ACTA
AMAZONICA

http://dx.doi.org/10.1590/1809-4392202103471

ORIGINAL ARTICLE

Soil phosphorus fractions and their relation to leaf litterfall in a central Amazonian *terra firme* rainforest

Emily Darc Andrade dos SANTOS[1*], David Yue Phin TNG[2,3], Deborah Mattos Guimarães APGAUA[2,3], Raul Reis ASSUNÇÃO[4], Antônio Ocimar MANZI[5]

[1] Instituto Nacional de Pesquisas da Amazônia, Av. André Araújo 2936, Aleixo,69060-001, Manaus-AM, Brazil

[2] Centre for Rainforest Studies, The School for Field Studies, PO Box 141, Yungaburra, QLD 4884, Australia

[3] James Cook University, College of Science and Engineering, Centre for Tropical, Environmental and Sustainability Sciences, 14-88 McGregor Rd, Smithfield Qld 4878, Australia

[4] Universidade Federal de Lavras, Aquenta Sol, 37200-900, Lavras-MG, Brazil

[5] Instituto Nacional de Pesquisas Espaciais, Rod. Presidente Dutra, km 40 SP/RJ, 12630-970 Cachoeira Paulista-SP, Brazil

* Corresponding author: emilyandrad@gmail.com; https://orcid.org/0000-0001-5127-7390

ABSTRACT

Phosphorus (P) cycling is an important yet poorly studied aspect of the macronutrient balance in tropical rainforest ecosystems. As soil P occurs in different organic and inorganic forms (fractions) with varying degrees of lability, we hypothesized that these fractions will vary between soil types, and temporally within soil types. Additionally, we hypothesized a direct influence of leaf litterfall P input on soil total P and soil P fractions. We collected soil and leaf litter samples from three soil types in a central Amazonian lowland rainforest in Brazil over five months, and used a modified Hedleys fractionation method to determine six organic and inorganic soil P fractions, and also total, labile and residual P. Leaf litterfall P concentrations were determined colorimetrically. Soil inorganic and organic P fractions varied between soil types and across months, but soil type and month interactions were mostly non-significant. Some inorganic P fractions (P_i-NaOH) peaked while the organic fractions (P_o-NaOH) fell and vice versa. Leaf litterfall production and leaf litterfall P input peaked around two months following the wettest month. Leaf litterfall P input was a significant predictor of P_o-$NaHCO_3$, a bioavailable P fraction. Future studies on P cycling in terrestrial ecosystems should examine the roles played by individual soil P fractions as they cycle asynchronistically and differently across soil types.

KEYWORDS: nutrient cycling; leaf litter; tropical soil

Frações de fósforo no solo e sua relação com a serrapilheira em uma floresta de terra firme na Amazônia central

RESUMO

A ciclagem de fósforo (P), mesmo sendo pouco estudada, é importante para o equilíbrio de macronutrientes em ecossistemas de floresta tropical úmida. Como P no solo ocorre em diferentes formas orgânicas e inorgânicas (frações), com diferentes graus de labilidade, supomos que essas frações variam temporalmente entre os diferentes tipos de solo. Além disso, hipotetizamos uma influência direta da serrapilheira no aporte de P no solo. Coletamos amostras de solo e folhas em três tipos de solo em uma floresta tropical na Amazônia central no Brasil durante cinco meses e usamos o método de fracionamento modificado de Hedley para determinar seis frações orgânicas e inorgânicas de P no solo, bem como P total, lábil e residual. As concentrações de P na serrapilheira foram determinadas pelo método de colorimetria. As frações de P inorgânico e orgânico do solo variaram entre os tipos de solo e ao longo dos meses, mas as interações entre tipo de solo e meses foram majoritariamente não significativas. Algumas frações de P inorgânicas (P_i-NaOH) atingiram o pico enquanto as frações orgânicas (P_o-NaOH) caíram e vice-versa. A produção de serrapilheira e a entrada de P atingiram o pico por volta de dois meses após o mês mais chuvoso. A entrada de P da serrapilheira foi um preditor significativo de P_o-NaHCO3, uma fração de P biodisponível. Futuros estudos sobre a ciclagem de P nos ecossistemas devem examinar o papel desempenhado pelas frações individuais de P no solo, à medida que circulam de forma assíncrona e diferente entre tipos de solo.

PALAVRAS-CHAVE: ciclagem de nutriente; serrapilheira; solo tropical

CITE AS: Santos, E.D.A.; Tng, D.Y.P.; Apgaua, D.M.G.; Assunção, R.R.; Manzi, A.O. 2022. Soil phosphorus fractions and their relation to leaf litterfall in a central Amazonian *terra firme* rainforest. *Acta Amazonica* 52: 104-113.

INTRODUCTION

Phosphorus (P) is an essential macronutrient for plant growth and development, and the cycling of P is an important component of global biogeochemical cycles (Wang *et al.* 2010; Reed *et al.* 2015). In a forest ecosystem, for example, the cycling of P involves the uptake of P from the soil by plants, followed by the return of P to the soil in the form of leaf litter, the breakdown of leaf litter by microbial action and the subsequent release of P into the soil (McGrath *et al.* 2000; Mooshammer *et al.* 2012; Prescott and Vesterdal 2021). The input of P from leaf litter and its influence on soil P fractions is an important component of P cycling in tropical forests. Knowledge about how nutrient pulses aboveground are synchronized with nutrient availabiliy and plant strategies belowground can greatly improve our understanding of the dynamics of the nutritional system that underlies forest function (Janssen *et al.* 2021).

Although P is ubiquitous in natural systems, it is considered a limiting nutrient in most tropical soils, which are typically highly weathered (Lambers *et al.* 2008; Turner 2008). Essentially, soil P may be divided into inorganic P (Pi) which is primarily derived from weathering of primary minerals, and organic P (Po) which comes from the deposition of organic matter (Smeck 1985; Rheinheimer *et al.* 2000). Both Pi and Po can be further broken down into subcategories or fractions of P which vary in their bioavailability (Vance *et al.* 2003). However, the P-cycle is poorly represented in most global biogeochemical models, one reason being the limited data available on the dynamics of different P fractions (Wang *et al.* 2010; Reed *et al.* 2015).

Different soil types are known to vary in relative content of P forms, but the extent of this variation is poorly known, especially in tropical forest ecosystems (Quesada *et al.* 2010; Ahmed *et al.* 2018). In tropical forests, soils can vary drastically in texture and composition across short distances (e.g. at plot level) due to differences in parent material, topography and drainage (Quesada *et al.* 2011). Moreover, since the decomposition rate of organic matter can also vary across soil types (Van Veen and Kuikman 1990), it is important to understand the short-term temporal changes in the concentration of organic and inorganic fractions of P across soil types.

As tropical soils vary in their physical and chemical properties, we hypothsized that P fractions vary among soil types and with time and that there is a close coupling of leaf litterfall P input with the concentration of soil P fractions. To test these hypotheses, we analyzed the temporal changes in six P forms defined through P fractionation methods and their relation with leaf litter P input in three soil types in a central Amazonian forest.

