

Does nutrient cycling differ between fragments of Atlantic Forest with distinct structural aspects? A case study in the state of Rio de Janeiro, Brazil

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ABSTRACT

In this study, we evaluate litter biomass and nutrient inputs, as well as nutrient use efficiency (NUE), in two fragments of dense montane rain forest within the Atlantic Forest Biome in the northern region of the state of Rio de Janeiro, Brazil. The total annual average litter production for the two fragments (designated M1 and M2) was 7.72 and 7.56 t ha⁻¹ year⁻¹, respectively. The annual nutrient return rate was 146.67, 4.84, 21.41, 64.93, and 17.25 kg ha⁻¹ year⁻¹ for N, P, K, Ca, and Mg, respectively. No differences in NUE were observed between the studied fragments, except for that of P. The average NUE for N, P, K, Ca, and Mg, respectively, was 51, 1426, 367, 111, and 428 in fragment M1, compared with 51, 1890, 360, 126, and 472 in fragment M2. The litter biomass input did not differ between the forest fragments studied, indicating that the differences in elevation and forest biomass did not affect nutrient cycling. However, a difference in the litter deposition rate between the dry and rainy periods was observed in fragment M2.

Key words: Decomposition, forest fragment, litter, nutrient input, nutrient use efficiency

Introduction

The Atlantic Forest of Brazil originally comprised a coastal belt extending up to 200 km inland, between the latitudes of 6°N and 30°S, ranging from the state of Rio Grande do Norte in the north to that of Rio Grande do Sul in the south and covering an area of approximately 1 million km² (Mata Atlântica, 1991). In the northern region of the state of Rio de Janeiro, the Atlantic Forest remains as isolated fragments of secondary forest and (rarely) primary forest, the latter situated in inaccessible mountain areas (Leitão Filho 1982). In that same region, especially in Desengano State Park, the Atlantic Forest is defined by its variation in elevation (Moreno *et al.* 2003). Cunha *et al.* (2009) studied the biomass and carbon (C) content of two fragments located at different elevations and found a higher tree density in the fragment located at 900 m, although the fragment located at 600 m had a higher biomass.

Nutrient cycling consists of the exchange of elements between the biota and the environment (Attiwil & Adams 1993). For terrestrial ecosystems in particular, the majority of energy flow (element exchange) occurs through soil-plant interactions (Proctor 1987). Nutrient cycling involves a great number of individual processes, from the nutrient uptake, transport, and translocation of the plant

to throughfall, organic matter production, and decomposition (Attiwil & Adams 1993). At the intermediate stages of nutrient cycling in terrestrial ecosystems, relationships are developed between the vegetation, the microbiota, the edaphic fauna, and the soil (Vitousek 1982; Proctor 1987). Litter production, one of the complex relationships developed in this process, is recognized as one of the main indicators of forest productivity (Figueiredo-Filho *et al.* 2003; Köhler *et al.* 2008). Litter production varies throughout the year with the amount of rainfall (Sanches *et al.* 2009; Köhler *et al.* 2008) and the minimum temperature (Köhler *et al.* 2008), and it is the main biological pathway for the transfer of chemical components into the soil (Xu & Hirata 2002).

Because nutrient cycling involves synchrony between nutrient availability and demand, an understanding of the process is an important element in the development of strategies for the sustainability of planted forest systems (Gama-Rodrigues & Barros 2002; Cunha *et al.* 2005) and natural forests (Moraes *et al.* 1999; Cunha *et al.* 2009; Pinto *et al.* 2009; Pimenta *et al.* 2011). The study of nutrient cycling may inform management strategies for forest restoration or the improvement of existing forest fragments, as well as for the restoration of portions of the forest massif in degraded pasture lands (Gama-Rodrigues & May 2001).

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Fragmentation of forest stands has been the basis for the development of agriculture in Brazil since colonial times (Dean 2002). Many of the currently featured fragments comprise areas for preservation and are more protected because they commonly occupy areas of relevant size, such as national parks within the Atlantic Forest. However, smaller forest fragments, in addition to still being subjected to the effects of human activities, are more vulnerable to climatic variations (Murcia 1995; Kapos *et al.* 1997) and are less biodiverse (Harper *et al.* 2005). It remains, however, to determine whether the patterns of nutrient cycling, considered fundamental to the sustainability of forests, are altered under such circumstances.

