Linking nitrogen and phosphorus dynamics in litter production and decomposition during secondary forest succession in the eastern Amazon

Vinculação da dinâmica do nitrogênio e do fósforo na produção e decomposição de serapilheira durante a sucessão da floresta secundária na Amazônia oriental

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Abstract: Land-use change, including tropical deforestation for agriculture and subsequent agricultural abandonment, may change the stoichiometry of nutrient cycling in tropical secondary forests relative to mature forests. While phosphorus (P) is conservatively cycled in these mature forests, nitrogen (N) losses during an agricultural phase may provoke conservative N cycling processes in young secondary forests. Here we explore differences in nutrient cycling properties among secondary and mature forests of the eastern Amazon, including litter nutrient concentrations and rates of litter production and decomposition. In a chronosequence of successional forest age, N production in litterfall and N loss during litter decomposition were low in young forests but increased with increasing forest age, whereas P was conservatively cycled in all forest ages. Litter N concentration was positively correlated with the rate of mass loss in a litterbag study and with a mass balance estimate of litter decomposition based on annual litterfall and litter stock measurements. Therefore, while P is conservatively cycled and may limit or co-limit productivity in these forests, variation in N content of litter among forest successional stages may be related to differences in decomposition rates and mean residence times of litter, thus linking N availability with rates of litter decomposition and P cycling.

Keywords: Litterfall production. Decomposition. Tropical forests. Nutrient cycling. Forest succession.

Resumo: A mudança do uso da terra (desmatamento-agricultura-abandono agrícola) pode alterar a estequiometria da ciclagem de nutrientes nas florestas secundárias em relação às florestas maduras. Enquanto o fósforo (P) tem um ciclo conservador nas florestas maduras, a perda do nitrogênio (N) na fase agrícola pode provocar processos conservadores do seu ciclo nas florestas secundárias jovens. Vamos explorar as diferenças da ciclagem de nutrientes entre florestas secundárias e maduras na Amazônia oriental, incluindo concentrações de nutrientes da serapilheira e as taxas de produção e decomposição. A produção e a perda de N durante a decomposição foram baixas nas florestas jovens, mas aumentaram com a idade da floresta, enquanto o P foi constante em todas as idades. A concentração de N teve correlação positiva com a taxa de perda de massa e com a estimativa de decomposição baseada na produção anual e no estoque da serapilheira. Portanto, enquanto P tem um ciclo conservador e pode limitar ou co-limitar a produtividade, a variação do teor de N entre os estágios sucessionais florestais pode influenciar diferenças nas taxas de decomposição e tempos de permanência na serapilheira, que liga a disponibilidade de N com as taxas da decomposição e o ciclo de P.

Palavras-chaves: Produção de serapilheira. Decomposição. Florestas tropicais. Ciclagem de nutriente. Sucessão florestal.

INTRODUCTION

Mature lowland tropical forests growing on highly weathered acid soils are known for conservative P cycles (Hedin *et al*., 2003; McGroddy *et al*., 2004; Reich & Okeksyn, 2004; Vitousek, 1984; Walker & Syers, 1976). More recently, several indices of N cycling, including foliar concentrations and isotopic signatures, soil inorganic-N, and N_2O emissions, were used to demonstrate that N limitation can be provoked in these tropical landscapes by repeated disturbance, resulting in conservative cycles of both N and P in chronosequences of young secondary forests regrowing after agricultural abandonment (Davidson *et al*., 2007).

Secondary forests generally represent only a small fraction of the Amazonian landscape, because they are frequently re-cut for agriculture and establishment of cattle pastures (Neeff *et al*., 2006). Even in areas of slash-and-burn agriculture, where secondary forests are common features of the landscape, recent trends are towards decreases in secondary forest cover (Almeida *et al*., 2010). Nevertheless, secondary forests cover significant areas of the region are important reservoirs of biotic diversity in the Amazon region (Vieira *et al*., 2003), they affect local climate through establishing rates of evapotranspiration similar to mature forests (Hölscher *et al*., 1997), they conserve and accumulate nutrients for slash and burn agriculture (Sommer *et al*., 2004). Rates of Amazonian regrowth of secondary forests have been negatively correlated with the number of burns experienced during agricultural phases (Zarin *et al*., 2005). Where agriculture use was intense and/or fires frequent, the rate of forest regrowth increased and the dominance of pioneer tree species was prolonged following N addition (Davidson *et al*., 2004; Siddique *et al*., 2010). Actively cycling N re-accumulates during secondary succession, gradually alleviating the N limitation and returning the maturing secondary forest to predominant P limitation (Davidson *et al*., 2007). Hence, the legacy of management during agricultural phases can affect nutrient cycling processes and the vigor of forest regrowth.

