

Litter flux in a successional forest ecosystem under nutrient manipulation in Eastern Amazon**Fluxo de serapilheira em um ecossistema florestal sucessional sob manipulação de nutrientes na Amazônia Oriental**

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ABSTRACT

The aim of this work was to evaluate the dynamics of Ca and Mg cations, via litter, in a successional forest ecosystem, on the middle plateau of the Apeú river, in Castanhal, northeast of Pará (1°19' S, 47°57' W). The magnitude of this phenomenon can be explained by the functional role of the floristic structure, with dominant species, *Myrcia sylvatica* (G. mey) DC., *Myrcia bracteata* (Rich) DC., *Miconia ciliata* (Rich) DC., *Lacistema pubescens* Mart., *Lacistema aggregatum* (Berg.) Rusby, *Vismia guianensis* (Aubl.) Choisy, *Cupania scrobiculata* Rich. and *Ocotea guianensis* Aubl, which consisted in the determinant factors, associated to the natural hydroperiodic effect. The evaluation of analytical results, in litter removal treatment, of the mean mass of Ca ranged from 0.018 to 0.076 g m⁻²month⁻¹, while Mg varied from 0.006 to 0.028 g m⁻²month⁻¹, being significantly (P<0.05) different from control in treatment and time. However, the flux distribution was influenced by the

season, being higher in the dry period. The flux values of Ca ($0.047 \pm 0.015 \text{ g m}^{-2}\text{month}^{-1}$) were significantly higher ($P < 0.05$) than those of Mg ($0.015 \pm 0.004 \text{ g m}^{-2}\text{month}^{-1}$), independently of the manipulation via treatment, phenomenon explained by the dynamics of Calcium in the biogeochemical cycle.

Keywords: Eastern Amazon, biogeochemistry, secondary forest, litter removal, litter.

RESUMO

O objetivo deste trabalho foi avaliar a dinâmica de cátions Ca e Mg, via serapilheira, em um ecossistema florestal sucessional, no planalto médio do rio Apeú, em Castanhal, nordeste do Pará ($1^{\circ}19' \text{ S}$, $47^{\circ}57' \text{ W}$). A magnitude desse fenômeno pode ser explicada pelo papel funcional da estrutura florística, com espécies dominantes, *Myrcia sylvatica* (G. meyer) DC., *Myrcia bracteata* (Rich) DC., *Miconia ciliata* (Rich) DC., *Lacistema pubescens* Mart., *Lacistema agregatum* (Berg.) Rusby, *Vismia guianensis* (Aubl.) Choisy, *Cupania scrobiculata* Rich. e *Ocotea guianensis* Aubl, que consistiu nos fatores determinantes, associados ao efeito hidroperiódico natural. A avaliação dos resultados analíticos, no tratamento de remoção de serapilheira, da massa média de Ca variou de 0,018 a 0,076 $\text{g m}^{-2} \text{ meses}^{-1}$, enquanto o Mg variou de 0,006 a 0,028 $\text{g m}^{-2} \text{ meses}^{-1}$, sendo significativamente ($P < 0,05$) diferente do controle no tratamento e no tempo. No entanto, a distribuição do fluxo foi influenciada pela estação, sendo maior no período seco. Os valores de fluxo de Ca ($0,047 \pm 0,015 \text{ g m}^{-2} \text{ meses}^{-1}$) foram significativamente maiores ($P < 0,05$) do que os de Mg ($0,015 \pm 0,004 \text{ g m}^{-2} \text{ meses}^{-1}$), independentemente da manipulação por tratamento, fenômeno explicado por a dinâmica do cálcio no ciclo biogeoquímico.

Palavras-chave: Amazônia Oriental, biogeoquímica, floresta secundária, remoção de serapilheira, serapilheira.

1 INTRODUCTION

The nutrient scarcity in tropical rainforests is a reflection of the intense weathering which rocks and soils are submitted to in a humid tropical environment. The high temperatures and rainfall promote the leaching of soil elements, with the preferential loss of Na, K, Ca, Mg and Si by the system. Intense leaching, besides nutrient loss, favors the formation of clay minerals with low cation retaining capacity (Jordan, 1985), also leading to the relative enriching of the soil in Fe and Al oxides.