The present work examines the nutrient cycling process by quantifying the litter biomass and nutrient inputs, as well as the nutrient use efficiency (NUE), for two fragments of dense montane rain forest within the Atlantic Forest of the northern region of the state of Rio de Janeiro. We hypothesized that forest fragments with distinct characteristics of size, dendrometry, and biomass can be functionally similar in terms of nutrient cycling.

Material and methods

The present study was conducted in two forest fragments of Atlantic Forest in Desengano State Park, located in the municipality of Santa Maria Madalena, in the northern region of the state of Rio de Janeiro, Brazil (21°37'S; 42°05'W). As described by Cunha *et al.* (2009), the first forest fragment (designated M1) covers approximately 200 ha at an elevation of 900 m and is interconnected with a forest continuum of 25,000 ha (Brasil 1983). The second forest fragment (designated M2) covers approximately 10 ha at an elevation of 600 m. Both fragments are located on the Atlantic side of a mountain range. The two forest fragments, both of which are approximately 40 years old, may be classified phytoecologically as dense montane rain forest. Data were collected from May 1999 to April 2000 and from May 2000 to April 2001.

The two forest fragments can be distinguished by their dendrometry and biomass (Cunha *et al.* 2009). The M1

fragment has a density of 927 individuals ha⁻¹, a basal area of 33.25 m² ha⁻¹, and a biomass of 148.41 t ha⁻¹, whereas fragment M2 has a density of 733 individuals ha⁻¹, a basal area of 27.13 m² ha⁻¹, and a biomass of 167.86 t ha⁻¹. Although Cunha (2002) described some species for the purposes of studies of nutrient balance, we did not conduct a detailed floristic and phytosociological survey of the forest fragments. Only nine genera and five species occurred simultaneously in both forest fragments. In fragment M1, the largest biomass accumulators were *Moldenhawera floribunda* Schrad., *Hyeronima alchorneoides* Allemão, and *Meliosma sellowii* Urb., whereas *Copaifera langsdorffii* Desf. was the largest biomass accumulator in fragment M2, where *Anadenanthera colubrina* (Vell.) Brenan was the most abundant species.

The local geological substrate is composed of pre-Cambrian granitoid gneisses from the Paraíba do Sul Complex (Brasil 1983). The climate has been classified as Cwa and is characterized by an average annual rainfall of 1440 mm, according to the historical data series (1961-1990), with a dry season lasting from May to August. According to data from the local weather station, made available by the Brazilian National Institute of Meteorology, the total rainfall during the two observation periods was 1783 mm and 1106 mm, respectively (Fig. 1). The soil of the forest fragments is a dystrophic medium loam Haplic Cambisol Tb with strongly undulating relief (Embrapa, 1999), with chemical characteristics as indicated in Tab. 1.

The forest fragments were chosen based on their conservation status, as indicated by the presence of a significant number of trees with diameter at breast height (DBH) > 10 cm. Three 25 × 20 m plots were established in each forest fragment. The quadrats were established on the hillside, with a vertical orientation from the top to the base, at distances of approximately 500 m from the edge of fragment M1 and 150 m from the edge of fragment M2. The following variables were measured in each plot: monthly production of litter, litter stock over the soil, annual nutrient flow through litterfall, NUE, litter residence time, and nutrient mineralization rate. To evaluate the litter production, litter collectors (1 × 1 m) were installed in May