MATERIAL AND METHODS

Study area

The study was conducted in the Adolpho Ducke Forest Reserve (59°52'40"–59°58'00"W; 03°00'00"–03°08'00"S), located 25 km from the city of Manaus, Amazonas state, Brazil. The vegetation in the reserve is predominantly undisturbed lowland *terra firme* rainforest (Sotta *et al.* 2004). The forest canopy is about 35 to 40 m high, with few emergent trees from 40 to 45 m high (Ribeiro *et al.* 1999). The climate in the region is humid tropical, with an annual precipitation of 1800-2800 mm (Leopoldo *et al.* 1987), a rainy season from December to May and a dry season from June to November. The rainiest months are between March and April (monthly average > 300 mm of rain) and the driest between July and September (monthly average <100 mm). The average annual temperature is 26 ºC with minimum and maximum temperatures of 19 ºC to 39 °C, respectively. The isothermal temperature condition is a high relative humidity range of 77-88%, with an annual average of 84% (Leopoldo *et al.* 1987). The altitude of the study area ranges from 50-110 m a.s.l.

Sediments found in this region have their origin in the Tertiary-Cretaceous period (~ 100 Mya) (Quesada *et al.* 2011). The Adolpho Ducke Forest Reserve encompasses a range of geomorphologies and comprises a sedimentary plain dissected by a network of drainage systems, resulting in a mosaic of plateaus, rounded top hills, and valleys with convex slopes. In terms of soil types, acrisols and ferralsols are clayey soils that prevail on hill slopes and plateaus, respectively (Quesada *et al.* 2010, 2011; Table 1), and are derived from weathering of kaolinitic materials derived from the ancient Guiana Shield in the Tertiary era (Hammond 2005). Podsols predominate in the valleys, and are typified by dark grey hydromorphic soils with

Table 1. Characteristics of sampling plots for three soil types and leaf litter in a *terra firme* rainforest in the central Amazon in Brazil, and particle size distribution in a composite sample of five subsamples of 0-5-cm top soil from each plot.

Soil type	Topographic position	Altitude (m)	Drainage	Particle size distribution (%)		
				Sand	Silt	Clay
Acrisol	Hill slope	82	Good	32.1	7.4	54.5
Ferralsol	Plateau	99	Good	10.8	9.5	79.7
Podsol	Valley	62	Poor	94.3	0.1	5.5

sandy texture (Hammond 2005; Table 1). Soil nomenclature follows the IUSS Working Group WRB (2015).

Soil and litterfall sampling

We used a 25-km² (5 x 5 km) trail grid forming 25 1-km² grid cells established by the Research Program on Biodiversity (www.ppbio.inpa.gov.br). The grid was set up as a long-term ecological research site (see Magnusson *et al.* 2005 for more details). Within the grid, 25 standard sampling plots are installed at 1-km intervals along the east-west trails. Each plot consists of a 125-m central transect that follows the slope gradient line of the terrain. We chose three sampling plots, one on a "plateau" (ferralsol), one on a slope (acrisol) and one in a valley (podsol) located in three adjacent grid cells. In each of these plots, we sampled soil and leaf litter at five points (n = 5 per plot) at 25-m intervals along the 125-m transect. We only had resources to sample soil and litterfall for a 5-month period, therefore we decided to conduct our field sampling from April to August 2012, as this period encompassed the transition from the wet to the dry season.

To test how leaf litterfall P input affects soil P, it was necessary for our individual soil samples to be coupled with our litterfall collection. To accomplish this, in March 2012 we installed five leaf litter traps in each plot (15 traps in total, each with an area 0.25 m²). Each trap consisted of four PVC pipes (20 cm diameter) forming the corners of a 0.6 m x 0.4 m area and a shade cloth net (1-mm nylon mesh) affixed on the top of the stakes to form a leaf litter collecting basket suspended 0.6 m above the ground to avoid contamination by soil. The traps were installed along the 125-m transects at 25-m intervals. Leaf litterfall intercepted by the traps was collected monthly from April to August 2012 and processed in the laboratory. We classified and sorted the litter debris into three components (leaves, reproductive material, and branches), but, for our purposes, we used only the leaf component. After removing dust or litter residues using a brush, the leaves were oven-dried at 60 °C for 72 hours and weighed.

Because we were interested in examining how litterfall P would influence P in the top mineral layer of soil, we collected surface soil samples to a depth of 5 cm on the west side of each litterfall trap (5 soil samples per plot, per month – 25 samples in total) using an auger (Eijkelkamp Agrisearch Equipment BV, Giesneek, Netherlands). This was done after first sweeping away the organic layer. The soil samples were then air-dried and sieved through a 2-mm pore size sieve before analysis. Soil particle size classes were determined for the first collection month (April) using compound samples of the replicates within each plot (thus soil type), using the pipette method (Gee and Bauder 1986).

Soil and leaf P analysis

We used the sequential P fractionation method developed by Hedley *et al.* (1982) and modified by Tiessen and Moir (1993) to obtain P fractions for each soil sample, based on the chemical solubility and increasingly stronger extraction solutions. We estimated inorganic P (P_i) by fractionation into P-resin, P_i-bicarbonate (henceforth Pi-$NaHCO_3$), P_i-NaOH, and P-HCl following Hedley *et al.* (1982) and Rheinheimer *et al.* (2000). These respective P_i forms were sequentially extracted by the following extractants: anion exchange resin (AER) (AR 103 QDP 434 Ionics Inc.), $NaHCO_3$ 0.5 mol L^{-1} at pH 8.5, 0.1 mol L^{-1} NaOH, and 1.0 mol L^{-1} HCl. Organic P (P_o) was determined after digesting the extracts for organic P release with 0.9 M H_2SO_4 and ammonium persulfate. We extracted the bicarbonate and hydroxide organic P fractions P_o-bicarbonate (henceforth P_o-$NaHCO_3$) and P_o-NaOH. Total P (P-Total) was determined as part of the sequential P fractionation method through a process of extraction in concentrated H_2SO_4 + H_2O_2 (Tiessen and Moir, 1993). Labile P (P-Labile) was calculated as the sum of the fractions of P-resin, P_i-$NaHCO_3$, and P_o-$NaHCO_3$. Finally, the residual P (P-Residual) was determined by the difference between the P-Total and the sum of all the aforementioned inorganic and organic P fractions (Quesada *et al.* 2010).

To relate soil P with leaf litterfall attributes, we first calculated and extrapolated the leaf litter production per hectare (kg ha^{-1} day^{-1}) for each sampling in each soil type. Next, we obtained the P concentration from the leaf litter samples collected for each sampling period (mg g^{-1}). The dried leaf litter samples were weighed and then crushed into a fine powder using a laboratory mill (Thomas-Wiley Mini-Mill 3383-L10; Thomas Scientific, Swedesboro, NJ, US). We then weighed 100 mg of ground leaf litter powder, digested it with HNO_3 + $HClO_4$, and determined the P concentration in the digested solution colorimetrically using the molybdate–ascorbic acid method (Olsen and Sommers 1982). Finally, we calculated the leaf litter P input into the soil (kg ha^{-1}) for each month as a product of leaf litterfall production and its P concentration. All leaf litter and soil samples were processed, analyzed and deposited in the collection of the Laboratory of Soils and Plants at Instituto Nacional de Pesquisas da Amazônia (INPA).