Therefore, the predominant geochemical processes in humid tropical ecosystems tend to promote the loss of cationic nutrients. However, studies on nutrient cycling, usually performed in forests, have demonstrated the high efficiency of this natural process in the ecosystems maintenance. In rainforests, many strong interactions occur between vegetation and soil through nutrient cycling (Golley, McGinnis, Clements, Child, & Duever, 1978), considering that transformations in this compartment of the biogeochemical cycle are the ones which most affect the energy flux within the system, from a holistic perspective (Pritchett, 1979).

Vitousek (1984) considers that nutrient cycling in an ecosystem is efficient when most part of the nutrients released by plants is rapidly absorbed by the roots, mycorrhizas and decomposers, and retained within the system, despite the amount of nutrients cycled between the plant and the soil.

According to León & Osório (2014), in a relatively short period it is possible to notice an improvement in many soil properties, influenced by litter production and decomposition.

Litter acts on the soil surface as an entrance and exit system of nutrients to the ecosystem, through the processes of production and decomposition. These processes are particularly important in the restoration of soil fertility in areas at the beginning of ecological succession (Ewel, 1976; Herrera, Jordan, Klinge, & Medina, 1978). The patterns of litter deposition introduce temporal and spatial heterogeneity in the environment, which can affect the structure and dynamics of plants communities (Facelli & Pickett, 1991).

During cycling, nutrients are transferred from a compartment to another in a series of processes within one or more natural cycles. The conceptual models which describe them are complex and, invariably, involve three fundamental systems of nutrient movement: plant, animal and soil.

The litter-soil system works as a valve where all elements and most part of the energy fixed by producers would pass, conditioning its productivity and stability, affecting its resilience regarding natural or anthropic disturbances. For this reason, litter has been studied for its help in understanding the dynamics of ecosystems through estimates of productivity, nutrient flux, nutrient chemical composition and phenology of arboreal species (Proctor, 1983), which may contribute to determine the ecosystem fragility, before the increasing anthropic pressure.

The quantification of biomass nutrients, as well as its cycling pattern, allows the evaluation of the magnitude of reflections caused by anthropic intervention or natural phenomena, enabling, through studies on nutrient cycling, the quantification of exits or losses of nutrients (Oki, 2002; Vitousek, 1982). Nonetheless, each ecosystem has its characteristic form of storing and cycling nutrients within their compartments.

Brazil has approximately one third of the remaining rainforests of the world, but the impact of anthropic actions on the managed environments has affected important ecosystems (Dionisio et al., 2016; Dionisio et al., 2017), mainly due to the increase of deforestation rates in Brazilian Amazon (INPE, 2016). The search for sustainable production systems has been a fundamental element of strategies for the development of the Amazon region (Leão et al., 2017).

Thus, knowledge concerning the nutrient cycling process and its relation to the natural resources of each environment allows the development of simplified models of the ecosystems, enabling, in this way, the planning of its use for agricultural purposes. Also, this knowledge contributes for a better use of this process, as in an economic perspective, for the rational use of fertilizers to efficiently replace the nutrients exported in tillages, as in an environmental perspective, considering the highest possibilities of promoting ecosystem sustainability.

For this, we have the following question: which are the causes and differences on the dynamics of calcium and magnesium, in the structural foliar component in a successional forest ecosystem? In order to answer this question, we formulated the following hypothesis: if the increase of organic matter and chemical elements have a different nature determined by the litter biogeochemical matrix, therefore, the relative isolation of biogenic factors which control the accumulation functions is possible, considering a successional forest ecosystem.

2 MATERIAL AND METHODS

The study was developed in the Manipulation of Moisture and Nutrient Availability in Young Regrowth Forests in Eastern Amazonia Project (MANFLORA), which began in 1999, when forest regeneration was 12 years old. The experiment was carried out at the Fresh Water Fish Farming Station (EPAD), which belongs to the Federal Rural University of the Amazon (UFRA), in the region of the middle Apeú River, Castanhal, in the Praquiquara River basin (1°19 'S, 47°57' W), 80 km away from Belém.

The surrounding landscape is marked by secondary forests, agroecosystems and pastures. According to Falesi, Baena, & Dutra (1980), in the Bragantina Zone there existed the humid tropical forest that, with colonization and agriculture practice, through successive cuts and burnings, was modified, which caused the formation of a mosaic of different successional stages, with predominance of several agroecosystems, mainly pasture. The settlement under study was modified due to shifting agriculture, that includes the cultivation cycle of corn, cassava and bean, for 1 to 2 years, followed by fallow, which was abandoned in 1987.