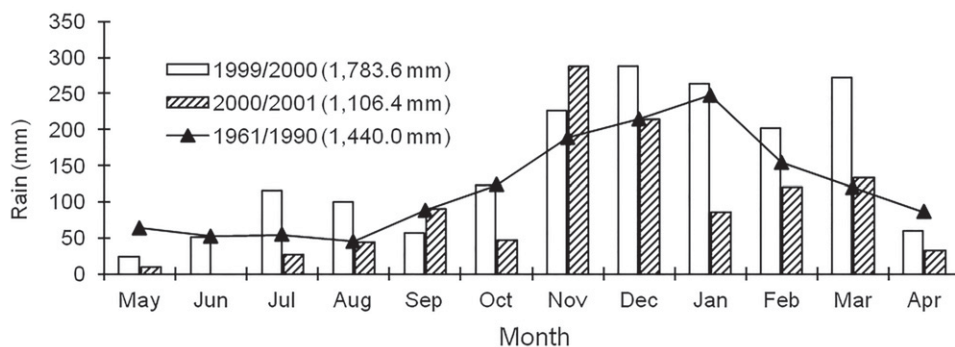


Figure 1. Rainfall in the municipality of Santa Maria Madalena, located in the state of Rio de Janeiro, Brazil, at an elevation of 620 m (21°37'S; 42°05'W).

Table 1. Soil chemical characteristics of the study sites. Averages in the same column in each depth followed by same letter are not significantly different according to the t test at $p < 0.05$.

Fragments	Depth	pH	C	P	K	Ca	Mg	Al	H+Al
	cm	H ₂ O	g kg ⁻¹	mg kg ⁻¹			cmol _c kg ⁻¹		
M1	0-5	4,05	60,3 a	6,3 a	51 a	0,43 a	0,66 a	1,49 a	14,89 a
M2		3,81	42,5 b	5,7 a	38 b	0,48 a	0,80 a	1,65 a	13,54 a
M1	5-10	4,20	46,9 a	6,0 a	42 a	0,33 a	0,54 a	1,29 b	11,97 a
M2		3,87	32,1 a	5,2 a	29 a	0,43 a	0,57 a	1,68 a	12,13 a

1999. The collectors were constructed from wooden slats and nylon screens with a 1 mm mesh and were installed 1 m above the ground, supported by four wooden slats. Five collectors were placed randomly in each of the sampling plots for a total of 30 collectors. The collection period ended in April 2001.

Litter collection was performed every 30 days, and the collected material was placed in paper bags and air dried. The material was then separated into leaves, twigs with a diameter < 2 cm, flowers and fruits, bark, and other smaller or unidentified materials. The separated material from each collector was dried to a constant weight in a convection oven at 70°C. The standing litter was sampled twice per year (1999/2001 dry season and rainy season) in four random replicates per plot, using a wooden square of 0.25 m². The collected material from these samplings was also dried to a constant weight in an oven at 70°C.

In the collected litter and soil, we determined the contents of K, using flame photometry; P, using the colorimetric method of the phosphomolybdic acid complex reduced with ascorbic acid, modified according to Braga & Defelipo (1974); Ca and Mg, using atomic absorption spectrometry following nitric-perchloric acid digestion; and N, using the Kjeldahl method, according to Bataglia *et al.* (1983). The soil analysis was performed according to the guidelines established by the Brazilian Agency for Agricultural Research (Embrapa 1997). The different fractions of the litter collected for each month (leaves, twigs, bark, fruits and flowers, and other materials) were analyzed separately. The annual nutrient flow through litterfall and the amount of nutrients stored on the forest floor were estimated by multiplying the nutrient concentrations of the different litter fractions by their dry masses.

The monthly NUE was calculated by dividing the litter dry matter by the litter nutrient content, according to Vitousek (1982). The average litter residence time was calculated as 1/KL, where KL is the ratio between the biomass of produced litter (kg/ha/year) and the standing litter (kg/ha). The mineralization rate was estimated by using the annual averages of the nutrient input by leaves and the annual average of the nutrients stored in standing leaf litter, according to the following formula:

$$K_E = \text{nutrient input (kg/ha/year)} / \text{nutrient stock (kg/ha)}$$

where K_E is the mineralization rate. Averages, standard deviations, and variation coefficients were calculated for each variable. Forest fragments were compared using a t-test for two independent samples.

Results

There were no significant differences between the two forest fragments in terms of the annual average litter production. Litterfall ranged from 7.72 to 7.56 t ha⁻¹ year⁻¹ in the M1 and M2 fragments, respectively (Tab. 2), leaves accounting for 66.45% and 69.17% of the total annual litter production, respectively, and representing the main component of the litterfall. The amounts of twig, bark, reproductive structures, and other structures returned to the soil were also similar in the two fragments.