Data analysis

The data of each P-fraction (mg kg^{-1}) are reported as the mean and standard deviation of five samples for each soil type and across the five month, and as the mean percentage relative to the soil P-Total. Due to unforeseen circumstances, the data for P-Total and P-Residual of our podsol soil samples in August were lost. Therefore, we analyzed and presented podsol P-Total and P-Residual data only for April to July. We used repeated-measures ANOVAs with soil type and month as factors to examine differences in P fractions between sites and months. All variables had non-normal distribution according to Shapiro-Wilk tests ($p < 0.05$), and were log-transformed to improve normality. When an ANOVA was significant for soil type and/or time, we used post-hoc Tukey HSD tests

(significance level α = 95%). All ANOVA analyses were performed in SPSS (Version 20; IBM Corp 2011).

Finally, because we were interested in testing how overall P input from leaf litterfall influences soil P attributes, we fitted linear mixed effects models to the data of each soil P fraction as response variable, and litterfall P input and soil type as fixed effects, and collection month as a random effect. All linear mixed effects models were fitted using the nlme package (Pinheiro *et al.* 2021) in the R statistical software (R Foundation for Statistical Computing, Vienna, AT; http://www.R-project.org/).

RESULTS

Soil particle size

In general, we found a wide textural gradient among soil types. The ferralsol (plateau) compound sample had the highest clay content (79.7%), followed by the acrisol (slope) (54.5%). In contrast, the podsol (valley) had very low clay content (5.5%), but the highest sand content (Table 1).

Phosphorus fractionation

Phosphorus fractions exhibited different patterns across soil types (Table 2). The overall mean P-Total over the five months was lowest in the podsol, intermediate in the acrisol, and highest in the ferralsol (Table 2). Non-labile P-Residual was the largest P-fraction and represented the largest proportion of P-Total in the three soil types, with the highest concentration in the ferrasol. The acrisol had approximately 1.5 times, and the ferralsol two times more P-Labile than the podsol (Table 2).

The inorganic fractions (excluding P-Residual) comprised less than 35% of P-Total. As expected, the contribution of P-Labile to the P-Total in the acrisol and the ferralsol was low (14.5% and 13.7% respectively), but in the podsol, P-Labile constituted approximately 27.8% of P-Total (Table 2). The P-HCl concentration was low in all soil types but was comparatively higher in the podsol (up to 3.1%). In the ferralsol and the podsol, P_o-NaOH occurred in higher concentration than its inorganic counterpart, and represented the second largest proportion of P-Total in all soil types (Table 2).

Variation in soil phosphorus fractions

Repeated measures ANOVA showed that soil type was a significant factor explaining most of the variation in P fractions, P-Labile, P-Residual and P-Total (Table 3; Figure 1). The month of collection was also a significant factor for concentrations of P-HCl, P_i-NaHCO, P_i-NaOH, and P_o-NaOH, but not for P-resin, P_o-$NaHCO_3$, P-Labile, P-Residual and P-Total (Tables 3 and 4). We found significant soil type and month interaction only for P-HCl ($F = 37.42$, $p < 0.001$; Table 3). The P-resin fraction varied conspicuously among soil types, with significant difference between acrisol and podsol, and ferralsol and podsols (Table 3; Figure 1a). The P_i- $NaHCO_3$ fraction did not vary significantly among soil types (Table 3; Figure 1b), but varied significantly through time, decreasing in concentration from April to May (Table 4; Figure 1b). P_i-NaOH conentrations were significantly higher in acrisol and ferralsol than in podsol, but did not differ significantly between acrisol and ferralsol (Table 3; Figure 1c). This P fraction also varied significantly among months, decreasing from May to July (Table 4; Figure 1c). P-HCl

Table 2. Phosphorus (P) fraction concentrations (mg kg^{-1}) within samples of three soil types in a *terra firme* rainforest in the central Amazon in Brazil. % P-Total = mean percentage of each fraction relative to the P-Total concentration. The values are the mean ± standard deviation of five composite samples (one sample per month from April to August, except P-Total and P-Residual of podsol, which are based on four samples from April to July) (see Material and Methods for details). Lowercase letters denote significant differences between soil types according to Tukey's post-hoc tests using data from April to August (to July for P-Total and P-Residual). See Table 4 for significant differences between months for each soil fraction within each soil type.

P-fraction	Acrisol	% P-Total	Ferralsol	% P-Total	Podsol	% P-Total
Inorganic						
P-resin	9.59 ± 0.82 a	8.9%	11.92 ± 1.08 b	7.7%	3.74 ± 0.42 c	11.1%
P_i-$NaHCO_3$	3.53 ± 1.80 a	3.4%	3.62 ± 1.53 a	2.5%	3.26 ± 1.47 a	9. 9%
P_i-NaOH	13.82 ± 4.65 a	14.6%	17.41 ± 5.16 b	12.1%	4.50 ± 2.29 c	13.6%
P-HCl	1.96 ± 0.7 a	1.7%	2.37 ± 0.86 b	1.4%	1.49 ± 1.12 c	3.1%
Organic						
P_o-$NaHCO_3$	2.44 ± 1.24 a	2.2%	4.75 ± 3.65 b	3.5%	2.4 ± 0.80 b	6.8%
P_o-NaOH	14.22 ±7.33 a	12.0%	21.70 ± 10.56 b	13.3%	8.26 ± 4.43 c	20.8%
Overall						
#P-Total	105.25 ± 8.68 a	NA	152.04 ± 2.79 b	NA	27.79 ± 3.92 c	NA
#P-Residual	59.69 ± 13.73 a	57.4%	90.26 ± 7.83 b	59.6%	10.20 ± 5.02 c	34.6%
P-Labile	15.55 ± 3.15 a	14.5%	20.29 ± 5.40 b	13.7%	9.40 ± 2.40 c	27.8%

Table 3. F-statistics and *p*-values (in parentheses) of repeated-measures ANOVA for the effect of soil type and sampling month on soil phosphorus (P) fractions in three soil types (acrisol, ferralsol and podsol) and leaf litter parameters in samples from a *terra firme* rainforest in the central Amazon in Brazil. Analyses are based on five samples per soil type from each of five months (April to August), except P-Total and P-Residual, which are based on four months (April to July) (see Materials and Methods for details). Degrees of freedom = 2, 12 in all cases. Significant statistics are in bold.