The successional forest ecosystem, in many serial stages, also known as secondary forest, and in the region of capoeira vegetation, is mainly derived from deforestation for shifting agriculture. In its early successional stages, it is characterized by arboreal and herbal species of rapid growth and wide distribution (Pires, 1973).

The region's relief is slightly wavy to wavy, under forest vegetation, mostly constituted by a flattened surface, dissected in flat top hills, with small altimetric variation (Tenório et al., 1999). It presents a dystrophic yellow latosol of clayey texture and concretionary laterites (Tenório et al., 1999), including both soils with textural B and latossolic B.

The profiles may be completely clayey or sandy-clayey in A-horizon and strongly acidic clayey with low base saturation in B, having good pore distribution and a subangular or massive block structure, masked by lateritic concretions (Brasil, 1974). Concretions represent 16% of the volume of superficial soil (0-10 cm), with organic pH of 5.0, organic C of 2.2 kg, organic C stock of 2.9 kg m⁻¹

², total N of 0.15 %, C:N 14.4, and Mehlich-1 extractable phosphorus 1.58 kg mg⁻¹ (Rangel-Vasconcelos, 2002).

The climate, according to the Köppen classification, is type Am3, with annual mean rainfall of 2000-2500 mm; 70-90% of the annual rainfall occurs between January and July, while the dry period occurs from August to December, with dry months being considered when rainfall was lower than 100 mm (Table 1). The analysis of the seasonal rainfall climatology confirmed previous results (Figuroa & Nobre, 1990; Rocha, 2001; Vieira et al., 2004), which demonstrated that most part of the Amazon shows two distinct periods: dry, with monthly mean rainfall below 100 mm, and rainy, with mean rainfall above 200 mm/month. The daily mean air temperature ranges from 24.7 to 27.3 °C, with a maximum of 30.1 to 32.7 °C and a minimum of 19.2 to 24.2 °C. Relative air humidity has annual mean values ranging from 78 to 90% (Martorano & Pereira, 1993).

Table 1. Variance analyses with associated significance values for the treatment effects (control and removal treatment), sampling time and its interaction on non-woody mass and nutrients in a secondary rain forest in Eastern Amazon, Brazil. The significance value is indicated (*: P < 0.05, **: P < 0.01, ns: not significant).

Litter removal Experiment			
Litter (non-woody)	Treatment	Time	Treat. x Time
Monthly mass	0.074ns	0.000**	0.993ns
Ca monthly mass	0.011*	0.000**	0.864ns
Mg monthly mass	0.001**	0.000**	0.999ns
Ca monthly concentration	0.000**	0.000**	0.603ns
Mg monthly concentration	0.000**	0.000**	0.993ns
Annual Mass	0.152ns	0.000**	0.247ns
Ca annual mass	0.040*	0.021*	0.107ns
Mg annual mass	0.009**	0.000**	0.232ns
Ca annual concentration	0.000**	0.317ns	0.023*
Mg annual concentration	0.000**	0.000**	0.119ns

The successional ecosystem has the following dominant species: *Myrcia sylvatica* (G. meyer DC.), *Myrcia bracteata* (Rich) DC., *Miconia ciliata* (Rich) DC., *Lacistema pubescens* Mart.,

Lacistema aggregatum (Berg.) Rusby, *Vismia guianensis* (Aubl.) Choisy, *Cupania scrobiculata* Rich. and *Ocotea guianensis* Aubl, which represent 71% of the sample area (Pantoja, 2002). In some species, such as *Annona paludosa* and *Rollinia exsucca*, deciduousness occurs during the dry season.

For this, a floristic survey was performed in the experimental plots, at the beginning of the project, in 1999, that is, when the forest was 12 years old, and later another, in 2006. The tree vegetation was inventoried in four 10 x 10 m plots, where individuals of tree species with a diameter of 1.3 m in height (DBH) \geq 1 cm were measured. Each measured tree was identified with a numbered metal plate and identified up to the species level. The botanical material was collected and herborized in the Herbarium of Embrapa Eastern Amazon.

The procedure of area selection for the collection of depositional flow samples from the biogeochemical matrix was performed at sites with full canopy cover and homogeneity of ecosystem characteristics to obtain a flow sample with greater accuracy. Sample collection was carried out following collectors' location, according to the experimental design of randomized blocks, with repeated measures through time.

The ecosystem was divided into four randomized blocks, with two treatments: control and removal. Each treatment plot measured 20x20 m, with central plots of 10x10 m, which contained three collectors of biogeochemical matrix (depositional litter). The experiment was evaluated during 2000 and 2006, while treatments remained during the interval of the evaluated years.

