calculated for each treatment based on mass remaining at each time point (*n* = 3 for each treatment at each time interval). Differences in mass remaining between treatments were compared using three-way analysis of variance (ANOVA) with time, soil texture, and fertilization treatment as factors. Significance was determined using Tukey-Kramer multiple comparison tests.

Nutrient content at each time point was calculated by multiplying the nutrient concentration by the mass remaining. Nutrient content was then reported as a proportion of the initial leaf content, with values greater than 1 reflecting an accumulation of nutrients through microbial immobilization or deposition. For both N and P, we calculated a mineralization rate based on the change in litter nutrient pool size over time. For the fertilized plots, we could not calculate a mineralization rate because we saw a pattern of P accumulation rather than loss at the 3- and 11-month time points, suggesting immobilization of P rather than mineralization. Differences in nutrient mineralization rates and differences in final nutrient pools in the litter were compared using a two-way ANOVA with soil texture and fertilization treatment as the main factors.

Stepwise multiple linear regressions were performed to determine if C-to-nutrient ratios and/or percent of the original C, N, and P remaining could be used to predict the percent of mass remaining. The relationship between the fraction of initial mass remaining and proportion of initial nutrients re-

maining at each time point were calculated using Pearson's correlation analysis. In addition, the relationships between the proportions of initial C, N, and P remaining at each time point were also calculated using Pearson's correlation analysis. Data were natural log-transformed where necessary to meet the assumptions of the models. All data were analyzed using SYSTAT (v. 8.0). Significance was set at *P* < 0.05 unless otherwise stated.

RESULTS

Initial Conditions

At the beginning of the experiment, there was significantly more available P, total P, and total C in the clay controls as compared to the sand controls (*P* = 0.016 for available P; *P* ≤ 0.001 for both total P and total C), but there were no significant differences in C:P ratios (Table 1). Fertilized clay plots had larger available and total P pools than did the controls (*P* < 0.001). Forest floor showed no significant differences between treatments in C or P pools or in C:P or C:N ratios (Table 1).

Decomposition of Leaf Tissue

Decomposition of leaf tissue was rapid in both sands and clays; approximately 50% of the total mass was lost after 11 months in all treatments (Figure 1). Exponential models were found to best describe decomposition rates (Table 2), predicting a rapid initial mass loss, followed by slower rates of loss after approximately 9 months. Mass remaining was significantly lower at each collection up to the 9-month time point (*P* ≤ 0.0001), but there was no significant decrease in mass between 9 and 11 months. There were no significant treatment effects on mass remaining at each time point.

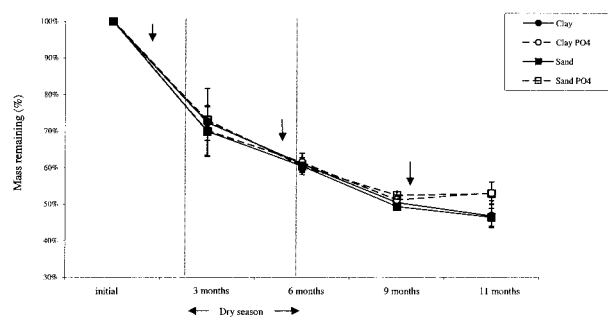


Figure 1. Percent of mass remaining for leaf litter in control and fertilized plot, for both sand and clay soils, in the Tapajós National Forest, Brazil. Bars indicate ± 1 SE. For each treatment, $n = 3$ at each collection point (each plot value is the mean of 15 replicate bags). Arrows indicate fertilization events; dashed lines indicate the approximate onset and end of the dry season. Slopes of the regressions and significant differences between treatments are given in Table 2.

