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Retention of phosphorus in highly weathered soils under a lowland Amazonian forest ecosystem

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[1] The low available phosphorus (P) pools typical of highly weathered tropical forest soils are thought to result from a combination of export of phosphorus via erosion and leaching as well as chemical reactions resulting in physically and chemically protected P compounds. Despite the low apparent P availability, these soils support some of the highest terrestrial net primary productivity globally. We followed different P fractions after P additions to two soil types, sandy loam and sandy clay, over 1 year in a lowland Amazonian forest. Of all the soil P fractions measured, only the $NaHCO_3$ and NaOH extractable fractions showed a significant increase following P additions, and this occurred only in sandy clays (+ 56.9 ± 15.1 kg ha^{-1} and + 2.8 ± 1.5 kg ha^{-1}, respectively). Our results indicate that intermediate rather than recalcitrant pools are the dominant fate of added P over an annual timescale even in fine-textured soils. Fine root and forest floor P pools increased more in the sandy loams following P additions suggesting a larger biotic P sink in these soils. Leaching of inorganic P from the surface soils was an unexpected and significant fate of added P in both soil types (9 ± 3% in the sandy loams, 2 ± 1% in the sandy clays). Significantly more of the added P was retained in the sandy clay soils than in the sandy loams (69 ± 20% versus 33 ± 7%) over the 1-year period.

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1. Introduction

[2] Humid lowland tropical forests are among the most species rich and productive terrestrial ecosystems [*Gentry*, 1992; *Melillo et al.*, 1993]. Net primary productivity (NPP) in these ecosystems is widely assumed to be limited by soil phosphorus (P) availability due to low primary mineral P in highly weathered soils, and the propensity of these soils to strongly bind P in forms unavailable to biota [*Sanchez*, 1976; *Cross and Schlesinger*, 1995]. Weathering depletes primary mineral P and, coupled with erosion and leaching, decreases the total P pool over the course of soil development [*Walker and Syers*, 1976; *Crews et al.*, 1995]. A significant fraction of the remaining soil P is bound to iron (Fe) and aluminum (Al) oxides and hydroxides and considered unavailable for biological uptake [*Walker and Syers*, 1976]. In addition, P can be adsorbed on soil surfaces and organic matter in reversible reactions, though some bonds are much more readily and rapidly released than others [*Sposito*, 1989]. Once absorbed, P can become move into more recalcitrant pools through metal or organic matter coating or occlusion in the crystalline structure of the minerals [*Barrow*, 1983; *Sposito*, 1989].

[3] In most deep, tropical soils, rock weathering no longer provides fresh inputs of P, and atmospheric deposition rates are usually small (<0.5 kg $ha^{-1}a^{-1}$) compared to annual uptake, particularly in the interior continental environment [*Walker and Syers*, 1976; *Williams et al.*, 1997]. Theory suggests that under these conditions, the vegetation depends mainly on the efficient cycling of existing P stocks to meet its requirements [*Dalal*, 1977; *Cole and Heil*, 1981; *McGill and Cole*, 1981; *Stewart and Tiessen*, 1987; *Tarafdar and Claassen*, 1988]. Efficient cycling of P in tropical forest soils, combined with high sorption capacity of the soils should result in very low rates of P leaching [*Bruijnzeel*, 1991].

[4] Studies of nutrient limitation in highly weathered soils have focused primarily on NPP and the role of plant and fungal-based strategies for P acquisition. The role of fine root morphological characteristics [*Powers et al.*, 2005], root exudates [*Tarafdar and Claassen*, 1988], and mycorrhizal associations [*Stark and Jordan*, 1978; *Bolan*, 1991] in plant P uptake have all been studied in P-limited ecosystems. Postfertilization P dynamics in agricultural systems in the tropics have been well-studied [*Yost et al.*, 1981; *Beck and Sanchez*, 1994, 1996; *Dobermann et al.*, 2002; *Buehler et al.*, 2002], but given that fertilization is usually accompanied by tilling and liming as well as crop removals and other disturbances, it is difficult to apply these findings

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Table 1. Characteristics of the Top 10 cm of Soil in the Floresta Nacional Tapajos, Pará, Brazil[a]

Soil	Bulk Density ($g\ cm^{-3}$)	Sand (%)	Silt (%)	Clay (%)	pH	Total P ($mg\ kg^{-1}$)	C (%)	N (%)	Fe_2O_3 ($g\ kg^{-1}$)
Sandy clay	1.10 (A) *(0.03)*	48.6 (A) *(1.4)*	4.0 *(1.6)*	47.4 (A) *(1.6)*	3.4 (0.02)	131 (A) *(7.3)*	2.48 (A) *(0.21)*	0.22 (A) *(0.01)*	50 *(6)*
Sandy loam	1.30 (B) *(0.05)*	89.8 (B) *(1.1)*	2.5 *(0.1)*	7.7 (B) *(1.0)*	3.4 *(0.04)*	68 (B) *(6.5)*	1.43 (B) *(0.07)*	0.10 (B) *(0.01)*	5

[a]Measurements reported here were made in April 1999 prior to fertilization with the exception of the Fe_2O_3 concentrations which are from *Rodrigues et al.* [1991]. For all measurements, N = 6, with standard error reported in parentheses. Uppercase letters indicate differences between soils significant at the 95% level.

directly to forest ecosystems. There have been surprisingly few field fertilization experiments in old–growth, lowland, tropical forest ecosystems and they have yielded mixed results with regard to NPP, and little information on the fate of P in the soil pool [*Mirmanto et al.*, 1999; *Li et al.*, 2006]. In laboratory experiments P additions increased microbial growth, respiration, and decomposition of dissolved organic carbon over hours to days in highly weathered soils from Costa Rica [*Cleveland et al.*, 2002]. On the same timescale, geochemical sinks exceeded microbial utilization of P tracers added to young mineral soils in Hawaii in the lab, while microbial immobilization dominated in organic soils [*Olander and Vitousek*, 2004].

[5] Much of the available P in tropical forest soils is thought to be supplied via mineralization of organic matter and the release of ester-bonded P [*Tate*, 1984; *Tiessen et al.*, 1984; *Stewart and Tiessen*, 1987; *Beck and Sanchez*, 1994]. However, recycling of the organic pool may be insufficient to maintain NPP, even with very low P losses from leaching [*Silver et al.*, 2000]. Recent evidence suggests that P previously thought of as biologically unavailable (bound to Fe and Al oxides and hydroxides) can be released during short-term, low redox fluctuations [*Peretyazhko and Sposito*, 2005; *Chacón et al.*, 2006]. Determining the fate of added P in soils will improve our understanding of nutrient dynamics and potential nutrient limitation in these productive ecosystems.

[6] In this study we used a field fertilization experiment to determine the effect of soil texture on the amount and form of P retained in the rooting zone of a mature tropical forest. Over the course of 1 year we measured changes in soil P fractions, microbial biomass, fine root biomass, and forest floor in response to P additions. At our study site highly weathered sandy clay Oxisol and sandy loam Ultisol interdigitate on the landscape. Owing to the co-occurrence of these soils at one site, several ecosystem state factors (sensu Jenny, i.e., relief, climate, and vegetation) are held constant allowing us to isolate the effects of soil texture and mineralogy on the fate of added P. We hypothesized that geochemical sorption and occlusion would be the dominant fate of added P in the sandy clay soils with their characteristic high Fe and Al concentrations and high particle surface area. In contrast, we predicted that root and forest floor P would be the largest sink of added P in sandy loam soils due to decreased reactive surface, higher root biomass, and lower soil Fe and Al content.