The collectors had an area of 1 m² (1 m x 1 m) and depth of 0.10 m, suspended from the ground at 0.3 m. The frequency of the collections was weekly in order to prevent the nutrient leaching process from happening in the samples while in the collector (Proctor, 1983). The litter removal treatment was performed every 15 days, when the litter was removed completely from the topsoil, manually, with the aid of plastic rakes (Figure. 1).



Figure 1. Removal procedure of deposited litter, in the litter removal plot in a secondary forest, Castanhal/PA.

Samples of fractions of the biogeochemical matrix were classified as: i) non-woody (leaf, flower, seed, fruit and miscellaneous) and ii) woody > 3 cm (branches). The plant materials collected in each litter collector were dried in the laboratory at 60-70 °C for 48 hours and weighed. At four-week intervals, materials from the same collector were mixed and then separated into woody and non-woody fractions.

Compounds from non-woody samples were grinded and stored in 60 ml glass bottles. For Ca and Mg analyses, 0.5 g subsamples were taken from an extract for chemical analysis of the elements, which was performed by atomic absorption spectrophotometry (Miyazawa et al., 1999; Rothery, 1986). The analyses were carried out at the Embrapa Eastern Amazon Soils Laboratory. The nutrient mass values were determined by multiplying the mean concentrations (ppm) of Ca and Mg by the dry mass values (g m^{-2}) of the biogeochemical matrix of weekly collected litter. The four collections were reunited and expressed monthly.

The analytical results were organized into sheets in the XLS format. MINITAB version 15 was used for all statistical analyses. We analyzed the treatment effects, time and the treatment x time interaction. When necessary, logarithmic and square root transformations were performed to meet the model requirements, such as normality tests and variance homogeneity, with significance criteria ($P < 0.05$).

3 RESULTS AND DISCUSSION

In the secondary forest, during the study period, there were found 2.744 individuals belonging to 24 families and 29 species with a mean DBH of 2.61 cm and a mean height of 4.86 m in 1999,

while in 2006 the mean DBH was 3.31 cm and the mean height was 6.82 m. The number of species found in this experiment was considered low, but it followed the pattern of the secondary forests of the Bragantina Zone, which have few species.

Higher plant diversity may reflect in better biomass quality, which is important for efficient nutrient recycling. In soil vegetation, nutrient storage increases in the following order: boreal < temperate < tropical forests (Waring & Schlesinger, 1985). In contrast, the mass and the nutrient content in the litter increases inversely as a result of less decomposition in cold weather or high latitude conditions.

The first species to occupy the area are little demanding about the quality of the environment. In the earliest successional stages, the community is formed by few species, with individuals of small diameter, rapid growth and intolerant to shade. With the advancement of succession, the pioneer species are replaced by those with slower growth and usually tolerant to shade. It is also observed an increase in the number of species and variety of epiphytic life forms (Budoswski, 1963), with a tendency to reconstitute the original vegetation (Klein, 1980).

Nonetheless, Lugo (1995) believes that tropical forests present resilience after suffering disturbances, but not the ability to return to the initial state of stability, that is, to return to the pre-disturbance state. Gomez-Pompa & Vazquez-Yanes (1981) described the regeneration process of tropical forests as complex and continuous throughout time, reason why it is difficult to divide it in stages, and it may present some stages of stability by the type of life cycle of the dominant species

The most representative families were Lacistmataceae and Myrtaceae, due to the large number of individuals of *Lacistema pubescens* (1,046) and *Myrcia sylvatica* (595), respectively, totaling more than 60% of the floristic composition of the area. The most abundant species in the area, besides the ones mentioned above, were *Vismia guianensis* (134), *Cupania scrobiculata* (131) and *Inga* sp. (87), which were also very abundant in the upper stratum of this forest (Pantoja, 2002; Lima, 2003). These species are considered pioneers in the secondary forests of Bragantina Zone (Oliveira, 1995; Vieira, 1996; Santana, 2000). The most peculiar habit of the vegetation was tree, which indicates that the forest is at a more advanced stage of succession (Smith, Larson, Kelty, & Ashton, 1997).

Ecological succession involves changes in the structure of species and processes of the community throughout time, being very directional and predictable. Succession is controlled by the community, and the environment determines the pattern and speed of change. The changes lead to increasingly complex and stable ecosystems, and if there is any external interference in the system, it will develop until stability is achieved again (Odum, 1988).