Leaf Tissue Phosphorus, Carbon, and Nitrogen Content

The patterns and rates of P release and accumulation during decomposition were dramatically different from those of mass loss (Figure 2A). At the end of the 11-month study, litter in the control plots in both sands and clays had only 30% less P than was contained in the original tissue. In the fertilized sand plots, the litter P pool at the final point was equal to that of the initial litter, even though P levels had decreased earlier in the study. The litter in the fertilized clay plots followed a trend similar to that observed in the sand fertilized treatment, with final litter P pools 30% higher than initial pools. In the fertilized plots, P content showed a strong seasonal pattern; there was a significant decrease between 3 and 6 months (peak of the dry season) and a return to original levels by 9 months (onset of the wet season). In the control plots, patterns were less markedly seasonal. After the first 3 months, there was no further significant decrease in P content in tissue in either sand or clay controls. The P mineralization rates were significantly slower than the decomposition rates in the controls ($P \leq 0.001$) (Table 3). In the control plots, the proportion of P remaining was correlated to the fraction of original N remaining ($r = 0.64$, $P \leq 0.0001$), the fraction of original C remaining ($r = 0.50$, $P = 0.05$), and less strongly to the fraction of original mass remaining ($r = 0.33$, $P \leq 0.001$).

There were no significant differences in remaining C and N content among treatments at any time point. The changes in C content in the leaf tissue

over time followed the patterns seen in total mass (data not shown). Rates for net N mineralization from the litter were significantly slower than the decomposition rates calculated ($P \leq 0.001$). Changes in leaf N content showed stronger seasonal effects than were seen in the biomass data (Figure 2B). There were no significant changes in N content between 3 and 6 months (the onset to peak of the dry season), whereas significant decreases were observed between 6 and 9 months (the onset of the wet season).

Carbon and N remaining and the C:N ratios of litter were strongly correlated with mass remaining for all treatments ($r = 0.93$, 0.94 , and 0.82 for C, N, and C:N, respectively; $P \leq 0.001$ for all) (Table 3). The correlations of N remaining to mass remaining were weaker in the P-fertilized plots than in the controls for both soils. Carbon and N remaining were also significantly and positively correlated with each other ($r = 0.87$, $P \leq 0.001$). Carbon:N ratios decreased by 30% after 11 months ($P \leq 0.0001$), but there were no significant differences between the control and fertilized treatments. After 11 months, litter C:P ratios decreased to less than half the original value in the fertilized plots and slightly more than half the original value in the control plots in both sands and clays ($P \leq 0.0001$ and $P = 0.06$ for sands and clays, respectively) (Table 4). The litter C:P ratios were significantly lower in the fertilized plots than in the control treatments at the 3- and 11-month collections; the litter C:P ratios in the dry season collections (September 2000 and December 2000) showed no significant treatment effect. Litter C:P ratios were positively correlated with mass remaining in both control ($r = 0.56$, $P \leq 0.05$) and fertilized plots ($r = 0.77$, $P < 0.001$). Stepwise regression analysis showed that the C and N remaining and C:N ratios were the best predictors of mass remaining for all four treatments ($P < 0.001$ for all).

DISCUSSION

Decomposition rates were not affected by differences in soil pools in this study. The lack of an effect of P availability comes as a surprise, given the low levels of available P at these sites and the relatively high C:P ratio of the initial leaf tissue (C:P = 1,434). By contrast, one survey of litterfall from tropical forests found an average C:P ratio of $1,124.3 \pm 109.3$ (calculating C as 50% of dry mass, [Vitousek 1984]), and another study (Aerts 1997) reported an average ratio of 902 ± 506 for tropical regions.

Patterns of P content in the leaf tissue during the decomposition process varied with both fertilization

Table 2. Decomposition Rates (k) for Marupá Litter in the Tapajós National Forest

Site/Fertilizer (combination)	Linear equation		Exponential Equation	
	k	(r ²)	k	(r ²)
Clay	-0.54 (0.04)	0.89	-0.77 (0.08)	0.93
Clay PO ₄	-0.49 (0.00)	0.86	-0.70 (0.01)	0.90
Sand	-0.54 (0.01)	0.86	-0.76 (0.03)	0.91
Sand PO ₄	-0.50 (0.02)	0.86	-0.69 (0.04)	0.89

Rates represent the slopes of the relationships between mass remaining and time (in y^{-1}), and are based on both linear and exponential models of decay. Regression statistics (r^2) are given for each model. All models were significant at $P \leq 0.001$.