2. Methods

2.1. Study Site

[7] The study was conducted in the Tapajós National Forest (FLONA Tapajós), a mature closed-canopy evergreen tropical lowland forest [*Parrotta et al.*, 1995], located 80 km south of Santarém, Pará, Brazil (2° 64′ S and 54° 59′ W). The region has a mean annual temperature of 25°C, and receives approximately 2000 mm of rain per year with a dry season lasting from August through November [*Hernández-Filho et al.*, 1993; *Parrotta et al.*, 1995]. For additional site description, see *Silver et al.* [2000], *Keller et al.* [2001], and *McGroddy et al.* [2004].

[8] The planalto area south of Santarém is dominated by well-drained distrophic yellow-brown lateritic Ultisols (Latossolo Amarelo textura muito argilosa in the Brazilian classification system), derived from the Alter do Chão formation (Cretaceous-Tertiary [*Irion*, 1984]). These soils are characterized by low pH (Table 1), low essential nutrient concentrations and relatively high aluminum concentrations. Cation exchange capacity is associated with organic matter concentration and highest in the O horizon suggesting most plant nutrient uptake occurs in the surface horizons. Soil structure is generally moderate with very fine to fine angular and subangular peds and dominated by 1:1 type clays (dominantly kaolinite with some gibbsite present [*Irion*, 1984; *Rodrigues et al.*, 1991]). In the mineral horizons, both CEC and base saturation are low. Extractable aluminum pools are high (0.8 to 5.4 cmol/kg soil) and dominate base saturation. Iron oxide concentrations in the top 10 cm of soil typically range from 41 to 61 $g\ kg^{-1}$ soil [*Rodrigues et al.*, 1991].

[9] In addition to the Ultisols, deep well drained sand/sandy-loam soils (Oxisols, Neossolos Quartzarenicos in the Brazilian soil classification system), developed from sandy sediments deposited during the Quaternary, occur in the same region [*Rodrigues et al.*, 1991]. These soils are characterized by a sandy or sandy loam texture to a depth of at least 2 m, with the sand component of the soil composed primarily of quartz with virtually no weatherable primary minerals. Both cation exchange capacity (1.2 cmol kg^{-1}), and base saturation (3–8%) are low in the sandy loams [*Rodrigues et al.*, 1991]. As with the co-occurring clay soils, 1:1 clays (primarily kaolinite) dominate the clay fraction of the sandy loams. Though most commonly located in the valleys and lower portions of the generally flat planalto, the sandy loams are not restricted topographically and the higher plateau areas are composed of approximately 70% clays and clay- loams and 30% sands and sandy loams [*Silver et al.*, 2000].

2.2. Experimental Design

[10] We used a combination of sequential soil samples, root ingrowth cores and root exclusion cores in control and fertilized plots in both the sandy loam and the sandy clay soils. The combination of root ingrowth cores and sequential cores was designed to increase our sensitivity to

potential changes in fine root biomass. Root exclusion cores allowed us to examine the effects of P additions on soils and microbial biomass in the absence of fine roots.

[11] Three study blocks (12 × 100 m) were established on level terrain in each soil type within the FLONA Tapajós. Blocks were divided into five 12 × 20 m plots with P addition and sampling restricted to the interior 4 × 20 m zone of the first, third and fifth plots, leaving the rest of the area as buffer. We randomly selected a pair of plots within each block for the installation of this study. Before initiating treatments, 3 soil cores (6 cm diameter, 0–10 cm depth) were collected from each plot to characterize baseline soil nutrient pools and physical characteristics. In addition, 5 samples of forest floor (the recently fallen litter and partially decomposed but still identifiable organic material above the soil surface) were taken from each plot for mass and nutrient analyses, using a 15 × 15 cm (interior dimensions) template.

[12] One plot in each pair was randomly selected to receive P additions. We added approximately 135 kg P ha^{-1} a^{-1} in the form of super triple phosphate (3 Ca $(H_2PO_4)_2$ H_2O) granules. Phosphorus was applied in equal quantities (approximately 45 kg ha^{-1}) in May and September 1999 and January 2000. This amount was chosen to allow us to detect an increase in the total soil P pool (~300–780 kg/ha, 0–40 cm, *Silver et al.*, 2000), and is similar to the P added in other tropical forest fertilization experiment on highly weathered soils [*Herbert and Fownes*, 1995; *Vitousek et al.*, 1993; *Cleveland et al.*, 2006; *Li et al.*, 2006]. In order to ensure that each core received an amount of phosphate proportional to its surface area, cores were individually fertilized and then covered while the remaining phosphate granules were distributed evenly across the experimental area (4 × 20 m).

[13] Given the importance of rainfall distribution in determining the seasonality ecosystem processes at this site, we designed our sampling schedule to capture the peak of each season (dry and wet) as well as the transition point between wet and dry seasons when rainfall inputs had been below putative evapotranspiration rates for a period of ~2 months potentially stressing the primary producers. Fertilizer was applied shortly after collection points to allow for maximum incorporation of fertilizer P into the soil and biotic pools prior to the next sampling point.

2.3. Root, Microbial, and Soil Phosphorus Dynamics

[14] Cores were 10 cm long and 6 cm in diameter and were constructed from plastic canvas (Darice 7 count plastic canvas, 2 × 2 mm mesh). A total of 360 root ingrowth cores (180 for fine root measurements, 180 for soil and microbial biomass measurements) and 180 root exclusion cores (plastic canvas cores lined with a double layer of root exclusion cloth) were constructed. Visual inspection of the root exclusion cores showed no fine root ingrowth after 8 months and minimal ingrowth after 1 year. We selected 216 cores for inorganic P leachate estimates; 3 ingrowth cores and 3 exclusion cores per plot and per collection point. The bottom of these cores were fitted with 6 cm dia. silk resin bags containing 3 g of Cl^- charged Biorad AG 85 anion exchange resin beads.

[15] For each core a soil sample of identical volume was collected from inside the plot. Visible roots and large pieces of organic material were removed by hand and the homogenized soil from each sample was packed into a plastic canvas core thus maintaining representative bulk densities. At each of 15 randomly selected locations within the plot a set of three cores was installed: one ingrowth core for fine root biomass measurements, one ingrowth core for soil and microbial biomass P pool measurements (in the presence of roots), and one root exclusion core for soil and microbial biomass P measurements. All cores (total of 180 sets or 540 cores) were installed in April 1999.

[16] Cores were collected 4, 8, and 12 months after installation (in August and November 1999 and April 2000). At each time point we collected 5 sets of cores; we also collected 6 quantitative bulk soil samples and 5 forest floor samples from each treatment plot for further estimates of soil, root and litter layer P dynamics. Three of the quantitative bulk soil samples were analyzed for fine root biomass and nutrient content and the other three for bulk density and soil and microbial P pools. Because we found no significant effect of sample type (root ingrowth, root exclusion and bulk soil) on P pools, all data were combined for statistical analyses.