For Ferraz, Filho, Imakawa, Varela, & Rodrigues (2004), the existence of ecological groups is based on the premise that the physiological, morphological and behavioral characteristics observed in certain species should be considered as adaptations due to their evolutionary history. The secondary succession is characterized by plant communities that occupy areas where there was originally primary vegetation that has undergone human intervention, reflecting time and land use (Velo, Rangel-Filho, & Lima, 1991). Native forest species of different ecological groups tend to behave differently in relation to nutritional requirements, whereas species from the early successional stages have a greater nutrient absorption capacity than those from subsequent successional stages.

The monthly variation of the mean litter production during the periods of January to December in 2000 and in 2006 in the control and removal plots is represented in Figure 2b. The total litter production in 2000 in the control treatment was 7.73 Mg ha⁻¹year⁻¹, with the lowest and highest deposition in the months of March and September (421.20 kg ha⁻¹ and 997.90 kg ha⁻¹), respectively, with a mean value of 644.40 ± 225.90 kg ha⁻¹; in 2006, the annual litter amount in the control treatment was 6.91 Mg ha⁻¹year⁻¹, ranging from 316.10 kg ha⁻¹ (January) to 937.90 kg ha⁻¹ (July), with a monthly mean of 575.96 ± 202.60 kg ha⁻¹. It is observed that litter production in both years studied were directly influenced by the hydroperiodic phenomenon (Figure. 2a).

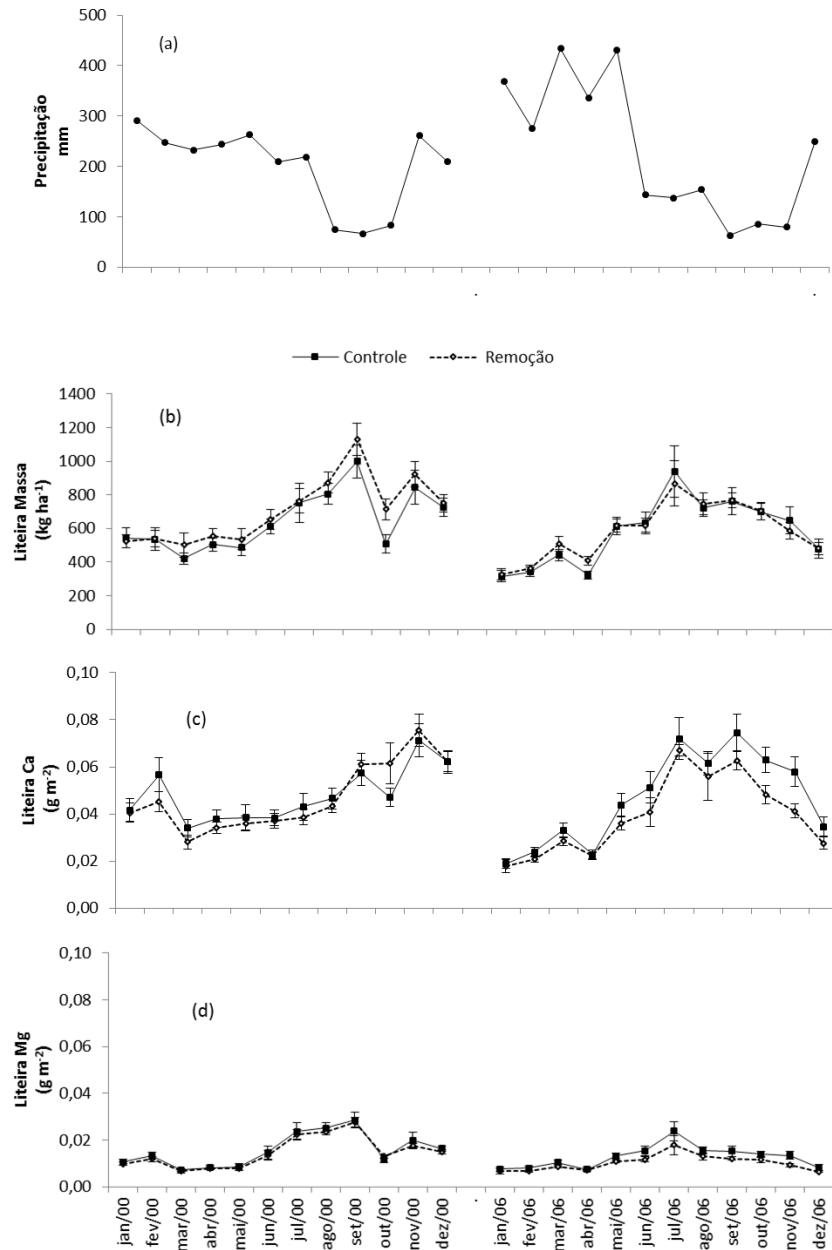


Figure 2. Dynamics of Ca and Mg masses in litter in control and removal treatments, in successional forest in Castanhal/PA. (a) Monthly rainfall, (b) non-woody litter mass, (c) Ca mass dynamics, (d) Mg mass dynamics.