To evaluate the behavior of the fragments toward the reduction of rainfall in the second year of the study, we compared the production of leaf litter between the driest and wettest trimesters in both of the years of the experiment (Tab. 3). It was found that, in both trimesters, leaf litter differed significantly between the two years of study in fragment M2, although the total production data had not revealed that difference (Tab. 2). Leaf senescence in that fragment was 23% and 30% higher in the driest and wettest trimesters, respectively, in the second year than in the first. We found differences in leaf litter production between the driest and the wettest trimesters for both forest fragments, which likely reflects the influence that fragment size and canopy density have on the preservation of humidity (Tab. 3). We observed a seasonal effect on litter production (Fig. 2), with the amount of standing litter biomass beginning to increase in September, which coincided with the dry season. In fragment M2, there was greater variation in leaf production (Fig. 2) throughout the year and the standard deviation was greater in the second year of study. In fragment M1 (Fig. 2), we observed a seasonal pattern of litterfall in both years. However, in both fragments, the annual pattern of senescence was well defined in each year, demonstrating sensitivity to variations in monthly production. Leaf litter exhibited seasonal patterns similar to those of total litterfall.

The annual N, P, K, Ca, and Mg inputs were not significantly different between the two forest fragments (Tab. 4).

Table 2. Litter production in forest fragments of the Atlantic Forest in the northern region of the State of Rio de Janeiro. Averages in the same column followed by same letter are not significantly different according to the t test at $p < 0.05$. The standard deviation is in brackets.

Fragments	Leaves	Twigs	Bark	Flower/fruits	Other	Total
	t ha ⁻¹ yr ⁻¹					
M1	5.13 (± 0,20)	1.58 (± 0,13)	0.25 (± 0,176)	0.54 (± 0,046)	0.22 (± 0,014)	7.72 a (± 0,27)
M2	5.23 (± 0,23)	1.73 (± 0,118)	0.09 (± 0,130)	0.23 (± 0,026)	0.28 (± 0,014)	7.56 a (± 0,30)

Table 3. Leaf litter in forest fragments of the Atlantic Forest in the northern region of the State of Rio de Janeiro for the driest trimester (July, August and September) and the wettest trimester (November, December and January). Averages in the same row in each trimester followed by same letter are not significantly different according to the t test at $p < 0.05$.

Fragments	Driest trimesters		Wettest trimesters	
	Year 1	Year 2	Year 1	Year 2
	t ha ⁻¹ yr ⁻¹			
M1	1.52 a	1.88 a	2.31 a	2.35 a
M2	1.55 b	2.03 a	1.76 b	2.53 a