2.4. Analytical Methods

[17] Soil pH was determined on fresh soils in a 1:1 slurry with 2 M KCl in April 1999. These samples were analyzed at the EMBRAPA soil labs in Belém, PA, Brazil. All further analyses were done at the University of California, Berkeley. Phosphorus sorption curves were developed for each soil type using six time points (0, 5, 10 min, 2, 8 and 24 h) and five PO_4^{3-} concentrations (0, 5, 10, 50, and 100 ppm PO_4) as KH_2PO_4 in a 0.02 M KCl solution (1:3 soil to solution ratio [*Bache and Williams*, 1971] (as modified by G. P. Asner, personal communication)). Soil texture was determined for one composite sample from each plot using the Bouyoucos hydrometer method [*Gee and Bauder*, 1986]. Total soil C and N were measured on air-dried, ground soils using a dry combustion- reduction method on a CE Instruments NC2500 soil analyzer (CE Instruments Lakewood NJ).

2.4.1. Soil Phosphorus Fractions

[18] Soil P fractions were determined using the modified Hedley fractionation method [*Tiessen and Moir*, 1993; *Frizano et al.*, 2002] on air-dried soil samples. Phosphorus concentrations of the extractant solutions were determined on a Lachat QuickChem 8000 Automated Ion Analyzer (Lachat Instruments Division of Zellweger Analytics, Inc. Milwaukee WI) and for the solutions with strong color on a Thermo Jarrell Ash axial IRIS ICP-AES (Thermo Elemental, Franklin MA). Due to strong discoloration of the $NaHCO_3$, and NaOH extractions, only total P is reported for each fraction. Based on work by *Cross and Schlesinger* [1995], we aggregated the fractions into 3 pools: the readily available P pool as the sum of the resin and $NaHCO_3$ extractable P, the intermediate pool as the sum of the NaOH and dilute HCl extractable P, and the recalcitrant P pool as the concentrated HCl extractable plus the P in the residual soil digest (Table 2). Sequential fractionation does not allow for the accurate distinction between occluded P, other insoluble inorganic forms and P tightly bound in recalcitrant organic forms [*Cross and Schlesinger*, 1995], but all of these pools are considered unavailable for uptake on a

Table 2. Chemical and Ecological Meaning of Sequential Soil P Fractions From the Modified Hedley Method[a]

	Extractant	Chemical Composition	Presumed Ecological Significance
Available Pool	Resin	Solution and labile P adsorbed on the surface of crystalline compounds	Directly exchangeable with the soil solution and available to plants for uptake
	$NaHCO_3$	Inorganic P absorbed on soil colloid surfaces and associated with Fe and Al. Easily mineralized organic P held at soil aggregate surfaces	Labile Pi in equilibrium with soil solution and easily mineralized organic P forms
Intermediate Pool	NaOH	P associated with amorphous and crystalline Fe and Al phosphates as well as inorganic P bound to sesquioxides and humic compounds	Inorganic forms more tightly bound to Al and Fe than in the previous fraction especially under acid conditions. Organic forms similar to but more stable than those removed with NaHCOs
	1M HCl	Calcium associated P, dominantly in inorganic forms	Slowly available to plants via dissolution
Recalcitrant Pool	Concentrated HCl	P in the form of Ca-phosphates and protected in sesquioxides	Stable forms of P with low solubility and low availability to the biota
	H_2SO_4 digest	Occluded P found in stable organics (humic acids and humus etc.) as well as physically encapsulated inorganic P	Slow turnover and highly recalcitrant P pool

[a]Definitions from *Tiessen and Moir* [1993] and *Cross and Schlesinger* [1995].

decadal to millennial timescale. The total soil P values by summation corresponded to the measurements by the HF method (estimated method precision of ±25% [*Dolezal et al.*, 1968; *Carmouze*, 1994]); regression analysis suggested that summing of fractions slightly overestimated total P at higher concentrations and underestimated P at lower concentrations.

2.4.2. Anion Exchange Resins

[19] Anion exchange resin bags were stored frozen until they could be analyzed. Bags were washed with distilled, deionized water to remove soil and debris, and then extracted with 50 ml of a 0.5 M HCl solution [*Sibbesen*, 1978]. Bags with holes due to either root or soil fauna activity were re-weighed to get an accurate assessment of mass. Approximately 15% of the bags from the final collection point were colonized by root biomass. Plant or fungal uptake of P in the root colonized bags may have caused an underestimation of P captured by the resin and these bags were excluded from the analyses. Orthophosphate in the extraction solution was determined using a molybdate blue analysis on a Lachat QuickChem 8000 Automated Ion Analyzer.

2.4.3. Microbial Biomass Phosphorus

[20] An index of microbial biomass P pools was determined using the chloroform fumigation direct extraction (CFDE) technique with acidified NH_4F as the extraction solution [*Brookes et al.*, 1982; *Oberson et al.*, 1997] on fresh soils. Phosphorus concentrations in the extraction solutions were determined on Thermo Jarrell Ash axial IRIS ICP-AES. CDFE-P was calculated as the difference between the P extracted from the fumigated sample and that from the non-fumigated sample. A correction factor for sorption of P released by fumigation was calculated by measuring recovery of a P spike (average recovery of 45% for a spike of 25 μg P g^{-1} soil in the form of KH_2PO_4), added to composite soil samples for each texture [*Morel et al.*, 1996]. All data are reported on a 105°C dry weight basis.

2.4.4. Root Biomass and Nutrient Content

[21] Roots were washed through a series of three Nalgene sieves (sieve opening sizes: 2.0, 0.5 and 0.2 mm respectively) to remove soil particles and extraneous organic material. Fine roots ($\leq$2mm dia.), considered most active in nutrient uptake, were sorted into live and dead categories based on appearance and tensile strength [*Vogt and Persson*, 1991], dried at 65°C and weighed to determine mass. Samples from replicate plots were bulked as necessary to provide enough tissue for nutrient analyses, and ground in a Wiley mill. Total tissue C and N were measured on a CE Instruments NC2500 soil analyzer (CE Instruments Lakewood NJ). Fine root tissue P concentrations were determined on a Thermo Jarrell Ash axial IRIS ICP-AES after a modified Kjeldhal digest [*Parkinson and Allen*, 1975].

2.4.5. Forest Floor Phosphorus and Soil Bulk Density, Carbon, and Nitrogen

[22] Forest floor samples were dried at 50°C for 3 days and weighed to determine mass. A set of subsamples was dried at 65°C and a conversion factor was developed to calculate mass on a 65°C dry weight basis. Samples were ground in a Wiley mill and passed through a 40 mesh. A 0.5 g subsample was ashed at 550°C for 4 h in order to determine the inorganic composition of each sample. Total P concentrations were determined as described for the root tissue and reported on a 65°C dry weight and ash free basis.