These results can be explained due to the leaves, the main component of the litter, since they are fundamental in the processes of photosynthesis and transpiration, that demand a large amount of water. In this way, plants lose their leaves as an adaptive mechanism to the water stress to which they are submitted. Hence, the increase of leaf fall in the dry season is influenced by climatic phenomena such as hydroperiodicity and solar radiation (Barros, 1979), with precipitation being one of the most important factors in the control of the ecological processes related to the discharge of biomass to the soil.

These results are coherent with the data reported in the seasonal semi-deciduous montane forest of Lavras-MG, with total litter production of $7.8 \text{ Mg ha}^{-1}\text{year}^{-1}$ (Dias & Oliveira Filho, 1997). Brun et al. (2001), in the Deciduous Seasonal Forest in Rio Grande do Sul, also carried out the quantification of accumulated litter biomass in different successional stages. The following stages of succession and accumulated litter were considered: "capoeirão" (5.1 Mg ha^{-1}), secondary forest (5.7 Mg ha^{-1}) and mature forest (7.1 Mg ha^{-1}).

The total amount of litter production in 2000 in the removal treatment was $8.46 \text{ Mg ha}^{-1}\text{year}^{-1}$, with a monthly average of $704.73 \pm 215.00 \text{ kg ha}^{-1}$, which ranged from $501.50 \text{ kg ha}^{-1}$ to $1131.40 \text{ kg ha}^{-1}$. However, in 2006, the mean monthly value was $582.36 \pm 170.50 \text{ kg ha}^{-1}$, ranging from $327.60 \text{ kg ha}^{-1}$ to $866.90 \text{ kg ha}^{-1}$, for a total of $6.99 \text{ Mg ha}^{-1}\text{year}^{-1}$ (Figure 2b). Tropical forests have very complex structure and floristic composition, which directly affect the production of litter, decomposition and release of nutrients to the environment (Alvarez-Sánchez & Guevara, 1999; Vasconcelos & Luizão, 2004). The litter production of an area depends primarily on the productivity of the plant community, and the main abiotic factor which is determinant for this production is climate, with precipitation and temperature being the main components (Facelli & Pickett, 1991).

The litter stores seeds of several species and provides shelter to communities of microorganisms that decompose organic matter, improving soil physical and chemical properties (Holanda, Feliciano, Marangon, Freire, & Holanda, 2015). For these reasons, litter is considered an indicator of the recovery of degraded areas, being the object of comparative studies among the ecosystems (Caldeira et al., 2013; Cunha Neto, Leles, Pereira, Bellumath, & Alonso, 2013; Silva et al., 2015).

The monthly and annual litter mass were highly significant ($P < 0.01$) only in time, being higher in the dry season than in the rainy season (Table 1, Figure 2b). In general, an increase in litter deposition was observed until the age at which the trees reach maturity or close their crowns. Afterwards, slight decrease or stabilization may occur (Bray & Gorham, 1964). Therefore, tree growth influences directly on nutrient cycling in forest ecosystems. The annual litter of control and of litter removal plots were poorly correlated with water inflow through rainfall (Table 1, Figure 2a).

The production of biomass in forest stands basically depends on light, water and adequate supply of nutrients. The dynamics of nutrients through the deposition of organic material is the most important route of the biogeochemical cycle. This cycle, along with the biochemical, allows forest trees to synthesize organic matter through photosynthesis, recycling nutrients, especially in highly weathered soils, where plant biomass is the main nutrient reservoir (Schumacher, 1992). As for the periodicity of deposition, this varies from species to species in tropical and subtropical regions, and climatic factors have a significant influence on this phenomenon.

