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Nutrient retranslocation in forest species in the Brazilian Amazon

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ABSTRACT. Internal retranslocation is an important mechanism for nutrient conservation in plants, which depends on different factors. However, there are little data about this subject, especially on tropical forest species. This study aimed to evaluate the macronutrient retranslocation dynamic and the influence of ecological (P: pioneer x NP: non-pioneer) and phenological (ND: non-deciduous x D: semideciduous / deciduous) characteristics on the macronutrient content of leaves of five tree species on monospecific plantations in the Brazilian Amazon: *Acacia mangium* Willd., *Parkia decussata* Ducke, *Dipteryx odorata* (Aublet) Willd., *Jacaranda copaia* (Aubl.) D. Don and *Swietenia macrophylla* King. Photosynthetically active green leaves and senescent leaves (leaf litter) were collected. Retranslocation was estimated through an equation proposed by Attiwill, Guthrie and Leuning (1978). The pioneer species presented higher foliar contents of N; the non-pioneer species presented higher contents of K, Ca and S; and the results were inconclusive for P and Mg. The deciduous species presented higher foliar contents of K and of P, whereas the foliar contents of N, Ca, Mg and S were virtually identical between the phenological groups. The internal retranslocation of foliar nutrients in pioneer and non-deciduous species was higher than that of non-pioneer and deciduous species.

Keywords: ecological groups, litterfall, nutrient cycling, phenological groups, plant nutrition.

Retranslocação de nutrientes em espécies florestais na Amazônia Brasileira

RESUMO. A retranslocação interna é um importante mecanismo de conservação de nutrientes nas plantas, que depende de diferentes fatores. Contudo, ainda são incipientes os dados desta natureza, principalmente para espécies florestais tropicais. O presente trabalho objetivou avaliar a dinâmica de retranslocação de macronutrientes e a influência dos grupos ecológico (P: pioneiras x NP: não-pioneiras) e fenológico (ND: não-decíduas x D: semidecíduas / decíduas) nas concentrações foliares de macronutrientes em cinco espécies arbóreas em monocultivo na Amazônia brasileira: *Acacia mangium* Willd., *Parkia decussata* Ducke, *Dipteryx odorata* (Aublet) Willd., *Jacaranda copaia* (Aubl.) D. Don e *Swietenia macrophylla* King. Para tanto, foram coletadas folhas verdes fotossinteticamente ativas e folhas da serapilheira. A retranslocação foi estimada segundo a equação de Attiwill, Guthrie e Leuning (1978). As espécies pioneiras apresentaram maiores concentrações foliares de N; as não-pioneiras apresentaram maiores concentrações de K, Ca e S; e os resultados foram inconclusivos para P e Mg. As concentrações foliares de K e de P foram maiores nas espécies decíduas, enquanto que as de N, Ca, Mg e S foram praticamente idênticas entre os grupos fenológicos. No geral, as espécies pioneiras e as não-decíduas foram mais eficientes na retranslocação de nutrientes.

Palavras-chave: grupos ecológicos, serapilheira, ciclagem de nutrientes, grupos fenológicos, nutrição de plantas.

Introduction

Nutrients are monitored in forest plantations to identify and correct imbalances by means of plant tissue analysis. Therefore, the evaluation of foliar nutrient content is one of the most widely used techniques in forest nutrition research (Araújo & Haridasan, 2007) as leaves are considered the most active and representative organs for plant nutritional status (Malavolta, 2006). Furthermore, foliar nutrient contents are influenced by their availability in the soil (Aerts, 1996). The mobile nutrients in

plants (N, P, K and Mg) are internally redistributed from senescent leaves before their abscission to growing regions such as new leaves (Bambi, Lobo, Dalmolin, & Dias, 2011; Almeida et al., 2014). This internal retranslocation process is especially important because it conserves approximately 60 to 85% of the total content of the nutrients absorbed when the soil availability of the nutrient is low (Malavolta, 2006). Information on this process may contribute to a better understanding of the nutrient conservation strategy in plants and the adaptation of

certain species to low-fertility soils (Magalhães & Blum, 1999).