[23] Bulk density was determined by measuring fresh weight of soil from 3 cores (282.6 cm^3 volume, 0–10 cm depth) from each plot and a fresh to oven dry (105°C) conversion developed from a subsample from each core. Air-dried soils from each collection were passed through a 2 mm sieve, ground, and analyzed for total C and N using the methods described for root tissue.

2.5. Statistical Analyses and Calculations

[24] Statistical analyses were performed using *SYSTAT* [1999]. Analyses were done on the mean of 3 replicates for each treatment plot for each collection point except for forest floor and microbial biomass P, which were done on the mean of 5 replicates per treatment plot. Data were log transformed to meet the assumptions of the analysis of variance (ANOVA). Using a 2 × 3 × 4 mixed-model, within-subjects, repeated measures ANOVA, we looked at the effect of treatment, and core type (ingrowth, exclusion or bulk soil) as well as interactions of these variables over time on the distribution of soil P, fine root and microbial P within each soil. Paired comparisons using Tukey's post hoc test were used to determine where significance occurred. All

Table 3. Mean and Standard Errors (N = 3) of Measured Soil P Pools in the Top 10 cm of Soils in the Floresta Nacional Tapajos, Para, Brazil[a]

	April 1999		August 1999		November 1999		April 2000	
P Pools	Control	+ PO_4	Control	+ PO_4	Control	+ PO_4	Control	+ PO_4
Sandy Clay Soils								
Resin	0.60 (1.1)	1.0 (AB) (0.1)	1.1 (0.4)	1.6 (A) (0.5)	0.05 (0.03)	0.2 (BC) (0.1)	0.5 (0.3)	0.0 (C) (0.0)
$NaHCO_3$	26.3 (A) (2.6)	24.0 (4.1)	**5.5 (B)** (1.5)	**29.8** (7.7)	**6.3 (AB)** (1.2)	**25.2** (4.1)	**8.0 (AB)** (2.1)	**35.3** (12.5)
NaOH	49.0 (A) (6.7)	42.6 (A) (1.9)	**24.5 (B)** (2.9)	**64.0 (A)** (10.6)	**39.6 (A)** (1.5)	**78.9 (AB)** (8.9)	**54.1 (A)** (1.7)	**111.1 (B)** (15.0)
1M HCl	2.0 (A) (0.4)	1.6 (A) (0.1)	1.5 (A) (0.2)	2.0 (A) (0.2)	8.4 (B) (2.0)	10.8 (B) (2.6)	1.4 (A) (0.2)	1.7 (A) (0.2)
Conc. HCl	45.3 (A) (3.1)	42.7 (A) (2.4)	69.3 (B) (1.2)	72.1 (B) (2.7)	34.6 (C) (1.8)	38.6 (A) (2.6)	70.5 (B) (2.5)	76.4 (B) (3.0)
H_2SO_4	19.3 (AB) *(5.1)*	16.8 (A) *(2.9)*	25.7 (A) *(2.3)*	27.2 (B) *(2.3)*	20.1 (AB) *(0.7)*	22.1 (AB) *(1.5)*	17.4 (B) *(0.9)*	20.2 (AB) *(1.5)*
Available	27.0 (A) *(2.6)*	25.0 *(4.1)*	**6.7 (B)** *(1.2)*	**31.4** *(7.6)*	**6.4 (B)** *(1.2)*	**25.4** *(4.1)*	**8.5 (B)** *(2.2)*	**35.3** *(12.5)*
Inter.	51.0 (A) *(7.1)*	44.7 (A) *(1.8)*	**26.0 (B)** *(2.9)*	**66.0 (AB)** *(10.7)*	**48.1 (A)** *(3.4)*	**89.6 (BC)** *(7.2)*	**55.5 (A)** *(1.6)*	**112.8 (C)** *(15.3)*
Recalc.	64.7 (A) *(8.3)*	59.4 (A) *(2.5)*	95.0 (B) *(3.2)*	99.2 (B) *(4.6)*	54.6 (A) *(2.3)*	60.7 (A) *(3.9)*	87.9 (B) *(3.2)*	96.5 (B) *(4.0)*
Total P	142.2 (AB) *(15.8)*	128.6 (A) *(4.1)*	127.7 (A) *(3.3)*	196.6 (AB) *(18.0)*	**109.0 (C)** *(3.8)*	**175.7 (AB)** *(14.2)*	**151.9 (B)** *(5.3)*	**244.6 (B)** *(26.2)*
Sandy Loam Soils								
Resin	1.2 (AB) *(0.1)*	1.0 *(0.3)*	2.1 (A) *(0.4)*	0.7 *(0.4)*	0.03 (B) *(0.06)*	0.2 *(0.1)*	0.9 (AB) *(0.6)*	0.3 *(0.3)*
$NaHCO_3$	37.3 (A) *(3.1)*	37.0 *(5.1)*	9.7 (AB) *(2.7)*	22.9 *(7.8)*	**5.2 (B)** *(0.9)*	**24.7** *(7.5)*	11.2 (AB) *(4.1)*	25.4 *(4.1)*
NaOH	26.3 *(6.1)*	17.1 *(2.8)*	18.4 *(2.5)*	24.3 *(7.0)*	**24.9** *(2.2)*	**39.2** *(5.0)*	23.9 *(5.9)*	40.7 *(5.2)*
1M HCl	2.0 (A) *(0.5)*	1.1 (A) *(0.2)*	1.5 (A) *(0.3)*	3.4 (A) *(1.8)*	12.4 (B) *(2.9)*	14.4 (B) *(3.3)*	**1.1 (A)** *(0.1)*	**2.4 (A)** *(0.4)*
Conc. HCl	20.1 (AB) *(6.0)*	14.8 *(1.3)*	32.7 (A) *(4.9)*	21.8 *(2.6)*	17.5 (B) *(2.6)*	17.7 *(1.5)*	27.2 (AB) *(3.5)*	23.3 *(2.9)*
H_2SO_4	14.6 (AB) *(2.2)*	9.2 (A) *(1.5)*	25.0 (B) *(3.2)*	20.1 (B) *(3.0)*	12.5 (A) *(1.2)*	11.5 (A) *(1.2)*	12.5 (A) *(1.6)*	12.7 (AB) *(1.1)*
Available	38.5 (A) *(3.0)*	37.9 *(4.9)*	11.8 (B) *(2.9)*	23.7 *(7.9)*	**5.3 (B)** *(0.9)*	**24.8** *(7.5)*	**12.1 (AB)** *(4.2)*	**25.6** *(4.1)*
Inter.	28.2 *(5.8)*	18.3 (A) *(2.9)*	19.8 *(2.5)*	27.7 (AB) *(6.7)*	37.3 *(4.7)*	53.6 (B) *(6.9)*	**25.0** *(5.9)*	**43.1 (AB)** *(5.5)*
Recalc.	34.7 (AB) *(7.6)*	24.0 *(2.4)*	57.8 (A) *(6.3)*	41.8 *(5.5)*	29.9 (B) *(3.5)*	29.2 *(2.6)*	39.7 (AB) *(4.6)*	36.0 *(3.6)*
Total P	101.4 *(15.0)*	80.2 *(10.0)*	89.4 *(5.4)*	93.2 *(17.9)*	**72.4** *(6.6)*	**107.5** *(13.9)*	76.9 *(13.5)*	104.7 *(10.0)*

[a]Fractions are identified by their extractant. The available pool is the sum of the resin and $NaHCO_3$ fractions, the intermediate pool is the sum of the NaOH and 1M HCl fractions and the recalcitrant pool is the sum of the concentrated HCl and H_2SO_4 fractions. Total is the sum of all the individual fractions. Units are in kg ha^{-1}. Uppercase letters indicate significant differences ($P \leq 0.05$) within a treatment over time; bold font indicates significant differences between control and treatment within a collection period.

results reported are significant at a $P \leq 0.05$ level unless otherwise stated. In the text, mean values and standard error are reported.