P-fraction	Soil type	Month	Soil type x month
Inorganic			
P-resin	**100.87 (< 0.001)**	3.92 (0.071)	0.03 (0.974)
P_i-$NaHCO_3$	0.448 (0.649)	**8.42 (0.013)**	2.62 (0.110)
P_i-NaOH	**93.66 (< 0.001)**	**26.99 (< 0.001)**	0.30 (0.746)
P-HCl	**37.42 (< 0.001)**	**329.86 (< 0.001)**	**21.36 (< 0.001)**
Organic			
P_o-$NaHCO_3$	**182.87 (< 0.001)**	1.79 (0.206)	1.04 (0.385)
P_o-NaOH	**30.04 (< 0.001)**	**30.72 (<0.001)**	1.16 (0.346)
Overall			
P-Total	**172.51 (< 0.001)**	2.38 (0.149)	0.57 (0.582)
P-Residual	**169.00 (< 0.001)**	3.76 (0.076)	1.33 (0.290)
P-Labile	**62.17 (< 0.001)**	0.179 (0.680)	0.37 (0.697)
Leaf litter			
Dry mass	**4.89 (0.028)**	**50.35 (< 0.001)**	**8.30 (0.005)**
Leaf P	1.22 (0.329)	0.45 (0.517)	0.94 (0.418)
Leaf P input	4.573 (0.172)	**14.54 (0.002)**	1.13 (0.356)

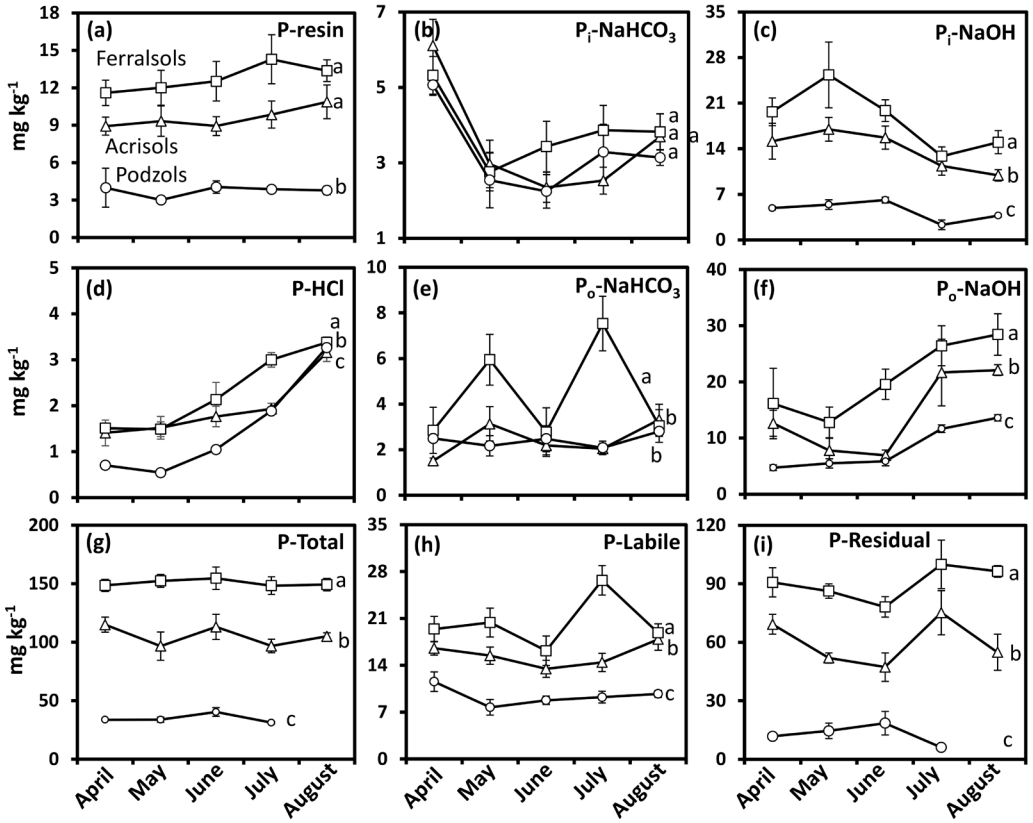

Figure 1. Monthly means of soil phosphorus (P) fractions in surface soil of three sampling plots representing three soil types in a central Amazon *terra firme* rainforest in Brazil. Soil types are acrisol (triangles), ferrasol (squares) and podsol (circles). Inorganic P fractions: P-resin (A); P_i-$NaHCO_3$ (B); P_i-NaOH (C); and; P-HCl (D). Organic P fractions: P_o-$NaHCO_3$ (E); P_o-NaOH (F). Overall soil fractions: P-Total (G); P-Labile (H); P-Residual (I). Error bars denote the standard error.

Table 4. Monthly phosphorus fraction concentrations (mg kg^{-1}) and leaf litterfall attributes for three soil types in a *terra firme* rainforest in the central Brazilian Amazon. Only attributes that varied significantly among months are shown (see Table 3). Values are the mean ± standard deviation of five sub-samples along a 125-m transect (see Material and Methods for details). The lowercase letters indicate significant differences between months within each attribute according to a Tuckey test. See Figures 1 and 2, respectively, for monthly variation in all soil P and leaf litter attributes.

Attribute	Collection month				
	April	May	June	July	August
Acrisol					
P_i-$NaHCO_3$	6.11 ± 1.55 a	2.97 ± 1.41 bc	2.35 ± 0.90 bc	2.53 ± 0.80 b	3.69 ± 1.37 ac
P_i-NaOH	15.15 ± 6.16 ab	16.98 ± 4.06 b	15.71 ± 3.98 ab	11.36 ± 3.17 ab	9.92 ± 1.95 b
P-HCl	1.41 ± 0.62 a	1.52 ± 0.55 a	1.77 ± 0.50 a	1.93 ± 0.27 ab	3.16 ± 0.43b
P_o-NaOH	2.85 ± 2.26 ab	5.94 ± 2.49 a	2.77 ± 2.39 a	7.53 ± 2.67 ab	3.04 ± 1.60 b
Leaf dry mass	4.88 ± 1.16 ab	9.19 ± 4.18 b	11.40 ± 8.05 b	10.76 ± 2.07 c	12.11 ± 5.22 d
Leaf P input	0.82 ± 0.21 a	2.13 ± 1.09 b	3.28 ± 1.80 c	2.95 ± 0.84 c	5.14 ± 1.27 c
Ferralsol					
P_i-$NaHCO_3$	5.32 ± 1.12 a	2.76 ± 1.12 bc	3.43 ± 1.49 a	3.87 ± 1.47 c	3.82 ± 1.08 a
P_i-NaOH	19.68 ± 4.75 a	25.34 ± 11.27 ab	19.87 ± 3.7 ab	12.86 ± 3.18 b	14.99 ± 3.97 ab
P-HCl	1.51 ± 0.25 a	1.49 ± 0.36 ab	2.14 ± 0.83 b	3.00 ± 0.35 c	3.38 ± 0.27 c
Leaf dry mass	7.3 ± 2.07 ab	9.32 ± 4.34 abc	12.97 ± 4.46 bc	25.75 ± 12.40 cd	26.45 ± 13.68 d
Leaf P input	1.50 ± 0.68 a	1.80 ± 0.63 ab	3.17 ± 1.11 ab	8.99 ± 5.90 b	6.07 ± 4.48 ab
Podsol					
P_i-$NaHCO_3$	5.07 ± 0.62 a	2.54 ± 1.64 bc	2.24 ± 0.99 bc	3.29 ± 1.64 ac	3.14 ± 0.47 ac
P_i-NaOH	4.89 ± 2.88 ab	5.43 ± 2.81 ab	6.13 ± 1.36 a	2.32 ± 1.26 b	3.74 ± 0.69 ab
P-HCl	0.70 ± 0.19 ab	0.54 ± 0.19 a	1.05 ± 0.32 b	1.89 ± 0.17 c	3.27 ± 0.65 d
P_o-NaOH	4.72 ± 1.92 ab	5.49 ± 3.20 b	5.86 ± 3.14 b	11.65 ± 2.63 b	13.60 ± 2.25 c