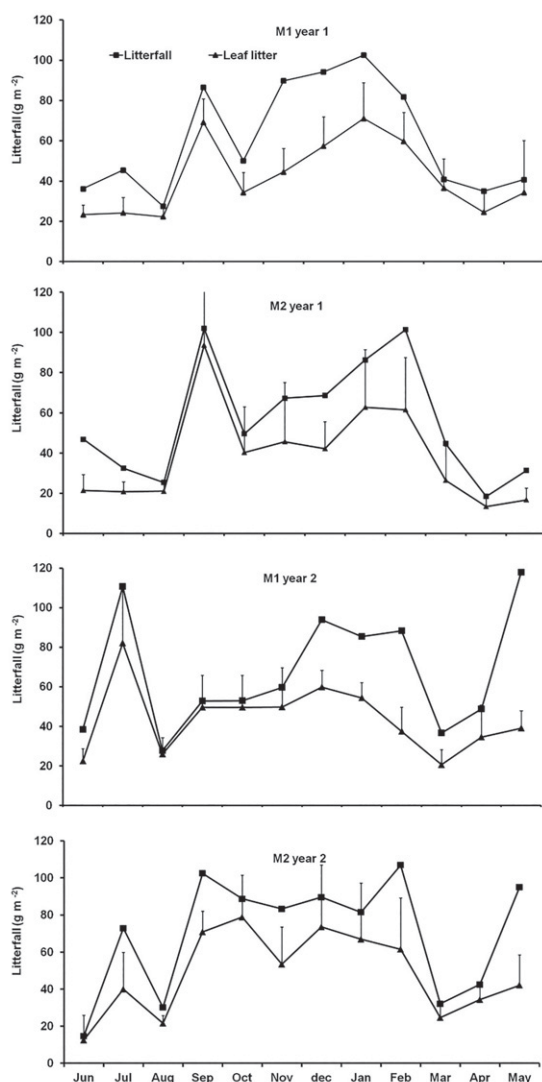


Figure 2. Monthly litter production in two fragments of Atlantic Forest in the northern region of the state of Rio de Janeiro, Brazil. Bars represent standard deviations.

The descending sequence of addition of nutrients by litterfall was N>Ca>K>Mg>P in both forest fragments. The sum of the nutrients (N + P + K + Ca + Mg) was 259.76 kg ha⁻¹ year⁻¹ in M1 and 250.42 kg ha⁻¹ year⁻¹ in M2. The leaves accounted for an average of 75%, 64%, 81%, 73%, and 70% of the transferred N, P, K, Ca, and Mg, respectively. The NUE was not significantly different between fragments M1 and M2 according to the t-test ($p < 0.05$), except for P. The average NUE values for for N, P, K, Ca and Mg, respectively, were 51, 1426, 367, 111, and 428 for fragment M1, compared with 51, 1,890, 360, 126, and 472 for fragment M2 (Fig. 3).

The quantity of standing litter varied between fragments and was considerably higher in the second year (Tab. 5). In the first year, standing litter was similar between the fragments, although the amount of leaf litter was higher in M2 fragment. In the first year, the proportion of leaves found on the ground was approximately 48% and 62% in M1 and M2, respectively, whereas it was 46% and 60%, respectively, in the second year. The plant residue biomass on the ground is an important nutrient stock, the sum of of N, P, K, Ca, and Mg being 231 kg ha⁻¹ in M1 and 240 kg ha⁻¹ in M2. The stock of nutrients did not differ significantly between the fragments. The sequence of inventory for both fragments was N> Ca> Mg> K> P, where Mg takes the position occupied by K in the sequence transferred by litterfall. The estimated average litter decomposition rate, as calculated from the residence time of the leaf litter, was approximately 25% higher in M1 than in M2 (Tab. 6). Therefore, the rate of mineralization of N was also significantly higher in M1. However, the average rate of mineralization was similar for all nutrients except K in both fragments.