[25] The amount of added P retained in each pool was estimated by dividing the difference between control and treatment plots by the cumulative amount of P that had been added up to that time point. The total amount retained by soil type was calculated by dividing the difference between the sum of P pools in the treatment and the control by the cumulative amount of P that had been added up to that time point. Microbial biomass pools were not included in this calculation as the P in the microbial biomass was also estimated in the soil P fractions.

3. Results

3.1. Initial Conditions: Sandy Loams Versus Clays

[26] Prior to P additions total C, N, and P concentrations in sandy clay soils were significantly higher than those in sandy loams ($P \leq 0.001$ for each, Table 1) while the sandy clays had significantly lower bulk densities ($P \leq 0.001$). As expected, sandy clay soils had significantly higher P sorption capacity compared to the sandy loams (57% more P sorbed g^{-1} soil after 24 h, absorption curves provided in Figure S1, available as auxiliary material).[1] Within soils we found no significant differences between plots selected for fertilizer treatment and those selected as controls.

[27] Resin-extractable P, the most biologically labile pool, was very low in both soil types representing a maximum of 3.3% of total soil P (Table 3). The Ca-bound P fraction (1 M HCl extraction) was also low in both soil types (less than 6% of the total soil P pool in both soils), which was expected given the acidic soil environment. Total soil P pools in the sandy clay soils were significantly larger than those found in the sandy loams ($P \leq 0.01$, Table 3). However, in the sandy loams, the available fraction was a significantly larger proportion of total soil P as compared to the sandy clays (18.3 ± 7.1% versus 8.9 ± 3.4% in sandy clays, $P \leq 0.01$). The recalcitrant fraction dominated the P pool in both soils, and was a slightly larger proportion of the total soil P pool in the sandy clays as compared to the sandy loams (58.6 ± 2.5% versus 50.8 ± 3.3%, $P = 0.06$, Table 3).

3.2. Response to Fertilization: Soil Phosphorus Pools

[28] Soil P pools in the two soil types responded very differently to P additions. After 1 year of treatment, total soil P in the sandy clay treatment plots had increased by 93 ± 27 kg P ha^{-1}, representing 68% of the added P ($P \leq 0.01$). In the sandy loams total P pools were significantly higher than the controls at the 8 month (peak dry season) collection ($P \leq 0.05$) but the difference was not significant at 1 year (Table 3). Added P in both soils was primarily found in the available and intermediate soil pools, specifically the $NaHCO_3$ and the NaOH extractable fractions (Table 3). There was no increase in the recalcitrant P fractions with P addition.

[29] Precipitation in this forest is strongly seasonal, and in the sandy clay control plots, available P pools were largest at the start of the experiment (the peak of the first wet season) after which values declined and stabilized (Figures 1a–1c). Intermediate soil P pools peaked in the late dry season (at 8 months, $P \leq 0.001$, and $P = 0.08$, for sandy clay and sandy loam respectively), while the recalcitrant fraction increased significantly during the early dry season (at 4 months, $P \leq 0.0001$ and $P \leq 0.01$ for sandy clay and sandy loam respectively). Total soil P declined from the

[1]Auxiliary materials are available in the HTML. doi:10.1029/2008JG000756.

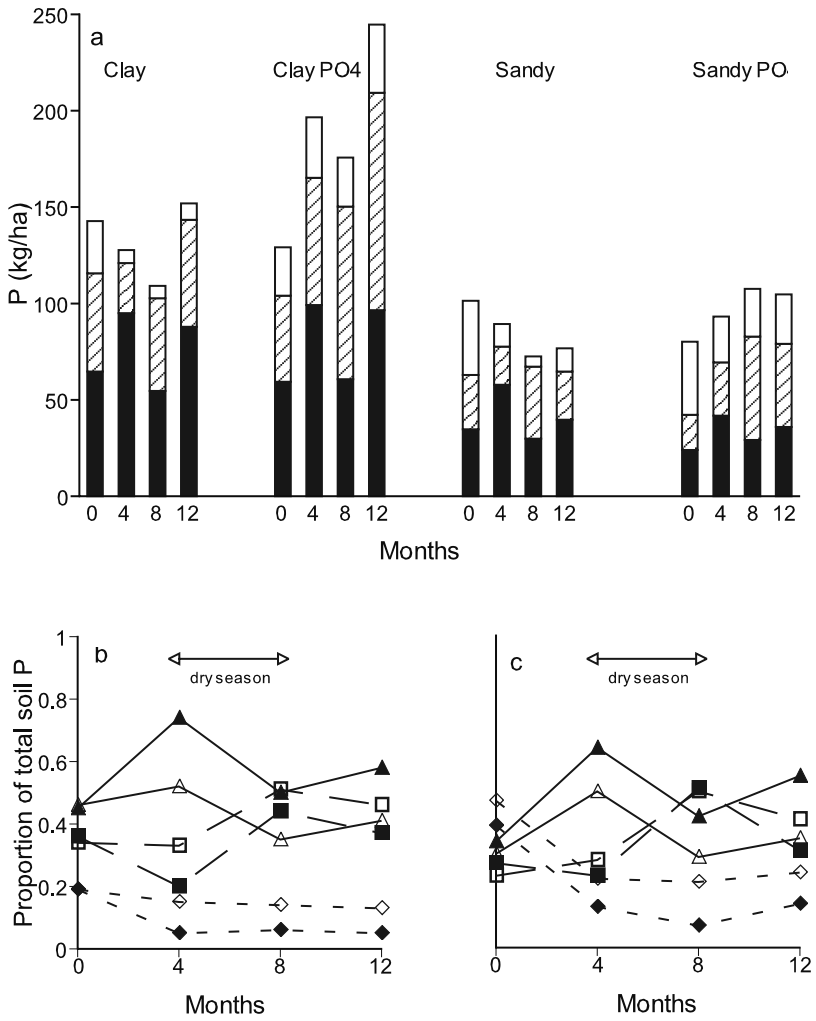

Figure 1. Soil P fractions in experimental plots in the FLONA Tapajós, Pará, Brazil. (a) Fractions have been bulked into three pools; available pool (resin and $NaHCO_3$ extractable fractions) represented by the open bar, intermediate pool (NaOH and 1M HCl extractable fractions) represented by the hatched bar and recalcitrant pool (concentrated HCl and H_2SO_4 extractable fractions) represented by the solid bar. (b and c) The available P pool (diamonds), the intermediate P pool (squares) and the recalcitrant P pool (triangles) are shown as percent of total soil P for sandy clays and sandy loams, respectively, with solid symbols representing the control treatments and open symbols representing the fertilized treatments. Time since the initiation of the study is noted on the *x* axis for all three graphs. The dry season is indicated by shading in Figures 1b and 1c.

initiation of the experiment (peak wet season) through the peak of the following dry season (8 month collection) and then returned to initial values at the peak of the following wet season ($P \leq 0.001$, Figure 1a). Although total P pools in the sandy loams showed a similar pattern, the differences were not statistically significant (Figure 1a). In both soils, P additions increased the variability in soil P pools and resulted in no statistically significant seasonal patterns (Figures 1a–1c).