concentrations varied significantly between acrisol and podsol, and between ferralsol and podsol, but not between acrisol and ferralsol (Table 3; Figure 1d). Overall, P-HCl concentrations increased significantly towards the dry season months (July and August) in all soil types (Table 4; Figure 1d).

Regarding organic P, the P_o-$NaHCO_3$ fraction varied significantly between acrisol and ferralsol (Table 3; Figure 1e). P_o-NaOH varied significantly among all soil types (Table 3; Figure 1f), increasing significantly towards the dry season months in acrisol and podsol (Table 4; Figure 1f).

P-Total varied among all soil types ($F = 172.51$, $p < 0.001$; all Tukey tests $p < 0.001$), but did not vary significantly through time (Table 3; Figure 1g). The same was observed for P-Labile ($F = 160.82$, $p < 0.001$; all Tukey tests $p < 0.001$) (Figure 1h) and P-Residual ($F = 169.00$, $p < 0.001$) (Table 3; Figure 1i) (Table 3).

Variation in leaf litterfall attributes

Repeated measures ANOVA showed that soil type was a significant factor determining leaf litterfall total dry mass ($F = 4.89$, $p = 0.028$; Table 3), but only acrisol and podsol differed significantly (Tukey test, $p = 0.046$; Figure 2a). Leaf litterfall P did not vary significantly among soil types or months (Table 3; Figure 2b). However, P input into the soil based on leaf litterfall P and leaf litter production per hectare varied among soil types ($F = 4.57$, $p > 0.001$) and months ($F = 1.13$, $p = 0.002$; Table 3; Figure 2c), with significant differences between acrisol and podsol (Tukey test, $p = 0.037$).

As expected, leaf litterfall total dry mass increased at the start of the dry season in June (Figure 2a), but this increase was only significant between May and June for acrisol, and between June and July for ferralsol (Table 4; Figure 2a). In the podsol, mean litterfall total dry mass appeared to increase in July, but the variation among months was not significant (Figure 2a).

Leaf litterfall P input to the soil varied significantly over the study period (Figure 2c), in tandem with the higher input of litter (Figure 2a) in the drier months (Table 4). These changes were most noticeable in August, when there was a drop in leaf litterfall P input to the ferralsol (Figure 2c). In the podsol however, the variation among months was not significant (Figure 2c). The linear mixed effects models showed that only P_o-$NaHCO_3$ was significantly explained by leaf litterfall P input, in addition to soil type effects (Table 5).

DISCUSSION

Overall, our soil P concentrations were typical for the geomorphological characteristics and highly weathered soils of the study area (McGroddy *et al.* 2008; Quesada *et al.*

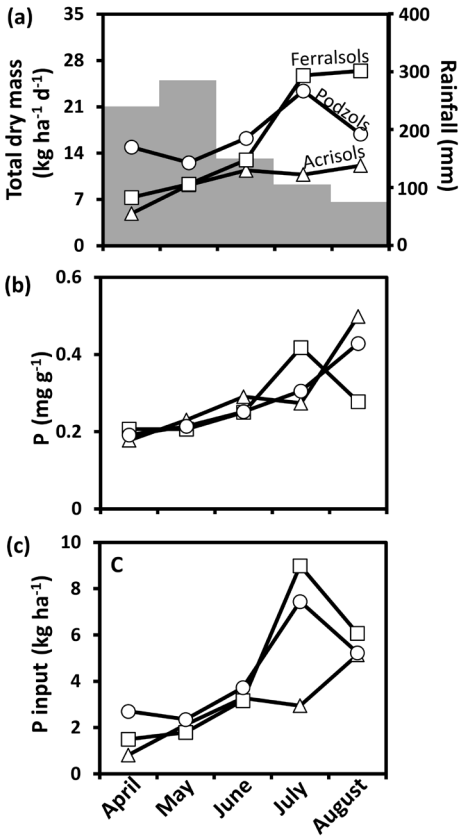

Figure 2. Monthly means of attributes of leaf litter sampled in a *terra firme* central Amazonian rainforest in Brazil in three soil types: acrisol (triangles), ferralsol (squares), and podsol (circles). A - monthly leaf litter production (lines) and rainfall (grey bars); B - P in the leaf litterfall; C - P input into the soil. Error bars denote the standard error. Different lowercase letters indicate significant differences between soil types according to Tukey's post-hoc tests using data from April to August. See Table 4 for significant differences between months for each soil fraction within each soil type.

2010), and fall within the range of soil P concentrations found in other parts of the Amazon (Rückamp *et al.* 2010; Costa *et al.* 2017). As expected, the podsol had very low P concentrations, since these soils are dominated by a very poor source material (quartz), and possess low charge density on the surface particles, and hence low P adsorption capacity (Cross and Schlesinger 1995). The ferralsol and acrisol in this region, on the other hand, have a high concentration of clay and Fe and Al oxides, as well as a large P adsorption capacity, which can reduce P bioavailability, but enable higher maintenance of P circulation in these soils (Cross and Schlesinger 1995).

Temporal variations in soil P fractions

Inorganic and organic phosphorus levels in forest soils are expected to change across seasons (Fabre *et al.* 1996; Chen *et al.* 2003; Schaap *et al.* 2021). Concordantly, we found a clear and significant temporal variation in some P fractions over the five months of study, in particular the inorganic and organic P-NaOH forms and P-HCl. Several studies have reported that P-NaOH and P-HCl forms can release large amounts of available P (Trolove *et al.* 1996; Bertrand *et al.* 1999), and others reported processing and use of these P forms in soils (Guo and Yost 1998; Nziguheba and Bünemann 2005).