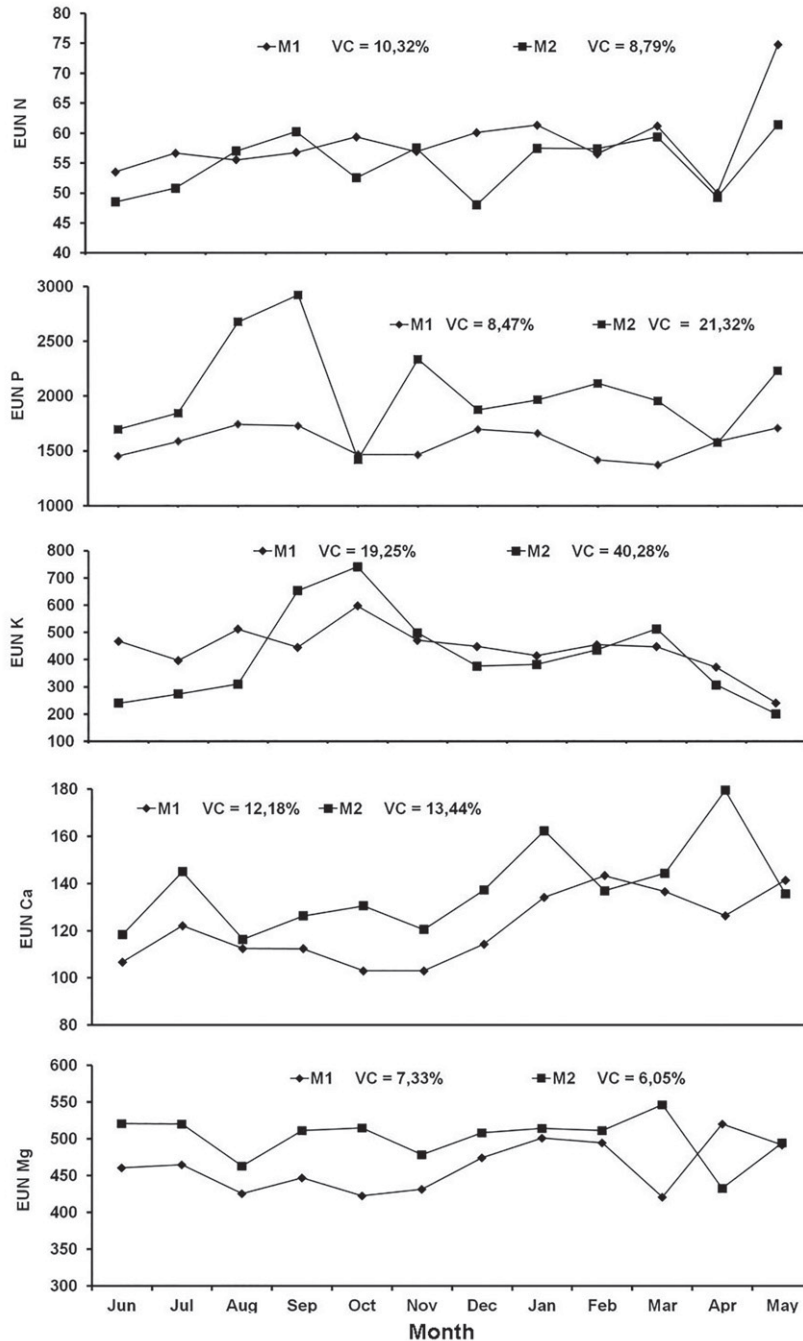
Discussion

The data presented on total litterfall fit well with those of other studies conducted in tropical forests in southeast Brazil. Domingos *et al.* (1997), found a contribution of 7.00 t ha⁻¹ year⁻¹ in rain forests in the state of São Paulo. However,

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Table 4. Total annual input of Nitrogen (N), Phosphorus (P), Potassium (K), Calcium (Ca) and Magnesium (Mg) by litter deposition in forest fragments of the Atlantic Forest in the northern region of the State of Rio de Janeiro. Averages in the same column followed by same letter are not significantly different according to the t test at $p < 0.05$. The variation coefficient is in brackets.

Fragments	N	P	K	Ca	Mg
	$t \text{ ha}^{-1} \text{ yr}^{-1}$				
M1	145.17 a (14,33)	5.41 a (15,57)	21.31 a (16,89)	69.66 a (12,58)	18.21 a (13,71)
M2	148.17 a (11,85)	4.27 a (13,52)	21.51 a (6,96)	60.19 a (16,25)	16.28 a (8,19)



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Figure 3. Nutrient use efficiency (NUE) for N, P, K, Ca, and Mg in two fragments of Atlantic Forest in the northern region of the state of Rio de Janeiro, Brazil. CV – coefficient of variation.

Table 5. Total standing litter, leaf litter, and litter nutrient content in forest fragments of the Atlantic Forest in the northern region of the State of Rio de Janeiro. Averages in the same column followed by same letter are not significantly different according to the t test at $p < 0.05$.

Fragments	Year 1		Year 2		Nutrient content				
	Total	Leaf	Total	Leaf	N	P	K	Ca	Mg
	t ha ⁻¹				kg ha ⁻¹				
M1	7.9 a	3.8 b	9.1 a	4.2 b	140 a	3.5 a	9.1 a	63 a	15.4 a
M2	8.3 a	5.2 a	9.3 a	5.6 a	156 a	3.3 a	7.8 a	59 a	14.3 a

Table 6. Residence time ($1/K_L$ = annual leaf litter production/annual average of standing leaf litter) and mineralization rates (K_E = nutrient input by leaf litter production/nutrient stocked in standing leaf litter). Averages in the same column followed by same letter are not significantly different according to the t test at $p < 0.05$.