[30] Mean soil C:P ratios did not vary significantly with soil type or treatment (392 ± 247 in the clays and 251 ± 58 in the sandy loams) and decreased over the course of the experiment for all treatments except the sandy clay control.

3.2.1. Fine Root Dynamics: Sequential Cores

[31] Fine root biomass at this site accounts for a significant component of the surface soil C pool with an estimated turnover time of 1–3 years [*Silver et al.*, 2000, 2005; *Trumbore et al.*, 2006]. Fine root biomass was consistently higher in the sandy loams than in the sandy clay soils ($P \leq 0.01$) and fertilization had no effect on fine root biomass in either soil (Table 4). Over the course of the experiment, fine root biomass increased in the control plots on both soils due primarily to increases in live fine root biomass ($P = 0.08$ for total fine root biomass, $P \leq 0.01$ for live fine roots, Table 4). No statistically significant trends were found in the treatment plots.

[32] Phosphorus additions resulted in significant increases in the fine root P pools in the sandy loams. Collection date, soil type and fertilization level were all significant factors in the analysis ($P \leq 0.001$ for all) with no significant interactions. The largest differences in fine root P pools between treatment and control plots occurred after 1 year of fertiliza-

Table 4. Fine Root Biomass and Phosphorus Pools in Experimental Plots in the Floresta Nacional Tapajós, Pará, Brazil[a]

			Sequential Cores			Ingrowth Cores		
Soil	Date	Treatment	Biomass	P Pool	C:P	Biomass	P Pool	C:P
Sandy clay	Aug.	control	1932 (443)	0.50 (0.10)	1877 (184)	1359 (201)	0.57 (0.09)	973 (32)
		+ PO_4	2854 (594)	0.97 (0.18)	1391 (8)	781 (A) (257)	0.43 (A) (0.19)	786 (A) (84)
	Nov.	control	2101 (205)	0.57 (0.09)	**1773** (123)	1404 (78)	0.50 (0.06)	**881** (71)
		+ PO_4	2221 (422)	0.87 (0.18)	**1018** (27)	2157 (B) (401)	1.13 (AB) (0.23)	**536 (B)** (11)
	Apr.	control	3185 (229)	1.17 (0.18)	**1235** (102)	1106 (118)	**0.70** (0.12)	684 (133)
		+ PO_4	2551 (710)	1.73 (0.26)	**633** (96)	1979 (B) (209)	**1.40 (B)** (0.12)	619 (AB) (44)
Sandy loam	Aug.	control	2884 (195)	1.03 (A) (0.09)	1328 (A) (82)	978 (151)	**0.53** (0.13)	767 (36)
		+ PO_4	4228 (664)	1.73 (0.38)	1124 (A) (63)	1447 (235)	**0.93** (0.09)	480 (A) (24)
	Nov.	control	2781 (314)	1.03 (A) (0.09)	1280 (A) (45)	1828 (134)	0.80 (0.06)	730 (38)
		+ PO_4	3863 (554)	1.60 (0.30)	1146 (A) (42)	3417 [1065]	2.00 (0.78)	705 (B) (34)
	Apr.	control	3081 (171)	**1.77 (B)** (0.18)	722 (B) (162)	1544 (378)	**0.80** (0.21)	813 (35)
		+ PO_4	3623 (545)	**2.67** (0.29)	625 (B) (113)	2160 (191)	**1.83** (0.30)	509 (C) (74)

[a]Biomass and P pools are reported in kg ha^{-1}. All ratios are mass-based. N = 3 for all values with standard errors reported in parentheses. Measurements that were significantly different ($P \leq 0.05$) within a treatment over time are indicated with uppercase letters; those that differed between fertilizer treatments within a soil at a given collection period are indicated by bold font. Differences were determined by ANOVA and paired t-tests using log transformed data where necessary.

tion ($P \leq 0.01$, Table 4). Fine root C:P and N:P ratios decreased as P concentrations increased, and C:P ratios were generally lower in dead as compared to live root tissue.

3.2.2. Fine Root Dynamics: Root Ingrowth Cores

[33] As in the sequential cores, root tissue P concentrations increased with P addition ($P \leq 0.001$ for live tissue; $P < 0.01$ for dead tissue). Live root tissue P concentrations increased over the course of the year in the treatment plots ($P \leq 0.001$) while dead root tissue P peaked at 8 months and then declined in both soils. In both soils total fine root P pools were significantly higher in the fertilized treatments after 1 year (Table 4). Fine root tissue C:P ratios showed no significant trends with fertilization in the ingrowth cores. At the initial collection, root tissue C:P ratios in the ingrowth cores were significantly lower than those measured in sequential soil cores ($P \leq 0.05$ for all control ($P \leq 0.05$ for live tissue and $P \leq 0.001$ for dead tissue).

3.3. Microbial Biomass and Forest Floor Phosphorus

[34] Microbial biomass P increased over the course of the experiment in the control plots ($P \leq 0.001$), with no significant differences between soils (Figure 2). In the treatment plots microbial biomass P pools peaked during the height of the dry season (at 8 months), and were significantly larger than the controls ($P \leq 0.01$ for sandy clays and $P = 0.08$ for sandy loams, Figure 2).

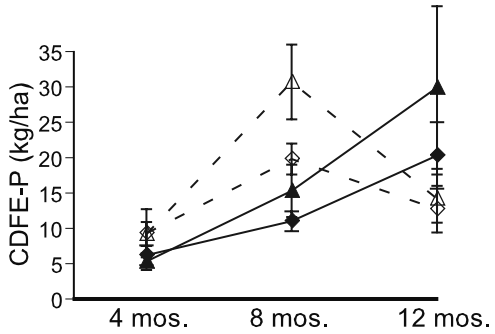

Figure 2. Chloroform fumigation-direct extraction P pools in experimental plots in the FLONA Tapajós, Pará, Brazil. Sandy clay soils are represented by diamonds and sandy loams by triangles. Solid symbols represent the control treatments, and open symbols represent the fertilized treatments. Bars represent ±1 standard error, and for all measurements N = 3. Time since the initiation of the study is noted on the *x* axis.

[35] Forest floor mass averaged 6.0 ± 5.8 Mg ha^{-1} with no significant differences between soils (Table 5). Four months after the first P addition the forest floor P pool in the sandy loams was significantly higher than both sandy loam controls at 4 months and other collections in the treatment plots ($P \leq 0.05$ for both).