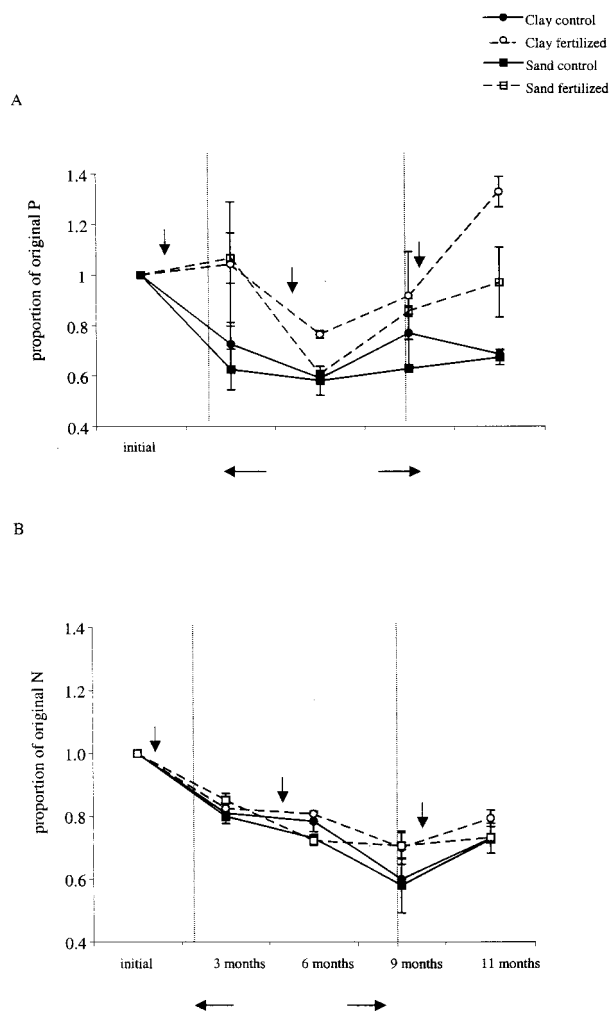


Figure 2. Remaining nutrient stocks as a fraction of the original nutrient stock in decomposing leaf tissue in the Tapajós National Forest, Brazil. Values greater than 1 represent immobilization; values less than 1 represent net mineralization. Letters represent significant differences among means at 11 months using Tukey's HSD multiple comparison test ($P \leq 0.05$). (A) Results for phosphorus (P). (B) Results for nitrogen (N).

and time and were significantly different from the patterns of mass loss. After approximately 1 year, the leaf tissue P pool was 100% to 130% of the initial litter P pool in the fertilized plots. The litter P pools in the controls represented over 65% of the initial pools, despite the 50% reduction in total mass in all treatments. The immobilization of nutrients during decomposition is an important process and has been reported in a variety of systems (Swift and others 1979; Staaf and Berg 1981; Ostersberg and Hobbie 1999; Hobbie and Vitousek 2000). White and Ayoub (1983) found that initial tissue C:P ratios were positively correlated with immobilization rates. The immobilization of limiting nutrients during decomposition is of particular interest in ecosystems where biological cycling is the primary source of nutrients for plant uptake. With immobilization, decomposition represents a net uptake of nutrients rather than release until the microbial biomass turns over. Rates of turnover of the microbial biomass can vary from 0.29 y to more than 1 y (Paul and Clark 1996) and are not well characterized in the field. White and Ayoub (1983) found no increase in plant-available P pools associated with the decomposition of even relatively P-rich litter in the short term.

In ecosystems on highly weathered soils, immobilization in the litter layer functions as a nutrient-retention mechanism (Went and Stark 1968; Stark and Jordan 1978). Organic P is less likely to be occluded by geochemical reactions with the soil surface. Although plants have not been shown to directly take up organic P, the organic P pool may play an important role in plant nutrition (McGill and Cole 1981; Stevenson and Cole 1999). Plants and microbes both produce extracellular phosphatases that readily mineralize most common organic P compounds into labile inorganic phosphates (McGill and Cole 1981). Immobilization may also be an important retention mechanism for N. Nitrate