Fragments	$1/K_L$ (year)		K_E (year)				
	Year 1	Year 2	N	P	K	Ca	Mg
M1	0.75	0.80	1.36 a	1.35 a	2.58 b	1.22 a	1.03 a
M2	1.11	0.97	0.98 b	1.11 a	2.98 a	1.10 a	1.10 a

smaller inputs, ranging from 4.4 to 5.5 10 t ha⁻¹ year⁻¹, according to the size of the fragment, were found in areas of Atlantic Forest in the mountains of the state of Rio de Janeiro (Gomes *et al.* 2010). However, Yang *et al.* (2005) pointed out difficulties in comparing results across studies, because litter production in forest ecosystems depends on several ecological factors, including climate, species composition, stand age, and site quality. In the present study, the average contribution of leaves to the total litterfall was 68%, similar to the 72% reported for rain forests by Domingos *et al.* (1997), and the 69% reported for montane forests by Gomes *et al.* (2010). A proportion of 66.9% was recorded in the state of Pernambuco (Espig *et al.* 2009). This proportion of leaves in deciduous material composition can contribute to nutrient availability through faster decomposition, because materials that are more lignin-rich retard the decomposition process (Melillo *et al.* 1982), as well as because the leaves are rich in nutrients (Pinto *et al.* 2009). Studying forests in Brazil, Domingos *et al.* (1997) reported average leaf production rates of 4.1–6.5 t ha⁻¹ year⁻¹ in the Atlantic Forest Biome of southeast Brazil.

Because M2 is a relatively small fragment with a lower population density (Cunha *et al.* 2009), its vegetation was likely more exposed to the drought stress observed in the second year of the study. In addition, the vegetation of the rain forest lacks morphological and physiological adaptations to drought stress. Rainfall decreased by 38% from the first year of the study to the second, and this decrease was 23% below the average in the 30-year historical data series, which represents a considerable reduction of water availability. The results for the total monthly litter production in the second year (Fig. 2) also support the influence of the climate on the forest fragments: between the months of July and November, the total monthly litter production in M2 was 125%, 20%, 1%, 79%, and 23% higher, respectively, than in the same months of the previous year. In a three-year study of a transitional tropical forest, Sanches *et al.* (2009)

observed a 32% increase in litter production in the year in which rainfall was lowest and the dry season was the most severe. Gomes *et al.* (2010) reported a similar pattern in other Atlantic Forest fragments, several additional studies in tropical forests have also observed a significant correlation between litter deposition and rainfall (Köhler *et al.* 2008; Sanches *et al.* 2009; Espig *et al.* 2009). The peaking of leaf litter production during the dry season may help the vegetation prevent water loss (Haines & Foster 1977). Low water availability activates biological mechanisms of water loss restriction, one of the most common of which is foliar abscission (Borchert *et al.* 2002). Leaves are the main component of the total litter, and the pattern of leaf deposition is therefore responsible for the seasonal variations observed in total litter production (Fig. 2). These two processes cannot be dissociated, as has been observed in a wide variety of environments (Yang *et al.* 2005; Köhler *et al.* 2008; Sanches *et al.* 2009; Pinto *et al.* 2009; Gomes *et al.* 2010). This association makes leaf litter a potential indicator of litter production in different forest ecosystems (Pinto *et al.* 2009), as well as an indicator of the state of conservation or disturbance of different natural areas (Gomes *et al.* 2010).

Some authors have stated that there is no direct relationship between litterfall and rainfall distribution (Varjabedian & Pagano 1988; Oliveira & Lacerda 1993). However, Espig *et al.* (2009) found an inverse relationship between litterfall and rainfall. Although annual litterfall did not differ significantly between the two years of evaluation in the present study, a more detailed analysis of the driest and wettest trimesters might better elucidate the effects that reduced rainfall has of the litterfall.