In a previous study (Davidson *et al*., 2007), climate and plant functional types were the same across study sites within the humid, evergreen tropical forest region of the eastern Amazon, but stand age and successional stage were varied among selected chronosequences of secondary forest stands of 3-70 years age as well as mature forests. Here we add litterbag decomposition studies to one of those chronosequences of forest age from 6-40 years plus a mature forest, and we take advantage of differences in nutrient cycling properties among secondary and mature forests to further explore differences in litter production rates, litter nutrient concentrations, and decomposition rates. It has been suggested that nutrients may limit decomposition more strongly in low-P than in low-N ecosystems (Hobbie & Vitousek, 2000). In addition to a conservative P cycle, the Ca cycle has also been shown to be conservative in highly weathered, acidify tropical forest soils (Markewitz *et al*., 2004). The N concentration of litter has been shown to be a dominant controller of rates of decomposition across biomes, from tropical evergreen forests to Arctic tundra (Parton *et al*., 2007). We hypothesized that N production in litterfall and N loss during litter decomposition would both increase with increasing forest age, whereas P and Ca would be conserved for all forest ages in these highly weathered, acidic tropical soils, with little variation across forest ages in P and Ca flux in litterfall or P loss during decomposition. Therefore, while P and Ca would be conservatively cycled and may limit or co-limit productivity in these forests, we proposed that variation in N content of litter among forest successional stages accounts for differences in decomposition rates and mean residence times of litter. Hence, N availability may also affect rates of P cycling.

MATERIALS AND METHODS

STUDY AREA

This study was carried out in the municipality of Capitão Poço, Pará, Brazil (47° 20' W, 2° 12' S), where a large
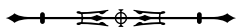
(3.700 ha) remnant of mostly undisturbed, dense mature forest remains standing in this region of widespread deforestation (Almeida *et al.*, 2010; Figueiredo *et al.*, 2010). Secondary forest of six, ten, 20, and 40 years of age were selected in the surrounding countryside, based on interviews with local farmers to determine the date of agricultural abandonment and that no fertilizers had been used on the site. Mean annual temperature is 26 °C with little seasonal variation. Mean annual precipitation is 1.960 mm, with a significant dry season of 3-5 months (Figure 1). Soils in upland areas have been classified as Latossolos Amarelos-Vermelhos in the Brazilian system or Oxisols in the United States Department of Agriculture (USDA) system (Wiesenmuller, 2004). Soil pH (in water) ranges from 4.5 in the mature forest to 5.5 in the young secondary forests (Davidson *et al.*, 2007).

This study area was part of a broader regional study of land-use change, species composition, and biogeochemistry (Almeida *et al.*, 2010; Davidson *et al.*, 2007; Vieira *et al.*, 2003). Fine litterfall was collected at all of these sites, but the litterbag study reported here was conducted only on a single chronosequence located in the southern section of the municipality of Capitão Poço, including a large remnant mature forest. Five farms were identified, which collectively provided a range of secondary forests of known age and land-use history, plus a mature forest. The litter layer material was collected from those plots and the litterbag incubations were conducted *in situ* in the same plots from which the litter was collected.

LITTER LAYER STOCKS AND LITTERFALL COLLECTIONS

In January 2004, six samples of the litter layer were randomly collected from each forest stand, using a 0.5 x 0.5 m square area for each sample. Six fine litterfall collectors (0.25 m²) were also installed per stand, and all fallen leaves, branches and reproductive structures < 2 cm diameter were collected every 15 days, from February 2004 to January 2005. The two collections per month were composited to a single sample per month for each collector. All material was dried in an oven at 65 °C until the weight was constant. After drying and weighing, the samples were ground in a Wiley mill with a screen of 1 mm. The mass of litter was corrected for silica content by incinerating 1 g material in a muffle furnace at 550 °C.

LITTERBAG STUDY

Recently fallen leaf litter was collected from each site (except the six-year-old site) and dried at 65 °C until the weight was constant. Nylon litterbags were 20 cm x 30 cm with a 2 mm mesh, and each was filled with 10 g dry litter and sealed. Four sets of five bags per set were placed within the litter layer in each forest age. One of five bags from each of the four sets was retrieved after 30, 60, 120, 180, and 270 days, so that there were four collections per date and per forest age. The retrieved litterbags were returned to the laboratory, where they were dried, weighed, and ground as described above.

NUTRIENT ANALYSES

All analyses followed standard protocols in the Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Laboratory of Plant Ecophysiology and Plant Propagation (EMBRAPA, 1999). Briefly, each ground sample from litterfall collectors and litterbags was mixed well, and then a 0.1 g subsample was placed in 2 ml of sulfuric acid (95%) and hydrogen peroxide (30%) and then digested in a block digester at 280 °C. Concentrations were determined colorimetrically for N (Mulvaney, 1996) and P (Murphy & Riley, 1962), by photometry for K, and by atomic absorption spectroscopy for Ca and Mg (EMBRAPA, 1999).

STATISTICAL ANALYSES

Litter mass and nutrient mass in the litterbags were fitted to an exponential regression function:

$$X_t = X_0 e^{-kt}$$

where X_t is the percent mass remaining on day t, X_0 is initial mass (%), k is the decomposition constant (day^{-1}), and t is incubation time in days (Olson, 1963).