The monthly mass of Ca was significant ($P < 0.05$) and Mg was highly significant ($P < 0.01$) in treatment and time, as well as in the annual mass, but there was no interaction between them. During the periods of lower precipitation the amount of Ca was even higher than that of Mg (Table 1, Figure 2 c and d). Similar results were found by Caldeira, Vitorino, Schaadt, Moraes, Balbinot, & Caldeira (2008) independently of the successional stage, the accumulated litter in the Dense Ombrophylous Forest was the main mean of transfer of Ca > Mg to the soil. Temporal variations were observed for the studied nutrients, with a tendency of greater nutrient addition in the months of higher litter supply (August, September, October, November and December).

In the control treatment, the production of Ca and Mg in 2000 was of 5.74 kg ha^{-1} ($0.048 \pm 0.017 \text{ g m}^{-2}$) and 1.88 kg ha^{-1} ($0.016 \pm 0.007 \text{ g m}^{-2}$), respectively; in 2006, of 5.57 kg ha^{-1} ($0.047 \pm 0.017 \text{ g m}^{-2}$) and of 1.53 kg ha^{-1} ($0.013 \pm 0.005 \text{ g m}^{-2}$), respectively. In litter removal treatment, the production of Ca and Mg in 2000 were of 5.63 kg ha^{-1} ($0.047 \pm 0.015 \text{ g m}^{-2}$) and of 1.77 kg ha^{-1} ($0.015 \pm 0.004 \text{ g m}^{-2}$); in 2006, of 4.69 kg ha^{-1} ($0.039 \pm 0.017 \text{ g m}^{-2}$) and of 1.22 kg ha^{-1} ($0.010 \pm 0.004 \text{ g m}^{-2}$), respectively (Table 2).

Table 2. Annual production of Ca and Mg nutrients, via litter, under control and litter removal treatments, in 2000 and 2006 in $\text{kg ha}^{-1}\text{year}^{-1}$.

Period	Treatments			
	Control		Removal	
	Ca	Mg	Ca	Mg
2000	5.74	1.88	5.63	1.77
2006	5.58	1.53	4.69	1.22

Litter production and nutrient return in forest ecosystems are the most important route in the soil-plant system. This route is characterized, in the first stage, by the absorption of nutrients by the roots and their distribution by the different parts of the plant, being the absorption rate higher in the period in which the trees are in juvenile stage, which corresponds to the period of greater productivity within the succession process (Kimmins, 1993).

The study of the dynamics of nutrient cycling in a certain ecosystem involves measuring the amount and rate of transfer of a given chemical element from one compartment to another. Biogeochemical cycling, in general, is the way in which nutrients such as the low mobility Ca in the plant are cycled, since for this nutrient the biochemical cycling is little expressive, which is opposite

to what occurs for Mg, of high mobility in the plant (Caldeira, 2003). In addition, during the rainy season, plants tend to grow more when compared to the season of lower rainfall. So, they cycle and renew their leaves more intensely. Thus, the leaves that fall in the rainy season are older and, consequently, with higher Ca content.

Carpanezzi (1980) analyzed data from 20 different hardwood ecosystems from many parts of the world, obtaining the following means for macronutrient concentration, in g kg^{-1} : Ca = 13.4 and Mg = 3.1. The mean values of Ca content, of 0.92 g kg^{-1} (2000) and 0.95 g kg^{-1} (2006), are well below the average stipulated by that author, fact which also occurs for Mg: 0.28 g kg^{-1} and 0.26 g kg^{-1} for 2000 and 2006, respectively. The calcium concentration can be explained by the fact that this element presents low mobility in the plant tissue and is associated with the lignification and constitution of cell walls.

The nutrient content in the litter may vary for the same species depending on the site, the plant characteristics and the nutrient itself, which makes it difficult to compare different stands. Besides, the amount of nutrients is determined by the different parts of the trees (leaves, branches, bark and wood etc.), vegetation of the understory, litter and soil. Each part of a tree has different concentrations of chemical elements in its tissues. In general, the accumulation of nutrients in the tissues has the following order: leaves > bark > branches > wood (Schumacher, 1992). The mean concentrations of Ca (Figure 3) and Mg (Figure 3) were highly significant ($P < 0.01$) in time and treatment, but at the annual concentration, only Ca was not significant in time (Table 1, Figure 3).