3.4. Leaching

[36] Leaching of inorganic P from the surface soil was consistently below detection limits in the control plots (detection limit 0.2 kg ha^{-1}, Figure 3). Addition of P caused a significant increase in the amount of inorganic P leached from the surface layer, especially in the sandy loams. The average amount of P recovered from resin bags was equivalent to 2.7 ± 0.6 kg $ha^{-1}a^{-1}$ leached from sandy clays, which was significantly less than the 8.7 ± 1.9 kg $ha^{-1}a^{-1}$ leached from sandy loams ($P \leq 0.01$).

Table 5. Forest Floor Mass and P Pools in Experimental Plots in the FLONA Tapajós, Pará, Brazil[a]

Soil	Date	Treatment	Mass (Mg ha^{-1})	P pool (kg ha^{-1})
Sandy clay	Apr. 1999	Control	4.4 *(0.6)*	2.37 *(0.45)*
		+ PO_4	4.3 *(0.3)*	2.72 *(0.23)*
	Aug. 1999	Control	5.9 *(1.3)*	5.87 *(2.33)*
		+ PO_4	4.4 *(0.4)*	4.61 *(1.22)*
	Nov. 1999	Control	6.4 *(0.5)*	4.48 *(1.17)*
		+ PO_4	6.4 *(0.6)*	7.66 *(2.30)*
	Apr. 2000	Control	4.9 *(0.3)*	2.11 *(0.17)*
		+ PO_4	5.3 *(0.6)*	5.69 *(2.61)*
Sandy loam	Apr. 1999	Control	5.5 *(1.4)*	2.42 *(0.74)*
		+ PO_4	6.4 *(1.6)*	3.70 (A) *(0.82)*
	Aug. 1999	Control	4.7 *(0.7)*	**4.70** *(1.07)*
		+ PO_4	10.6 *(4.3)*	**12.96 (B)** *(3.05)*
	Nov. 1999	Control	6.9 *(0.5)*	4.19 *(1.02)*
		+ PO_4	8.9 *(1.9)*	6.61 (AB) *(0.89)*
	Apr. 2000	Control	4.4 *(1.3)*	2.95 *(0.19)*
		+ PO_4	6.0 *(1.4)*	6.15 (AB) *(2.25)*

[a]N = 3 for all values with standard errors reported in parentheses. Measurements that were significantly different ($P \leq 0.05$) within a treatment over time are indicated with uppercase letters; those that differed between fertilizer treatments within a soil at a given collection period are indicated by bold font. Differences were determined by ANOVA using log transformed data to meet the assumptions of the analysis.

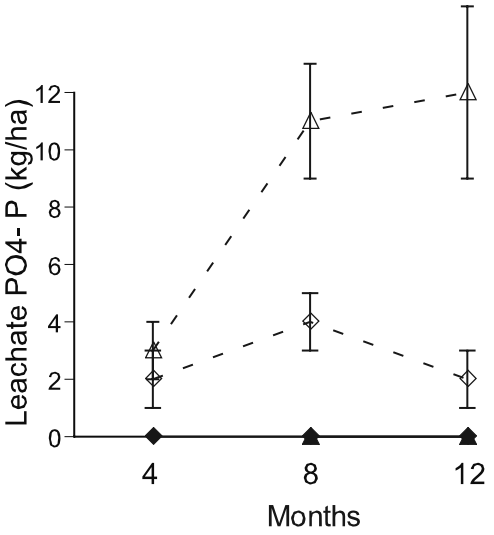

Figure 3. Phosphorus collected in anion exchange resin bags, in experimental plots in the FLONA Tapajós, Pará, Brazil. Bags were located at 10 cm depth beneath root ingrowth and exclusion cores. Sandy clay soils are represented by diamonds and sandy loams by triangles with solid symbols representing the control treatments and open symbols representing the fertilized treatments. Bars represent ±1 standard error, and for all measurements N = 3. Time since the initiation of the study is noted on the *x* axis.

3.5. Surface Soil Retention of Added Phosphorus

[37] The scope of this study was limited to the retention of added P in the surface soils, fine root and forest floor pools, so given other potential fates, such as plant uptake, we did not expect to account for all of the added P. After 1 year approximately 69 ± 20% of the added P was retained in the sandy clays, while only 33 ± 7% of the added P was found in the sandy loams (Figure 4). Added P in the sandy clay soils was found primarily in the available and intermediate soil P fractions rather than the recalcitrant fractions. In sandy loams, the intermediate soil P pools and leachate were the dominant fates for added P.

4. Discussion

[38] Given the high proportion of the recalcitrant fraction in both soils, we expected that most of the added P would move into recalcitrant soil pools, particularly in the sandy clay soils which are dominated by Fe and Al minerals. However, we found more of the added P in the $NaHCO_3$ and NaOH extractable fractions that make up the intermediate P pools over the 1-year study. Over short time periods (hours to weeks) microbial immobilization of labile P, Fe reduction and organic matter competition for both labile P and binding sites on soil particles have been shown to effectively reduce the geochemical sequestration of labile P in P-limited soils [*Walbridge et al.*, 1991; *Nziguheba et al.*, 1998; *Olander and Vitousek*, 2004; *Chacón et al.*, 2006]. All of these processes are likely to be important at our study site, and appear to be effective mechanisms for maintaining P in a relatively labile state over a 1-year period. While the microbial pool is characterized by rapid turnover the conversion of reactive inorganic P into less reactive organic compounds has longer term effects on P cycling in soils. Additionally fungal translocation of P to C rich sites [*McGroddy et al.*, 2004] can increase the probability of P being bound to organic matter. Studies in agricultural systems on highly weathered soils have reported similar increases in the NaOH extractable pools with fertilization [*Beck and Sanchez*, 1996; *Dobermann et al.*, 2002]. While the P associated with Al and Fe oxides and hydroxides is generally considered moderately stable [*Cross and Schlesinger*, 1995], it has been suggested that it is an important reservoir of P and in equilibrium with the labile P pool [*Tiessen and Stewart*, 1994; *Beck and Sanchez*, 1994, 1996; *Buehler et al.*, 2002]. As such it may play an important role in plant nutrient uptake especially in soils with high C inputs and potential redox fluctuations [*Peretyazhko and Sposito*, 2005; *Chacón et al.*, 2006]. In our study this pool was sensitive to rainfall seasonality which could reflect either shifts in soil redox states and/or biological demand. The intermediate pools were much stronger sinks for added P in the sandy clays than in the sandy loams, likely due to higher organic matter content and Al and Fe concentrations (Table 1), greater reactive surface area in the clay soils, and possibly more biological uptake in the sandy loams.

[39] Fine root, microbial biomass, and forest floor P pools were more sensitive to the addition of P in the sandy loams than in the sandy clays. However, the increases with P addition were generally small and/or transient unlike the changes measured in the soil pools in the clays. In studies of tropical ecosystems, P additions have resulted in both increases and decreases in fine root biomass, though root tissue P concentrations have generally increased with P additions [*Ostertag*, 2001].