For litterfall, an annual sum of total mass and mass of each nutrient was calculated for each litterfall collector (n = 6 per forest age class). Similarly, mass-weighted mean nutrient concentrations were calculated for each collector. An analysis of variance (ANOVA) was used to test the effect of forest age class on litterfall mass and nutrient concentrations, using Tukey's Honest Significant Difference post-hoc test to evaluate differences between means. An analysis of covariance (ANCOVA) using age as a continuous variable would be superior to an ANOVA for the purposes of testing our hypothesis, but, unfortunately, it is impossible to assign an age to the mature forest (see discussion in Davidson *et al.*, 2007). Multiple forest stands per age rather than multiple collectors per age would be desirable, especially for testing differences among age classes in an ANOVA, but is less necessary when testing for an age effect when age can be used as a continuous variable in an ANCOVA. As a compromise, we report and discuss significant differences from the ANOVA only when the differences among age classes follow a unidirectional trend with increasing or decreasing age.

RESULTS

LITTERFALL PRODUCTION AND NUTRIENT FLUX

Litterfall was highly seasonal, with the highest rates of litterfall measured during the dry season and lower rates during the wet season in all forest age classes (Figure 1). It is common for trees to drop old leaves and to produce a flush of new leaves before the end of the dry season in the evergreen forests of this region.

Nutrient concentrations in litterfall were also seasonal. The small quantity of litter that fell during the early wet season was rich in P and poor in K and Ca (Figure 2). In contrast, the large amount of litter that fell during the dry season was poor in P and rich in K and Ca. This pattern is consistent with phenologically related retranslocation of P prior to dry season litterfall. Litterfall N concentrations

followed a similar seasonal pattern as P, and Mg followed a pattern like Ca and K, but these were less pronounced.

Annual litterfall mass was similar among the secondary forests, but was significantly higher in the mature forest (Table 1). On a mass-weighted annual average basis, litterfall-N concentrations were higher in the mature forest and oldest secondary forest than in the younger secondary forests, whereas the opposite was true for Ca (Table 2). No differences in annual average litterfall concentrations were detected among forest ages for P, K, and Mg. Annual litterfall-N mass was nearly two times higher in the mature forest than the youngest forest (Table 1). A less pronounced increase with forest age was also measured for litterfall P mass, and a decrease was observed for litterfall-Ca mass.

LITTERBAG DECOMPOSITION

Rates of litter decomposition increased with increasing forest age (Figure 3A, Table 3). Rates of N loss from litter also increased with forest age (Figure 3B, Table 3). There was also a similar but less pronounced trend of increasing loss of K and Mg from litter with increasing forest age (Figures 3D, 3F, Table 3). In contrast, there was little loss of P or Ca in litterbags, except for some modest loss in the mature forest litterbags (Figure 3C, Table 3). The rate of mass loss in the litterbag study was positively correlated with the initial N concentration (Figure 4).

LITTER LAYER STOCKS AND DECOMPOSITION

The mass of the litter layer was greatest in the youngest forest and declined with forest age (Figure 5). As a consequence, mass balance decomposition rates of the litter layer (k = annual litterfall production/litter stock) were lowest in the young forests and increased with increasing forest age. Annualized litterbag decomposition rates were well correlated with mass balance decomposition rates, although the litterbag rates tended to under-predict mass balance rates (Figure 6A). Litter N concentrations were also good predictors of mass balance decomposition rates (Figure 6B). The 10- and 20-year-old forests had
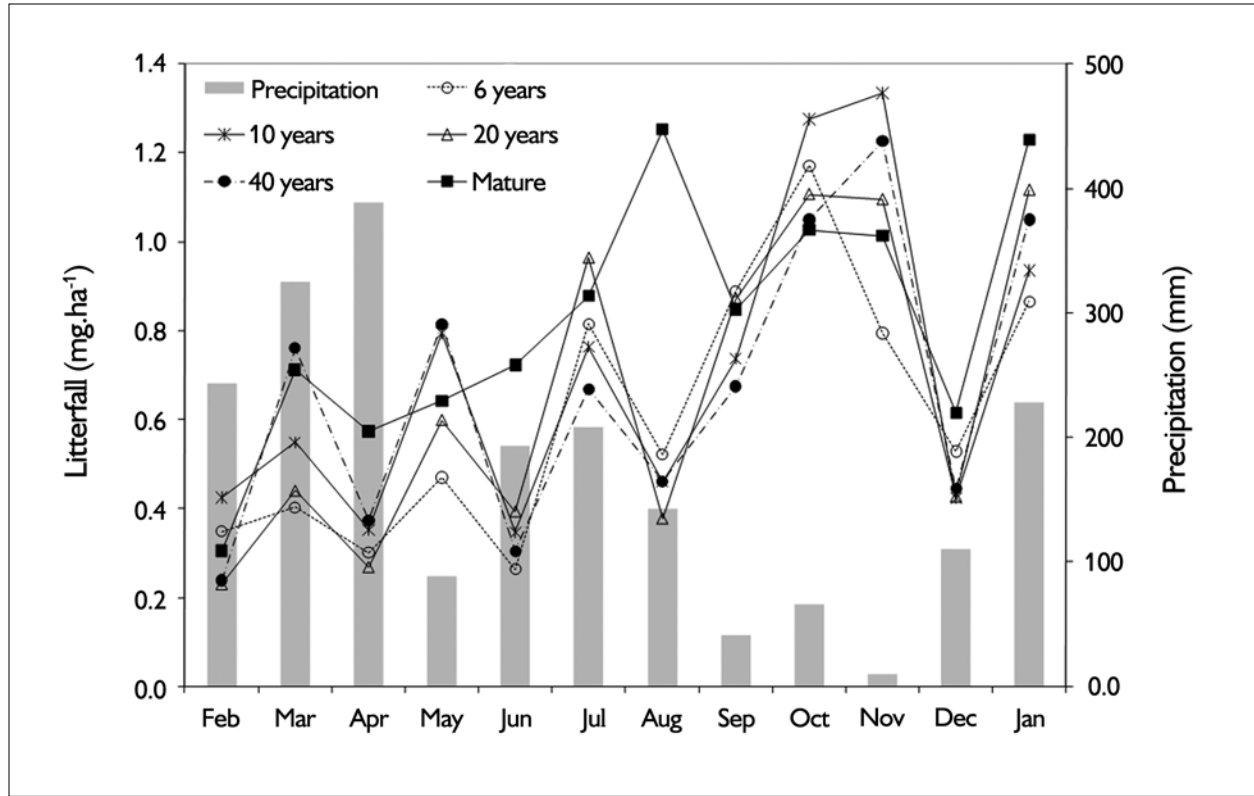
Figure 1. Monthly fine litterfall (points and left axis) in secondary forests of six, ten, 20, 40 years old and in a mature forest, and monthly precipitation (bars and right axis) for February 2004 to January 2005.