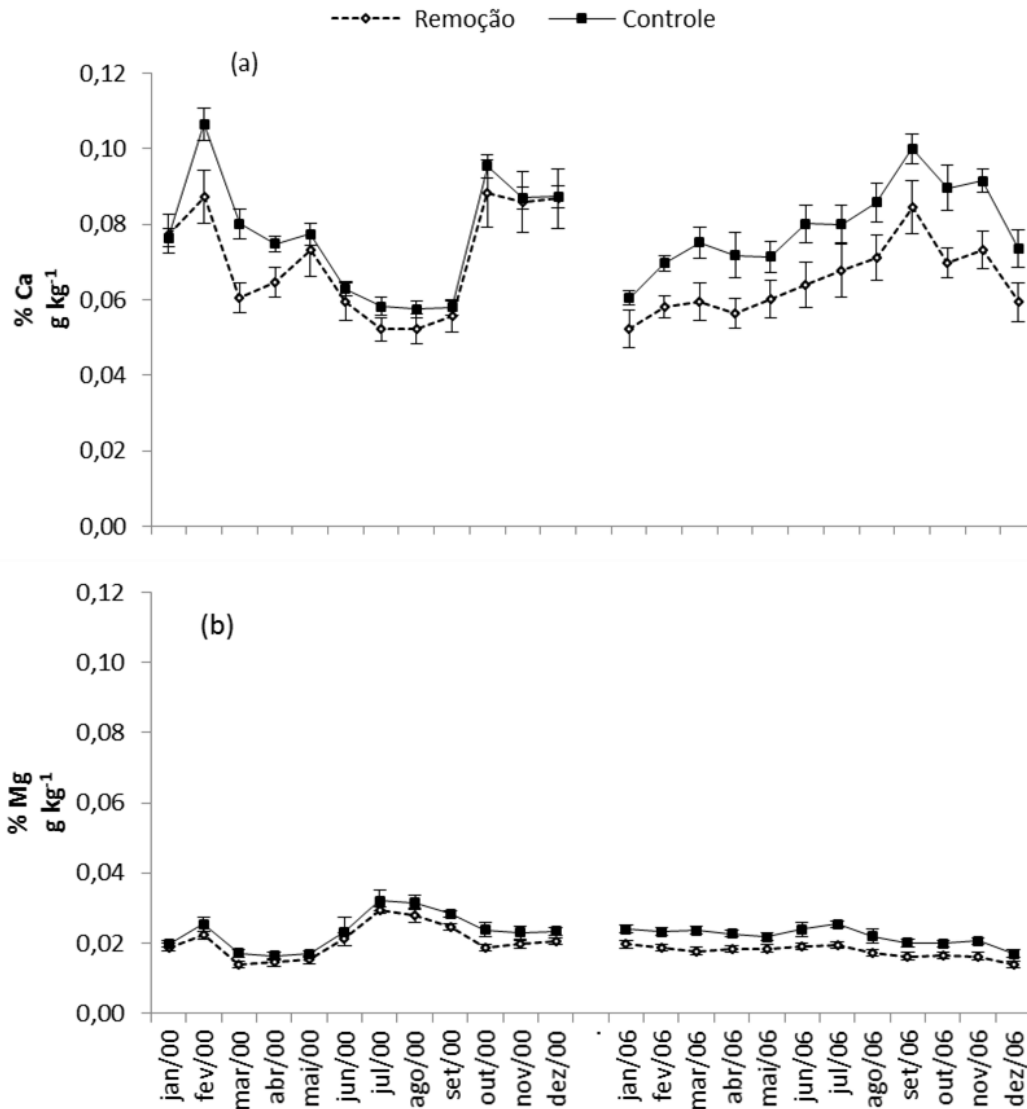


Figure 3. Dynamics of Ca and Mg concentration in control and removal treatments in successional forest in Castanhal/PA. (a) Ca concentration and (b) Mg concentration.

Effects of nutrient manipulation on ecosystem processes are generally not immediate, and studies of mass removal may have slower effects than fertilization studies (Campo & Vazquez-Yanes, 2004). According to Vasconcelos et al. (2008), it is possible that the extension of the litter removal time will further reduce the concentration of nutrients in the mass, leading to a critical point where productivity will be significantly reduced.

However, the seasonality of total litter production was significant, being higher in the dry season, regardless of the treatment. The annual litter production did not present significant differences between the control and removal treatments of the litter. The dynamics of Ca and Mg differed in quantity (production) and concentration, with Ca being higher, independent of time and treatment. There was an effect on the treatment of litter removal, as there were reductions in Ca and Mg

production and concentration. However, it is believed that a longer observation period may permit the observation of greater effects of litter removal, leading to probable nutritional deficiencies in the successional forest.

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