In agreement with Turner and Engelbrecht (2011), we found that organic P made up a substantial component of the soil P. In highly weathered soils such as those of our study sites, organic P is also the major form of P involved in P cycling (Tiessen *et al.* 1984; Turner *et al.* 2015). In such soils, P dynamics is driven mainly by organic P transformation to inorganic fractions (Reed *et al.* 2015). Notably, the inverse relationship between P_i-NaOH and P_o-NaOH suggests a strong mechanistic relation between inorganic and organic P in the soil, which may be mediated by microbial and plant

Table 5. Parameter estimates and random effect standard deviation (SD) for linear mixed effects models fitting phosphorus (P) fraction responses to leaf litter P input and soil type (acrisol, ferralsol, podsol) as fixed effects and collection month as a random effect. Analyses are based on five subsamples per soil type from each of five months (April to August), except P-Total and P-Residual for podsol, which are based on four months (April to July). Significant effects are marked in bold.

P fraction	Intercept	Leaf litterfall P input	Ferralsol	Podsol	Random effect (month) SD
Inorganic					
P-resin	**21.838 (< 0.001)**	0.017 (0.060)	**0.193 (0.016)**	**-10.002 (< 0.001)**	0.274
P_i-$NaHCO_3$	**10.878 (< 0.001)**	0.019 (0.207)	0.032 (0.772)	-0.100 (0.375)	0.379
P_i-NaOH	**26.138 (< 0.001)**	-0.014 (0.339)	**0.259 (0.015)**	**-11.968 (< 0.001)**	0.363
P-HCl	**0.585 (0.010)**	-0.003 (0.796)	0.185 (0.053)	**-4.802 (<0.001)**	0.327
Organic					
P_o-$NaHCO_3$	**0.602 (< 0.001)**	**0.051 (0.025)**	**0.411 (0.023)**	-0.011 (0.950)	0.615
P_o-NaOH	**23.984 (< 0.001)**	-0.009 (0.670)	**0.534 (< 0.001)**	**-0.505 (0.001)**	0.523
Overall					
P-Total	**4.641 (< 0.001)**	-0.002 (0.811)	**0.387 (< 0.001)**	**-1.110 (< 0.001)**	0.178
P-Labile	**3.728 (< 0.001)**	0.008 (0.220)	**0.353 (< 0.001)**	**-0.623 (< 0.001)**	0.177
P-Residual	**4.132 (< 0.001)**	-0.024 (0.225)	**0.447 (0.003)**	**-1.692 (< 0.001)**	0.441

action (Richardson *et al.* 2005). Since plants can only absorb inorganic orthophosphate (Raghothama 2005), mobilizing P_o forms first involves the liberation of P_o from precipitates and adsorption sites, followed by the mineralization of these P_o forms into plant available P_i through the action of phosphatase enzymes (Richardson *et al.* 2005; Clarholm *et al.* 2015; Schaap *et al.* 2021). However, P_i-NaOH can also be an important source of inorganic P in the P cycle, and may transfer a significant amount of P to other fractions or be taken up by plant roots in the form as orthophosphates. In fertilized and unfertilized cultivated plots in the Peruvian Amazon, P_i-NaOH in the fertilized plots released P quickly and maintained an adequate level of availability over time, while in the unfertilized plots the main source of P used by plants was organic P derived from organic matter (Beck and Sanchez 1994).

The other labile inorganic P form, P-HCl, despite being present in small amounts, varied significantly among soil types and months. Low concentrations of P-HCl are typical in highly weathered tropical soils, since virtually all of this P form is associated with soil matrix material (Smeck 1985). Because P-HCl is calcium-bound and calcium is a structural element in the leaves, we speculate that the increase in the P-HCl fraction concomitantly with litterfall input may be due to a P complexation process with Ca in the soil.

Another relevant point in terms of temporal variation in soil P is microbial activity. Soil microbes are known to be sensitive to P concentrations (Fanin *et al.* 2014), and declines in soil organic P have been correlated with declines in soil microbial biomass during the dry season (Chen *et al.* 2003; Turner *et al.* 2015). This may explain some of the declines in P_o-$NaHCO_3$ and P_o-NaOH levels in our ferralsol and acrisol sites during the drop in monthly rainfall in June, although extended studies are required to establish clearer trends. We also speculate that differential microbial action on different soil P fractions may be a reason for the temporal variation in P fractions. Microbial community variation across soil types may help explain differential temporal variation of soil P fractions accross soil types.

Litterfall input and P fractions

We found that only the organic P_o-$NaHCO_3$ fraction was significantly influenced by leaf litter P input, which may be expected given that leaf litter is the main source of organic P (Vicent *et al.* 2010; Wright *et al.* 2011). It is likely that the organic P fractions respond fastest to P input. For example, the P_o-$NaHCO_3$ fraction increased strongly after experimental leaf litter addition to forest soils (Mirabello *et al.* 2013). In another study, soil P_o-NaOH in a forest soil increased one month after experimental leaf litter addition (Kunito *et al.* 2018).

Seasonality may be another factor affecting soil P fractions (Schaap *et al.* 2021). In central Amazonian forests, leaf litter production was highest during the drier period of the year, mainly from June to October (Luizão and Schubart 1987), and our results on leaf litterfall production are in line with these observations. However, decomposition processes were more accentuated in the wet season (Luizão and Schubart 1987; Schaap *et al.* 2021), which suggests that the greatest extent of leaf litter P release into the soil takes place during the wet season. Indeed, seasonal microbial activity plays an important role in the conversion of leaf litter P into soil P fractions (Turner *et al.* 2013, 2015; Prescott and Vesterdal 2021). Increased input of leaf litter can lead to the proliferation of microbes, but, as our study was ended partway into the dry season, it is likely that soil microbial biomass was still low (e.g. Turner *et al.* 2015). Moreover, it is possible that plants may preferentially use inorganic or organic P at different times of the year, perhaps due to mycorrhizal activity (Bolan 1991) or as a result of resource partitioning of soil P by co-existing tree species (Turner 2008; Mayor *et al.* 2014). Studies combining spectroscopic and isotopic labelling (Helfenstein *et al.* 2018) could allow further clarification of the conversion pathways of leaf litter P to soil P fractions.

As a step towards greater representation of P cycling in biogeochemical models, future studies characterizing P fractions in different terrestrial ecosystems could be helpful, particularly if conducted alongside measurements of factors known to influence P mineralization and uptake such as decomposition, phosphatase activity and mycorrhizal colonization. Additionally, it may be instructive to concurrently examine aspects of nitrogen cycling, as it has been suggested that N and P cycles are closely coupled across terrestrial ecosystems (Marklein and Houlton 2012).

CONCLUSIONS

We found temporal variations in P fractions in different soil types within a central Amazonian *terra firme* rainforest, and that the changes in some organic and inorganic P fractions appeared to be asynchronous over the five-month study period. Leaf litterfall production, and the corresponding leaf litterfall P input do appear to influence peaks in individual soil P fractions, but the mechanism by which this occurs requires further investigation. Particularly, investigations on longer-term leaf litterfall dynamics can be useful in elucidating these trends and understanding the productivity of these forests. The role of soil microbes, soil invertebrate activity, different tree species, and in particular species with a high leaf production or with different mechanisms of P utilization (e.g. Inagaki and Ishizuka 2011) as contributors to the pool of leaf litter may be worthy of further study.