low values for litterbag decomposition rates, mass balance decomposition rates, and litter N concentrations, whereas the opposite was true for 40-year-old and mature forests.

DISCUSSION

Litterfall was measured in every month of the year, which has also been noted in several other studies of tropical forests (Campo & Vázquez-Yanes, 2004; Fernandes et al., 2007; Hermansah et al., 2002; Martius et al., 2004; McDonald & Healey, 2000; Teixeira et al., 2001; Santana et al., 2003). According to Martins & Rodrigues (1999), an increased production of litterfall during the dry season may be a response of the vegetation to hydrological stress, and the loss of leaves prevents loss of water through evapotranspiration. A similar explanation has been given by César (1993); Fernandes et al. (2007); Martins & Rodrigues (1999). Other

factors can also affect litter production, including nutriens (Morellato, 1992) and wind (Martins & Rodriges, 1999). However, the flush of new green leaves just before the initiation of the rainy season in many Amazonian forests such as the ones studied here suggests that soil water stores are sufficient for this production of new foliage.

The litterbag study presented here adds support to prior analyses of N cycling indices (Davidson et al., 2007), which indicated that N is conservatively cycled in young secondary forests regrowing from agricultural abandonment in this region of the eastern Amazon. The rates of N loss during litterbag decomposition increased with forest age (Table 3), indicating more leaky N cycle in the 40-year-old and mature forests compared to the younger forests. Consistent with the finding that initial N concentration is a good predictor of litterbag decomposition rates across
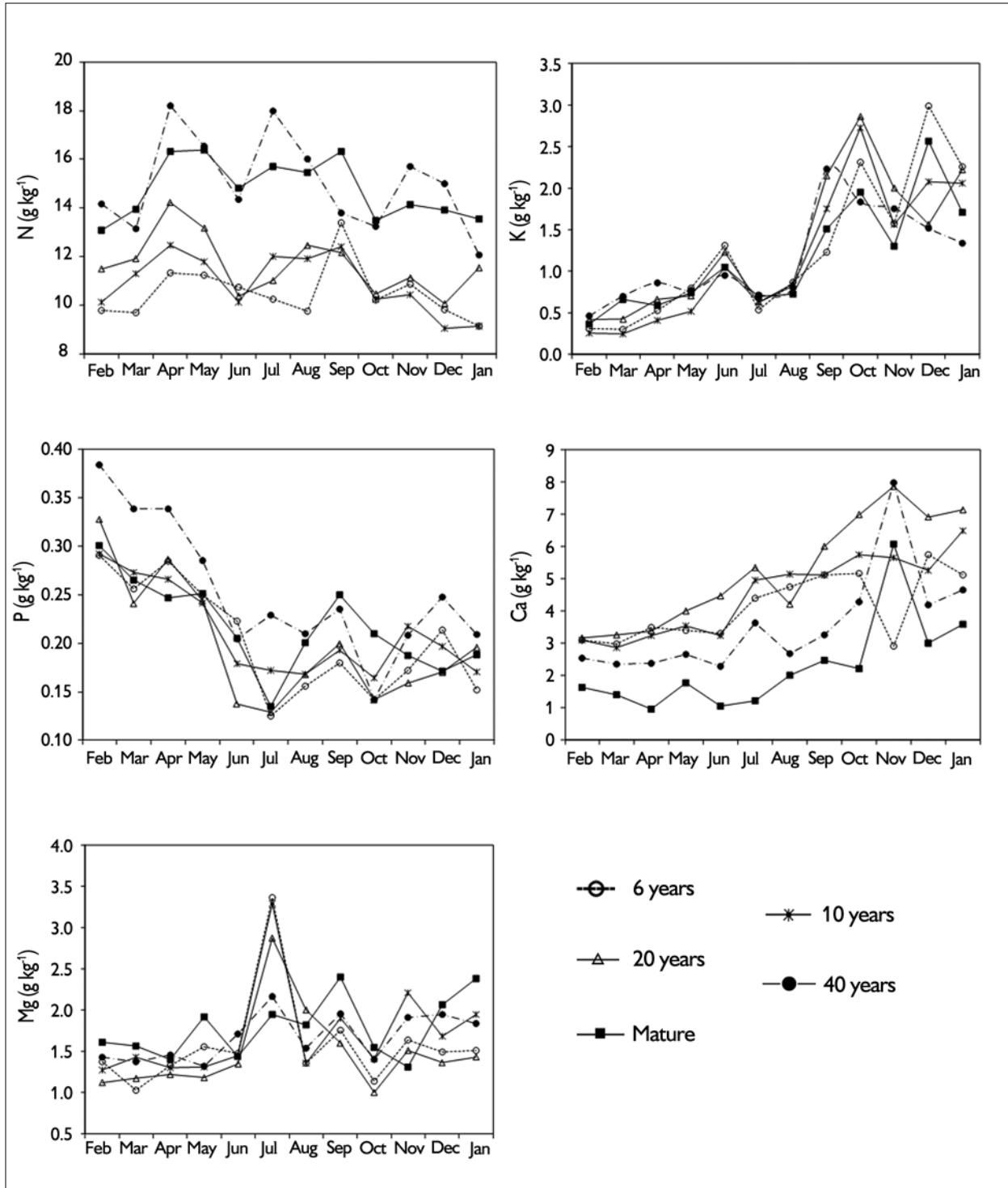
Figure 2. Mean monthly concentrations of nutrients in litterfall in secondary forests of six, ten, 20, 40 years old and in a mature forest for February 2004 to January 2005.