[40] A significant amount of added P moved out of the soil cores during the course of the experiment. Much of this P was likely taken up by both fine roots and mycorrhizal hyphae and incorporated into aboveground biomass. As a first approximation we estimated the potential sink for P in foliage by applying the relative increase in tissue P concentrations measured in roots from ingrowth cores to foliar production in plots. The foliar P pool accounted for an additional 16.3–27.4 kg P ha^{-1} (or 12 and 20% of added P for sandy clays and sandy loams, respectively; leaf litter productivity data from *Silver et al.* [2005], initial foliar concentrations from *Olander et al.* [2005]). Though there are few studies that have looked at the responses of both root and foliar tissues to P additions, data from a long-term fertilization study on highly weathered soils in Hawai'i suggest that leaf tissue is potentially more responsive to increased nutrient availability than root tissue despite higher initial concentrations [*Vitousek*, 2004], thus this value is likely to be an underestimate. Additional P uptake and storage in woody tissues and reproductive parts would account for a larger percentage of the added P.

[41] Significant quantities of inorganic P leached out of the surface layer of fertilized plots in both soils compared to low levels of leaching in the control soils. Phosphorus additions, although distributed over time, may have exceeded the capacity for root and microbial uptake, increasing leaching losses [*Chapin*, 1980; *Olander and Vitousek*, 2005]. The phosphate ion is generally considered to be highly immobile in soils [*Sposito*, 1989], and leaching of

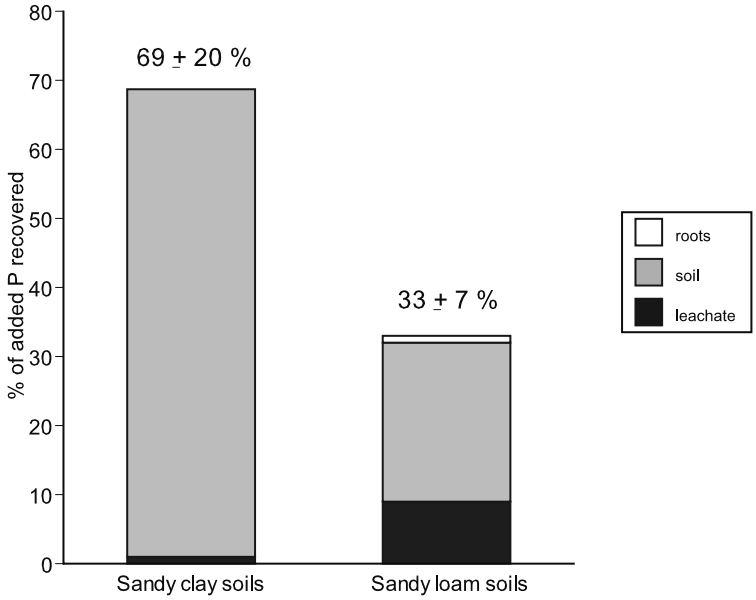

Figure 4. Retention of P added as super triple phosphate in surface soils at the FLONA Tapajós, Pará, Brazil. Retention is calculated as the difference between a given pool in the fertilized treatment and the same pool in the control treatment divided by the total amount of P added. Mean retention ±1 standard error is reported above each column.

inorganic P in P- limited systems has been considered minimal [*Neff et al.*, 2000], though there is some evidence of increased P mobility in sandy soils [*Weaver et al.*, 1988a, 1988b]. In nutrient-poor ecosystems, direct cycling of nutrients between plants and microbes in the forest floor [*Went and Stark*, 1968] may minimize leaching losses. The biota may not be able to rapidly adjust uptake rates to respond to after unexpected inputs, resulting in the leaching of key nutrients from the surface layers [*Chapin*, 1980]. Alternatively, preferential flow through macropores in clay soils has also been posited as a mechanism allowing significant leaching of PO_4-P in despite high sorption capacity [*Djodjic et al.*, 1999] though this is unlikely to be the mechanism in sandy soils. Leachate P was likely slightly underestimated because we did not consider particulate or organic P in soil solution [*Djodjic et al.*, 1999; *Uusitalo et al.*, 2001]. Organic P forms are known to be more labile than inorganic forms [*Frossard et al.*, 1989] and are important components of leachate from P-amended agricultural soils [*Sharpley and Smith*, 1989; *Toor et al.*, 2005].

[42] Previous work has described seasonal increases in soil P pools, particularly the organic and microbial P pools, associated with reduced rates of mineralization, microbial predation and plant nutrient uptake in the dry season [*Saunders and Metson*, 1971; *Srivastava*, 1992; *Fabre et al.*, 1996; *Campo et al.*, 1998; *Cleveland et al.*, 2004]. The organically bound components of both the labile and intermediate pools may be rapidly made available via phosphatase activity [*McGill and Cole*, 1981] which could result in the strong seasonal shifts in pool sizes measured in this study. While our data point to an accumulation of P in the microbial biomass and intermediate soil P pools, we also find total soil P generally lower in the dry season, particularly in the sandy loams. There has been recent work suggesting that plant productivity and therefore nutrient uptake may be quite high during the dry season across the Amazon Basin [*Huete et al.*, 2006], perhaps resulting in the reduced soil pools we measured.

[43] In addition to the patterns discussed above, we saw a decrease in the importance of available soil P pools over the course of this 1-year study, and almost linear increases in live fine root biomass in the sequential cores and in microbial P pools in the control treatments that did not correspond to seasonal patterns in precipitation. At the onset of this study, the central Amazon region was recovering from the 1997–1998 El Niño. We propose that the severe and prolonged dry season in 1998 caused a dieback in fine roots and microbial biomass and a decrease in plant P uptake. The measured increases in live fine root biomass and microbial P pools may represent recovery of the forest biota.

[44] Few studies have considered soil pools when accounting for P added as fertilizer. *Compton and Cole* [2001] and others working in a temperate Spodsol recovered between 77 and 98% of the 400 kg ha^{-1} P added in their study. *Beck and Sanchez* [1994] could account for 69–85% of P added over 13 years to agricultural plots on an Ultisol with a sandy topsoil layer. In the Beck and Sanchez study 25–43% of the P added was recovered in the plant biomass on the plots with the remaining 42–44% found in the soil pools. The P retained here in the sandy clay soils is comparable to that found in the study by Compton and colleagues. Less of the added P was retained in the sandy-loam soils, which appear to be more dynamic with regard to biological P cycling.

5. Conclusions

[45] Our data suggest that while soil physical characteristics can predict long-term patterns in P pools [*Sanchez*, 1976], retention of added P in soil on an annual timescale is largely driven by biological demand and reversible reactions

with organic matter and metal oxides and hydroxides. The organically bound and Al/Fe oxide bound components of the soil P pool appear to play a key role in preventing P losses via leaching as well as replenishing the more labile soil P pools [*Beck and Sanchez*, 1994] and may be the key to understanding the high rates of primary productivity in these ecosystems. More of the added P was retained in the finer textured soils; in sandy loams, lower soil OM pools, and coarser texture allowed for significant leaching of this essential nutrient from the surface soil layer. In addition to its role limiting primary productivity, recent work has suggested that soil P is linked to soil C sequestration capacity in highly weathered soils [*Giardina et al.*, 2004; *Li et al.*, 2006] although the relationship is not currently well understood. Our ability to predict the C fluxes in tropical forest ecosystems under changing climate conditions depends on our understanding of the interaction among soil P pools as well as the regulation of these pools and their relative size by soil environment.

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