ACKNOWLEDGMENTS

We thank Beto Quesada for his comments on previous versions of the manuscript. The research was supported by a scholarship from Conselho Nacional de Desenvolvimento

Científico e Tecnológico (CNPq) awarded to Emily Darc Andrade dos Santos.

REFERENCES

Ahmed, A.W.A.M.; Elsheikh, M.A.; El Mahi, Y.E.G. 2018. Relationship between phosphorus fractions of some selected Sudanese soil orders to phosphate availability. *Eurasian Journal Soil Science,* 7: 224–229.

Beck, M.A.; Sanchez, P.A. 1994. Soil phosphorus fraction dynamics during 18 years of cultivation on atypic paleudult. *Soil Science Society of America Journal,* 58: 1424–1431.

Bertrand, I.; Hinsinger, P.; Jaillard, B.; Arvieu, J.C. 1999. Dynamics of Phosphorus in the rhizhosphere of maize and rape grown on synthetic, phosphate calcite and goethite. *Plant Soil,* 211: 111–119.

Bolan, N.S. 1991. A critical review on the role of mycorrhizal fungi in the uptake of phosphorus by plants. *Plant Soil,* 134: 189–207.

Chauvel, A.; Lucas, Y.; Boulet R. 1987. On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. *Experientia,* 43: 234–241.

Chen, C.R.; Condron, L.M.; Davis, M.R.; Sherlock, R.R. 2003. Seasonal changes in soil phosphorus and associated microbial properties under adjacent grassland and forest in New Zealand. *Forest Ecology and Management,* 177: 539-557.

Clarholm, M.; Skyllberg, U.; Rosling, A. 2015. Organic acid induced release of nutrients from metal-stabilized soil organic matter -the unbutton model. *Soil Biology and Biochemistry,* 84: 168–176.

Costa, A.D.R.; Silva Júnior, M.L.; Kern, D.C.; Ruivo, M.D.L.P.; Marichal, R. 2017. Forms of soil organic phosphorus at black earth sites in the Eastern Amazon. *Revista Ciência Agronomônica,* 48: 1–12.

Cross, A.F.; Schlesinger, W.H. 1995. A literature review and evaluation of the Hedley fractionation: Applications to the biogeochemical cycle of soil phosphorus in natural ecosystems. *Geoderma,* 64: 197–214.

Fanin N.; Hättenschwiler, S.; Schimann, H.; Fromin, N. 2014. Interactive effects of C, N and P fertilization on soil microbial community structure and function in an Amazonian rain forest. *Functional Ecology,* 29: 140–150.

Fabre, A.; Pinay, G.; Ruffinoni, C. 1996. Seasonal changes in inorganic and organic phosphorus in the soil of a riparian forest. *Biogeochemistry,* 35: 419–432.

Gee, G.W.; Bauder, J.W. 1986. Particle-size Analysis. In: Klute, A. (Ed.). *Methods of Soil Analysis Part 1*. Soil Science Society of America Book Series 5, Madison, Wisconsin, USA, p.383-411.

Guo F.; Yost, R.S. 1998. Partitioning soil phosphorus in to three discrete pools of differing availability 1. *Soil Scienc,* 163: 822–833.

Hammond, D.S. 2005. Biophysical features of the Guiana Shield. In: Hammond, D.S. (Ed.). *Tropical Forests of the Guinea Shield. Ancient Forests in a Modern World*. CABI, Wallingford, p.15–194.

Hedley, M.J.; Stewart, J.W.B.; Chauhan, B.S. 1982. Changes in inorganic and organic soil phosphorus fractions induced by cultivation practices and by laboratory incubations. *Soil Science Society America Journal,* 46: 970–976.

Helfenstein, J.; Tamburini, F.; von Sperber, C.; Massey, M.S.; Pistocchi, C.; Chadwick, O.A.; *et al.* 2018. Combining spectroscopic and isotopic techniques gives a dynamic view of phosphorus cycling in soil. *Nature Communications,* 9: 3226.

IBM Corp. 2011. IBM SPSS Statistics for Windows, Version 20.0. IBM Corp, Armonk, NY.

Inagaki, M.; Ishizuka, S. 2011. Ecological impact on nitrogen and phosphorus cycling of a widespread fast-growing leguminous tropical forest plantation tree species, *Acacia mangium*. *Diversity,* 3: 712–720.

IUSS Working Group WRB. 2015. World Reference Base for Soil Resources 2014, update 2015 International soil classification system for naming soils and creating legends for soil maps. World Soil Resources Reports No. 106. FAO, Rome.

Janssen, T.; van der Velde, Y.; Hofhansl, F.; Luyssaert, S.; Naudts, K.; Driessen, B.; Fleischer, K.; Dolman, H. 2021. Drought effects on leaf fall, leaf flushing and stem growth in the Amazon forest: reconciling remote sensing data and field observations. *Biogeosciences*, 18: 4445–4472.

Kunito, T.; Hiruta, N.; Miyagishi, Y.; Sumi, H.; Moro, H. 2018. Changes in phosphorus fractions caused by increased microbial activity in forest soil in a short-term incubation study. *Chemical Speciation Bioavailability,* 3: 9–13.

Lambers, H.; Raven, J.A.; Shaver, G.R.; Smith, S.E. 2008. Plant nutrient-acquisition strategies change with soil age. *Trends Ecology Evolution,* 23: 95–103.

Leopoldo, P.R.; Franken, W.; Salati, E.; Ribeiro, M.N.G. 1987. Towards a water balance in Central Amazonian region. *Experientia,* 43: 222–233.

Luizão, F.J.; Schubart, H.O.R. 1987. Litter production and decomposition in a terra-firme forest of Central Amazonia. *Experientia,* 43: 259–265.

Magnusson, W.E.; Lima, A.P.; Luizão, R.; Luizão, F.; Costa, F.R.C.; Castilho, C.V.; Kinupp, V. F. 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. *Biota Neotropica,* 5:19–24.

Marklein, A.R.; Houlton, B.Z. 2012. Nitrogen inputs accelerate phosphorus cycling rates across a wide variety of terrestrial ecosystems. *New Phytologist,* 193: 696–704.

Mayor, J.R.; Wright, S.J.; Turner, B.L. 2014. Species-specific responses of foliar nutrients to long-term nitrogen and phosphorus additions in a lowland tropical forest. *Journal of Ecology,* 102: 36–44.

McGrath, D.A.; Comerford, N.B.; Duryea, M.L. 2000. Litter dynamics and monthly fluctuations in soil phosphorus availability in an Amazonian agroforest. *Forest Ecology and Management,* 131: 167–181.

McGroddy, M.E.; Silver W.L.; de Oliveira Jr., R.C.; de Mello, W.Z.; Keller, M. 2008. Retention of phosphorus in highly weathered soils under a lowland Amazonian forest ecosystem. *Journal of Geophysical Research,* 113: g04012.

Mirabello, M.J.; Yavitt, J.B.; Garcia, M.; Harms, K.E; Turner, B.L.; Wright, S.J. 2013. Soil phosphorus responses to chronic nutrient fertilization and seasonal drought in a humid lowland forest, Panama. *Soil Research,* 51: 215–221.