Table 1. Annual fine litterfall flux of mass and of nutrients in secondary forests and a mature forest from February 2004 through January 2005. The standard deviation for six plots per forest age is given in parentheses. Means within a column followed by the same letter are not significantly different, using Tukey's honest significant difference (p = 0.05).

Forest age	Mass (mg.ha^{-1})	N (kg.ha^{-1})	P (kg.ha^{-1})	K (kg.ha^{-1})	Ca (kg.ha^{-1})	Mg (kg.ha^{-1})
6 years	7.37 (0.49) a	77.5 (±14.9) a	1.34 (±0.33) a	10.6 (±3) a	31.5 (±5.7) ab	11.3 (±2.3) a
10 years	8.40 (0.80) a	93.9 (±16.6) ab	1.75 (±0.44) ab	12.17 (±4.1) a	42.0 (±8.3) a	15.2 (±1.1) abc
20 years	7.89 (1.05) a	89.8 (±9.61) ab	1.42 (±0.37) ab	12.6 (±3.8) a	46.5 (±11.8) c	11.9 (±3,29) a
40 years	8.06 (0.76) a	126 (±17.1) bc	1.91 (±0.14) bc	10.5 (±2.0) a	33.5 (±6.4) abc	13.5 (±2.2) abc
Mature	9.82 (0.92) b	143 (±15.8) c	2.01 (±0.26) c	11.7 (±1.7) a	23.8 (±4.8) b	17.4 (±2.8) c

Table 2. Mean annual nutrient concentrations (g kg^{-1}), followed by standard deviations (n = 6) of fine litterfall of secondary forests and a mature forest. Means within a column followed by the same letter are not significantly different, using Tukey's honest significant difference (p = 0.05).

Forest age	N	P	K	Ca	Mg
6 years	10.52 (±0.61) a	0.20 (±0.05) a	1.25 (±0.18) a	4.13 (±0.81) ac	1.49 (±0.15) a
10 years	10.92 (±1.11) a	0.21 (±0.05) a	1.17 (±0.38) a	4.53 (±0.89) ac	1.69 (±0.20) a
20 years	11.68 (±1.24) a	0.20 (±0.05) a	1.31 (±0.37) a	5.23 (±1.19) c	1.46 (±0.30) a
40 years	15.02 (±0.98) b	0.25 (±0.02) a	1.16 (±0.15) a	3.57 (±0.34) ab	1.64 (±0.15) a
Mature	14.77 (±0.97) b	0.22 (±0.02) a	1.15 (±0.19) a	2.28 (±0.46) b	1.76 (±0.26) a