Table 3. Correlations between Remaining Mass and Remaining Nutrient Pools

Variables	All Treatments	Control	Fertilized
Mass remaining × C remaining	0.93 ^b	0.95 ^b	0.92 ^b
Mass remaining × N remaining	0.94 ^b	0.94 ^b	0.91 ^b
Mass remaining × P remaining	0.33 ^b	0.60 ^b	s 0.48 ^b /c 0.28 ^a
Mass remaining × C:N	0.82 ^b	0.83 ^b	0.82 ^b
Mass remaining × C:P	0.61 ^b	0.56 ^a	0.77 ^b
C remaining × N remaining	0.87 ^b	0.91 ^b	0.81 ^b
C remaining × P remaining	0.22 ^a	0.50 ^a	s 0.12 ^b /c 0.22 ^a
P remaining × N remaining	0.48 ^b	0.64 ^b	s 0.57 ^b /c 0.51 ^b

C, carbon; N, nitrogen; P, phosphorus; S, sand; C, clay

Litter was decomposed in fertilized and control plots in both sand and clay soils.

Where there were no significant differences between soil types, treatments were lumped for analyses.

Remaining P did differ significantly between fertilized clay and fertilized sand plots at two of the five time points; for these analyses, correlations are reported separately, with analyses for clay plots indicated with a "c" and those for sands with an "s".

Correlations were tested for significance using Bonferroni probabilities.

^aSignificant at 95% confidence level.

^bSignificant at 99.9% confidence level.

Table 4. Litter C:P Ratios during Decomposition in the Tapajós National Forest

	Initial	3 mo	6 mo	9 mo	11 mo
Clay	1434:1 (268)	1193:1 ^{ab} (117)	937:1 (28)	782:1 (123)	847:1 ^a (29)
Clay PO ₄	1434:1 ^A (268)	976:1 ^{Ba} (260)	735:1 ^B (55)	711:1 ^B (153)	510:1 ^{Bb} (17)
Sand	1434:1 ^{AB} (268)	1355:1 ^{Ab} (131)	919:1 ^{AB} (142)	913:1 ^{AB} (46)	810:1 ^{Ba} (26)
Sand PO ₄	1434:1 ^A (268)	886:1 ^{ABab} (83)	964:1 ^{AB} (12)	712:1 ^B (18)	687:1 ^{Bab} (116)

C, carbon; P, phosphorus

Litter was decomposed in four different treatments—fertilized clay soils (Clay PO₄), fertilized sand soils (Sand PO₄), and controls for each soil type.

Values are reported as mean (± SE).

Differences significant at the 95% confidence level between treatments at each time point are indicated with lower-case letters; differences within each treatment over time are indicated with upper-case letters.

is readily leached from the biologically active zone of the soil, whereas organic N is much less mobile.

Most studies report significant immobilization only in the initial stages of decomposition (although see Ostertag and Hobbie 1999), but here we found greater immobilization of nutrients later in the decomposition process. Immobilization of P showed strong seasonal patterns. Decreased moisture in the litter layer and surface soils can lead to reduced plant and microbial nutrient uptake in the dry season (Kieft and others 1987; Lodge and others 1994; Paul and Clark 1996). The increased retention of P compared to N, especially at the onset of the second wet season, probably reflects the relative scarcity of P at this site, as well as differences in their solubilities.

In this study, rates of decomposition started to decline, with only a 30% net loss of both initial P and N litter pools, and despite further mass loss, N and P pools in the litter remained relatively constant for the last 6 months of the study. For the final 3 months of this study, the C content of the leaf

tissue also remained constant at approximately 50% of the original stock. The apparent decrease in decomposition and mineralization rates may be a result of the fact that the mass measured was a mixture of both remaining leaf tissue and colonizing microbial biomass, including mycorrhizal hyphae (Sylvia and others 1998). As the leaf tissue mass decreased, the microbial biomass increased, along with the microbial nutrient pools. Conversion from leaf mass to microbial biomass increases N and P content because C:N and C:P ratios of microbes are lower than those of plant tissue (Paul and Clark 1996).

In conclusion, differences in P availability did not affect decomposition rates, but P additions increased rates of P immobilization dramatically. In contrast to other studies that have shown the highest rates of immobilization in the initial stages of decomposition, we found higher rates of P immobilization later in decomposition. The later stages of decomposition in this study coincided with the onset of the rainy season, and seasonal increases in

microbial biomass may have driven this pattern. Our results suggest that rates of decomposition and net nutrient mineralization may be decoupled in ecosystems with low nutrient availability, providing an important nutrient-retention mechanism.

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