As stated by Yang *et al.* (2005), litter dynamics is a primary mechanism of nutrient recycling in natural and plantation forest ecosystems. It plays a vital role in maintaining soil fertility, and determining the rates at which this return occurs is essential to an understanding of forest nutrient

cycling. The forest fragments studied here not only show many similarities in terms of the dynamics of plant residue fall but are also remarkably similar in terms of the content of the nutrients transferred to the forest floor. The leaves transfer most of the nutrients contained in the litterfall, so this fraction, because of its higher concentration of nutrients and biomass, plays the most important role in the dynamics of nutrient cycling. That makes the leaf litter fraction the most accurate indicator of forest nutrient cycling, a result that is in agreement with the observations of Domingos *et al.* (1997) and Yang *et al.* (2005). In the present study, the averages annual return rates were 146.67, 4.84, 21.41, 64.93, and 17.25 kg ha⁻¹ year⁻¹ for N, P, K, Ca, and Mg, respectively. That same sequence of nutrient input was found by Domingos *et al.* (1997), except by reason of quantification of S, the contribution of which was higher than was that of K, Mg, or P. In other fragments within the same biome, also in the state of Rio de Janeiro, Gomes *et al.* (2010) observed averages annual return rates of 3.05, 16.20, 71.60 and 15.60 kg ha⁻¹ year⁻¹ for P, K, Ca, and Mg, respectively.

The NUE (Vitousek 1982) is a good indicator of the nutrients required to sustain a single mass unit of litter. Higher NUE values indicate a larger quantity of litter transferred to the soil per nutrient unit (Yang *et al.* 2005). Although the present study sites differ in dendrometric characteristics and floristic composition (Cunha 2002) the NUE was similar among sites, except for P, which was used more efficiently in fragment M2. In another area of Atlantic Forest, Domingos *et al.* (1997) found an NUE of 44 for N, whereas Smith *et al.* (1998) found the NUE for N to be 85 in the Amazon rain forest. Therefore, the NUE for N found in the present study is within the normal range for tropical forests.

The variation in the amount of litter between years was likely due to the decrease in rainfall, which has been shown to reduce the decomposition rate (Costa *et al.* 2005). The average standing litter stock was 8.5 and 8.8 Mg ha⁻¹ in M1 and M2, respectively. Pinto *et al.* (2009) found an average standing litter value of 7.0 Mg ha⁻¹ in mature fragments of semideciduous forest, higher values corresponding to periods of greater litter deposition. Although the total standing litter was not significantly different between the two fragments, a greater quantity of leaf litter was observed in M2. The nutrient accumulated in the greatest quantities was N, followed by Ca, Mg, K and P (Tab. 5).

The lower decomposition rate observed in M2 may have been due to a local microclimate effect resulting from the lower tree density of this forest fragment (Cunha *et al.* 2009), together with its smaller area and consequently greater edge effect, which would have resulted in a greater loss of soil humidity. Because decomposition decreases during dry periods, a loss of soil humidity would partially restrict the decomposition rate (Villela & Proctor 2002). The nutrient mineralization rate was not different for P, Ca and Mg, although N was higher in M1 and K was higher in M2. A higher mineralization rate translates to a higher rate of nutri-

ent cycling, which would result in the soil partially retaining its high nutrient availability. This result is in agreement with those of Yang *et al.* (2005), who emphasized the importance of litter dynamics in maintaining soil fertility. The nutrient found to be transferred to the soil in the greatest quantities was K, confirming its susceptibility to lixiviation (Dent *et al.* 2006); this element is not a part of any plant structural component (Gama-Rodrigues *et al.* 2007).

Conclusion

The litter biomass input did not differ between the two forest fragments studied, indicating that their different elevations and biomasses did not affect nutrient cycling. However, a difference in litter deposition between the dry and rainy seasons was observed in fragment M2, indicating a spontaneous microclimatic effect on nutrient cycling. The nutrient transfer through the litter also did not differ between fragments, although the NUE for P was higher in fragment M2. The litter residence time was lower in fragment M1, indicating higher rates of decomposition and mineralization of N. Our results indicate that the two forest fragments studied are functionally similar in terms of nutrient cycling, despite their different characteristics.

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