biomes (Parton et al., 2007), this study demonstrates that N concentration was a good predictor of litterbag decomposition rates among litters of different forest ages within the same local study area (Figure 4). The 10 and 20-year-old forests cluster together and the 40-year-old and mature forests cluster together in this relationship, indicating that the temporal transition to higher rates of litter decomposition with increasing N availability may be nonlinear, but we have too few forest ages in this study to evaluate this possibility. The N concentrations and litterbag decomposition rates fell between the intermediate and high end of the range in the Long-Term Intersite Decomposition Experiment Team (LIDET) study of Parton et al. (2007). This is not to suggest that N is the only important nutrient affecting litter decomposition in tropical forests. Litter decomposition rates have also been shown to covary with ratios of
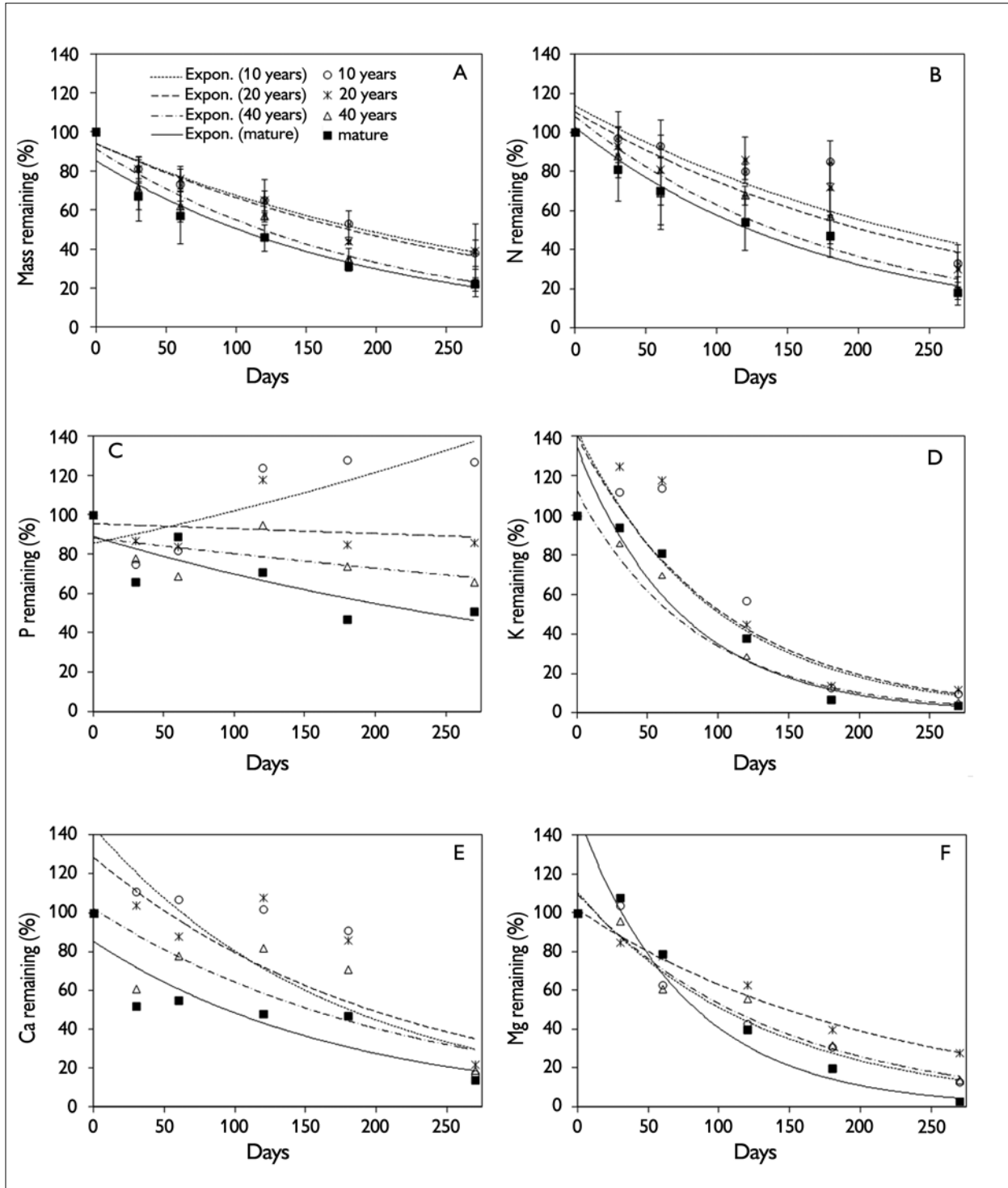
Figure 3. Remaining mass and nutrient stocks in litterbags during 270 day incubations. The lines plot the exponential fits indicated in Table 3. Mass remaining (A); N remaining (B); P remaining (C); K remaining (D); Ca remaining (E); and Mg remaining (F).

Table 3. Regression coefficients for exponential fits ($X = X_o * e^{(-kt)}$) of the percent remaining litter mass and nutrient mass in secondary and mature forests during 270 days incubation *in situ*. The significance of the regression fit is indicated as: ns when $p > 0.05$; * when $p < 0.05$; and ** when $p < 0.01$.