Mooshammer, M.; Wanek, W.; Schnecker, J.; Wild, B.; Leitner, S.; Hofhansl, F.; *et al*. 2012. Stoichiometric controls of nitrogen and phosphorus cycling in decomposing beech leaf litter. *Ecology,* 93: 770–782.

Nziguheba, G.; Bünemann, E.K. 2005. Organic phosphorus dynamics in tropical agroecosystems. In: Turner, B.L.; Frossard, E.; Baldwin, D.S. (Ed.). *Organic Phosphorus in the Environment.* CABI Publishing, UK, p.243–268.

Olsen, S.R.; Sommers, L.E. 1982. Phosphorus. In: Page, A.L.; Miller, R.H.; Keeney, D.R. (Ed.). *Methods of Soil Analysis*. Part 2, 2nd ed. American Society of Agronomy, Madison, p.403-430.

Pinheiro, J.; Bates, D.; DebRoy, S.; Sarkar, D.; R Core Team. 2021. *nlme: Linear and Nonlinear Mixed Effects Models*. (https://CRAN.R-project.org/package=nlme).

Prescott, C.E.; Vesterdal, L. 2021. Decomposition and transformations along the continuum from litter to soil organic matter in forest soils. *Forest Ecology and Management*, 498: 119522.

Quesada, C.A.; Lloyd, J.; Anderson, L.O.; Fyllas, N.M.; Schwarz, M.; Czimczik, C.I. 2011. Soils of Amazonia with particular reference to the RAINFOR sites. *Biogeosciences,* 8: 1415–1440.

Quesada, C.A.; Lloyd, J.; Schwarz, M.; Patiño, S.; Baker, T.R.; Czimczik, C.; *et al*. 2010. Variations in chemical and physical properties of Amazon forest soils in relation to their genesis. *Biogeosciences,* 7: 1515-1541.

Raghothama, K.G. 2005. Phosphorus and plant nutrition: an overview. *Phosphorus: Agriculture and the Environment*, 46, 353-378.

Reed, S.C.; Yang, X.; Thornton, P.E. 2015. Incorporating phosphorus cycling into global modeling efforts: a worthwhile, tractable endeavor. *New Phytologist,* 208: 324–329.

Rheinheimer, D.S.; Anghinoni, I.; Conte, E. 2000. Fósforo da biomassa microbiana em solos sob diferentes sistemas de manejo. *Revista Brasileira de Ciências do Solo,* 24: 589-597.

Ribeiro, J.E.L.S.; Hopkins, M.J.G.; Vicentini, A.; Sothers, C.A.; Costa, M. A.S.; Brito, J. M.; *et al*. 1999. *Flora da Reserva Ducke - Guia de Identificação das Plantas Vasculares de Uma Floresta de Terra-Firme na Amazônia Central*. Editora INPA, Manaus, 816p.

Richardson, A.E.; George, T.S.; Hens, M.; Simpson, R.J. 2005. Utilization of soil organic phosphorus by higher plants. In: Turner, B.L.; Frossard, E.; Baldwin, D.S. (Ed.). *Organic Phosphorus in the Environment*. CABI, Wallingford, p.165–184.

Rückamp, D.; Amelung, W.; Theisz, N.; Bandeira, A. G.; Martius, C. 2010. Phosphorus forms in Brazilian termite nests and soils: relevance of feeding guild and ecosystems. *Geoderma,* 155: 269–279.

Schaap, K.J.; Fuchslueger, L.; Hoosbeek, M.R.; Hofhansl, F.; Martins, N.P.; Valverde-Barrantes, O.J.; *et al*. 2021. Litter inputs and phosphatase activity affect the temporal variability of organic phosphorus in a tropical forest soil in the Central Amazon. *Plant and Soil*, 469: 423–441.

Smeck, N.E. 1985. Phosphorus dynamics in soils and landscapes. *Geoderma,* 36: 185–189.

Sotta, E.D.; Meir, P.; Malhi, Y.; Nobre, A. D.; Hodnett, M.; Grace, J. 2004. Soil CO_2 efflux in a tropical forest in the central Amazon. *Global Change Biology,* 10: 601–617.

Tiessen, H.; Stewart, J.W.B.; Cole, C.V. 1984. Pathways of phosphorus transformations in soils of differing pedogenesis. *Soil Science Society of America Journal,* 48: 853–858.

Tiessen, H.; Moir, J.O. 1993. Characterization of available P by sequential extraction. In: Carter, M. (Ed.). *Soil Sampling and Methods of Analysis*. Lewis, Boca Raton, p.75–78.

Trolove, S.N.; Hedley, M.J.; Caradus, J.R.; Mackay, A.D. 1996. Uptake of phosphorus from different sources by *Lotus pedunculatus* and three genotypes of *Trifolium repens*. *Australian Journal of Soil Research,* 34: 1027–1040.

Turner, B.L. 2008. Resource partitioning for soil phosphorus: a hypothesis. *Journal of Ecology*, 96:698–702.

Turner, B.L.; Engelbrecht, B.M.J. 2011. Soil organic phosphorus in lowland tropical rain forests. *Biogeochemistry,* 103: 297–315.

Turner, B.L.; Cade-Menun, B.J.; Condron, L.M.; Newman, S. 2005. Extraction of soil organic phosphorus. *Talanta,* 66: 294–306.

Turner, B.L.; Lambers, H.; Condron, L.M.; Cramer, M.D.; Leake, J.R.; Richardson, A.E.; Smith, S.E. 2013. Soil microbial biomass and the fate of phosphorus during long-term ecosystem development. *Plant and Soil,* 367: 225–234.

Turner, B.L.; Yavitt, J.B.; Harms, K.E.; Garcia, M.N.; Wright, S.J. 2015. Seasonal changes in soil organic matter after a decade of nutrient addition in a lowland tropical forest. *Biogeochemistry,* 123: 221-235.

Van Veen, J.A.; Kuikman, P.J. 1990. Soil structural aspects of decomposition of organic matter by micro-organisms. *Biogeochemistry,* 11: 213–233.

Vance, C.P.; Uhde-Stone, C.; Allan, D.L. 2003. Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytologist,* 157: 423–447.

Vincent, A.G.; Turner, B.L.; Tanner, E.V.J. 2010. Soil organic phosphorus dynamics following perturbation of litter cycling in a tropical moist forest. *European Journal of Soil Science* 61: 48-57.

Wang, Y.P.; Law, R.M.; Pak, B. 2010. A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. *Biogeosciences,* 7: 2261–2282.

Wright, S.J.; Yavitt, J.B.; Wurzburger, N.; Tuner, B.L.; Tanner, E.; Sayer, E.J.; *et al*. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. *Ecology,* 92: 1616–1625.

RECEIVED: 07/12/2021
ACCEPTED: 06/03/2022
ASSOCIATE EDITOR: Lucia Fuchslueger