Parameter	10 year	20 years	40 years	Mature
Litter mass				
X_o	94	94	92	86
K	0.0033	0.0035	0.0051	0.0053
R^2	0.98*	0.96*	0.97**	0.97**
Nitrogen				
X_o	114	110	109	103
K	0.0036	0.0039	0.0054	0.0058
R^2	0.75**	0.79**	0.86**	0.94**
Phosphorus				
X_o	85	95	88	89
K	-0.0018	0.0063	0.0010	0.0024
R^2	0.57 ns	0.04 ns	0.33 ns	0.68 ns
Calcium				
X_o	144	129	102	135
K	0.0059	0.0048	0.0047	0.0135
R^2	0.66 ns	0.64 ns	0.63 ns	0.94**
Magnesium				
X_o	111	102	110	152
K	0.0077	0.0048	0.0072	0.0132
R^2	0.98**	0.99**	0.97**	0.95*

initial lignin:N and lignin:P, and with K and micronutrient concentrations (Kaspari *et al*., 2008; Wieder *et al*., 2009).

By combing litterbag studies with measures of litter layer stocks and annual litterfall, we were able to demonstrate that litterbag decomposition rates and litter N concentrations correlate well with litter layer decomposition rates based on a mass balance approach (annual production rate/stock; Figure 6A and 6B). These data show the same clustering of young and older sites, as described above for Figure 4, again indicating that we had too few forest stand ages to determine the temporal pattern of transition to a high N and high decomposition condition. Annualized estimates of litterbag decomposition rates were lower than the mass balance decomposition estimates, which is consistent with possible artifacts caused by the nylon mesh of litterbags preventing contact with some soil fauna, fungal hyphae, and roots. The mass balance approach demonstrates that the young successional forests accumulated more litter mass relative to older forests, not because of higher litterfall inputs, but because of lower rates of decomposition, corroborated by litterbag studies and presumably due to lower N concentrations of young forest litter.

Mesquita *et al*. (1998) also reported lower rates of litter layer decomposition in a 10 year-old Cecropia-dominated second-growth forest, near Manaus, Brazil, compared to published values for mature forests. In contrast, Ewel (1976) found no trends in decomposition rates in a secondary forest chronosequences in
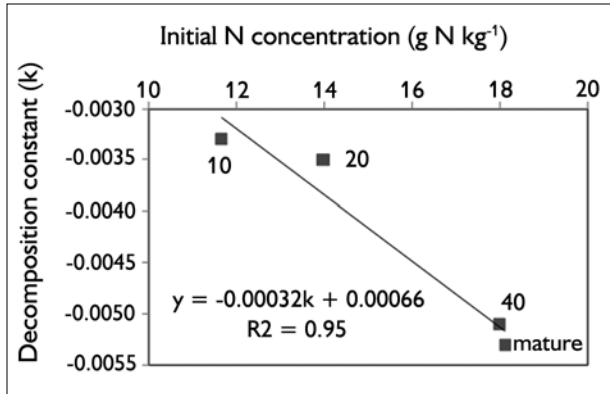
Figure 4. Relationship between initial N concentration of fine litter versus litterbag decomposition rates calculated for secondary forests of 10, 20, and 40 years age and a mature forest (ages shown near marker).
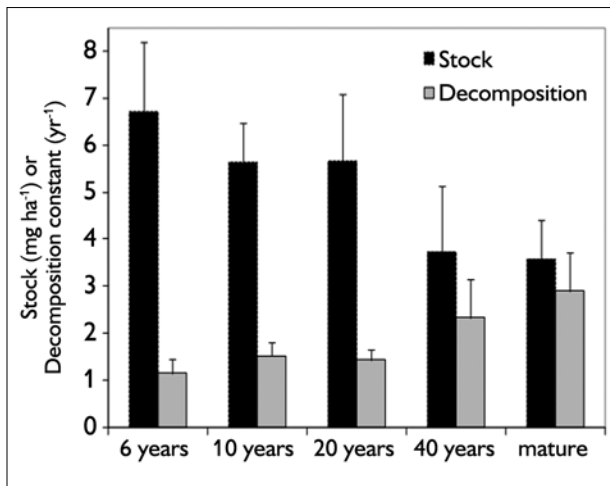

Figure 5. Litter layer stocks and mass balance decomposition constants (annual production/stock) for secondary and mature forest. Error bars indicate standard errors (n = 6).

Guatemala, although the oldest secondary forest in that study was only 14 years. The author also reported that all of the litterbags had been heavily invaded by roots, which may have accelerated decomposition and rates of nutrient removal. No differences were found in litterbag decomposition rates between a mature forest and a mid-successional forest in Puerto Rico (Zou *et al*., 1995). However, this result is actually consistent with the present study, because the mid-successional forest in the Puerto

Rico study was already 50 years old, which is older than the oldest secondary forest in the present study, and our 40-year old forest also had similar decomposition rates as the mature forest. In the present study, where secondary forest ages ranged from six to 40 years, litterbag and mass balance decomposition rates were lower in the young forests (six, ten, and 20 years) than in the older forests (40 years and mature).

While decomposition rates, N losses during decomposition, and N concentrations in fine litterfall varied with forest age, lack of such variation in P cycling characteristics suggest that P cycled conservatively for all forest ages. The high P concentrations measured in the small amount of litterfall early in the wet season presumably reflects foliar P concentrations of young leaves that fell due to partial herbivory or storm damage and before the plants actively reabsorb foliar P prior to most litterfall. In contrast, the large amount of litter that fell during the dry season had P concentrations that were about 50% lower (Figure 2), indicating a phenologically controlled retranslocation of foliar P prior to litterfall. This trend was true for all forest age classes. Furthermore, contrary to the near doubling of annual litterfall-N from youngest to oldest forest, annual P flux in litterfall increased only modestly with forest age (Table 2). Comparisons of foliar and litterfall N:P ratios have previously shown that retranslocation prior to litterfall is greater for P than for N in these forests, although some retranslocation of N does occur, especially in the young forests (Davidson *et al*., 2007). The conservative nature of the P cycle is further supported by either net retention of P or low rates of P loss during litterbag incubations observed in the present study, as has been observed for other tropical forest litterbag studies (Cleveland *et al*., 2006; Hobbie & Vitousek, 2000).

As expected for forest ecosystems on highly weathered acid soils, the calcium cycle also appears to be conservative. Because Ca is generally a non-mobile element, there was no Ca retranslocation before leaf drop. Instead, the seasonal litterfall concentration data show an increase in Ca concentration before leaf
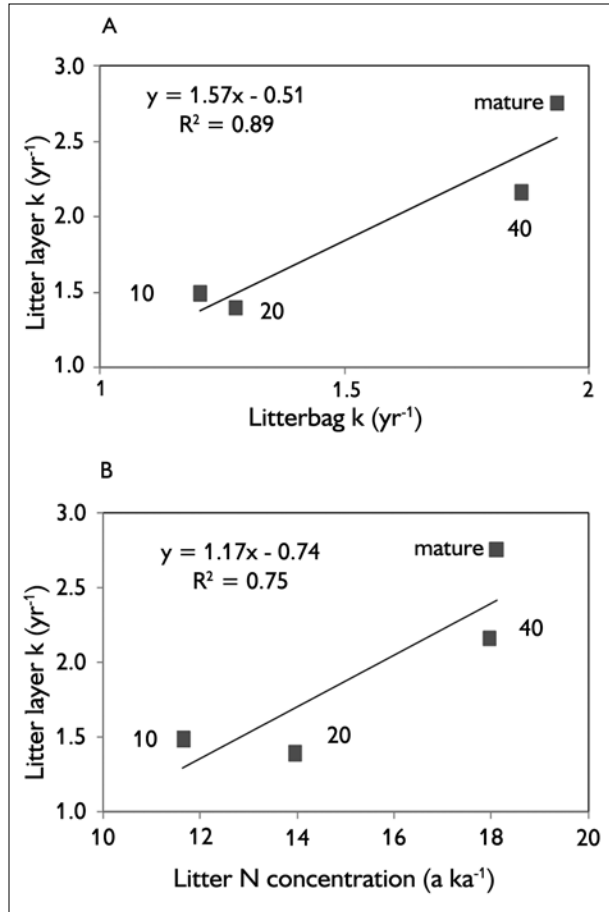
Figure 6. Relationship between annualized litterbag decomposition constants (values from Table 3 multiplied by 365 days/year) *versus* mass balance litter layer decomposition constants (k = annual input/stock; (A) and between initial N concentration of litter versus mass balance litter layer k (B). Forest ages are shown near their respective markers.

drop (Figure 2), probably because the plants actively retranslocate other constituents, leaving mostly Ca-rich structural tissues. Concentrations of Ca in litterfall were considerably lower in the older forests (Table 1), so much so that annual litterfall-Ca mass was lower in the mature forest even though total litterfall mass was highest there (Table 2). In other words, the Ca cycle was even more conservative than we had originally hypothesized. Amazonian pasture soils have been shown to retain most of the Ca that had been present in aboveground biomass before stand clearing and burning, with the soil

Ca and soil pH declining only gradually over decades (Markewitz *et al*., 2004; Moraes *et al*., 1996). The same trend was observed by these investigators for Mg, but less pronounced, whereas K was more rapidly lost – all patterns that are consistent with the litterbag study and annual litterfall rates reported in the present study.

While these results reaffirm a highly conservative P cycle in these forests on highly weathered lowland tropical forest soils, they also demonstrate that land-use change can provoke variation in N content of litter among forest successional stages, and this variation in N quality of the litter correlates with differences in decomposition rates and mean residence times of litter. Extracellar enzymes needed to break down litter require N, thus linking N availability with cycling of other nutrients bound in the litter (Vitousek *et al*., 2010).

Here we show that even where P may be a co-limiting nutrient to plant productivity, variation in N availability, in this case due to land use history and forest successional status, may affect litter decomposition rates in eastern Amazonian forests. Although the trees retranslocate about 50% or more of foliar-P before leaf drop, mineralization of the remaining litter-P must be dependent upon decomposition rates, which appear to be linked to N cycling processes.

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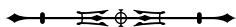
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