Pioneer species colonize infertile soils likely through the combination of two characteristics, low nutrient requirements and the efficient use of these elements (Boeger & Wisniewski, 2003), by increasing internal retranslocation, which is influenced by the continuous growth of these plants (Fife & Nambiar, 1997). Thus, pioneer species with fast growth may have higher nutrient retranslocation rates than the non-pioneer species in low-fertility soils. Therefore, pioneer tree species present lower nutrient contents in both green and senescent leaves (leaf litter) than the non-pioneer species (Boeger, Wisniewski, & Reissmann, 2005; Pinto, Martins, Barros, & Dias, 2009). Regarding plant phenology, it is known that deciduous or semideciduous plants generally have higher foliar nutrient contents because senescent leaves are lost before the internal retranslocation of nutrients compared with the non-deciduous phenological group in tropical or temperate forests (Aerts, 1996; Aerts & Chapin, 2000; Franco et al., 2005; Araújo & Haridasan, 2007). However, few studies have focused on nutritional retranslocation monitoring in forest plantations in the Amazon, especially related to native species (Magalhães & Blum, 1999). This study aimed to evaluate the influence of ecological and phenological groups on macronutrient foliar content and retranslocation in five tree species in monospecific plantations in the Brazilian Amazon: the exotic *Acacia mangium* Willd and the native species *Parkia decussata* Ducke, *Dipteryx odorata* (Aubl.) Willd., *Jacaranda copaia* (Aubl.) D. Don and *Swietenia macrophylla* King.

Material and methods

The experimental area was located at the coordinates 2° 56' 13" S and 58° 55' 55" W, 250 km from the AM-010 State Road in Itacoatiara, Amazonas State, Brazil. The local climate was classified as Am, defined by a high total annual rainfall with a short, less rainy period (Köppen, 1948). The average rainfall is 2,551 mm yr⁻¹, and the annual average temperature is 25.9°C. The local relief varies from flat to wavy, and the predominant soil is Oxisol. The original vegetation, an Ombrophilous Dense Forest (Veloso, Rangel Filho, & Lima, 1991), was intensively deforested to exploit the high economic value of some tree species, and the remaining vegetation was burned afterwards, followed by the establishment of *Bracharia humidicula* (Rendle) Schweickert pastures.

In December 2003, some areas on a farm called Nova Vida were selected for the establishment of

the experimental monospecific forest plantations. The pits (40x40x40 cm) were opened manually with a post hole digger. Calcitic limestone was applied (300 g pit⁻¹), and a month later NPK (2-18-20) was also applied (200 g pit⁻¹) according to a previous soil analysis. Weed control was performed by hoeing and periodic herbicide spraying, and leaf-cutting ants were controlled by pesticide application (sulfloramida). Thereafter, three plots of 128 m² (384 m² total area) per monospecific plantation were selected, and three individuals per plot were evaluated. The individuals selected presented the following average diameter at breast height (DBH), with the standard deviation: *A. mangium* (DBH = 8.5±1.9 cm) and *P. decussata* (DBH = 9.8±1.6 cm), both pioneer and non-deciduous species; *D. odorata* (DBH = 5.2±1.1 cm), a non-pioneer and non-deciduous species; *J. copaia* (DBH = 10.9±2.7 cm), a pioneer and semideciduous species; and *S. macrophylla* (DBH = 7.1±1.4 cm), a non-pioneer and semideciduous species.

In December 2006, approximately twenty-five photosynthetically active green leaves (GL) were taken from the newest branches, in the middle of the canopy, of each individual. The GL were bulked to obtain a composite sample per plot (three composite samples per forest species). Senescent leaves (SL) were collected monthly with litterfall traps (1.0 m² and composed of shading screens) installed near the trees, one per individual (three traps per plot). The SL were also bulked to obtain composite samples per plot. The samples of both GL and SL were placed in separate paper bags and dried in a forced draught oven at 65°C for 72 hours to estimate the dry mass. The dried material was ground in a Willey mill, and a portion was subjected to sulfuric acid digestion to determine the nutrient content (g kg⁻¹) of the obtained extract (Tedesco, Gianello, Bissani, Bohnen, & Volkweiss, 1995).

The macronutrient contents in the GL and SL were compared considering the species categorization in the ecological groupings (P: pioneer, NP: non-pioneer species, which included secondary and climax species) and the phenological groupings (ND: non-deciduous, D: deciduous, which included semi-deciduous species). The macronutrient internal retranslocation was estimated according to Attiwill et al. (1978): $NR\% = [(SL - GL) / GL] \times 100$, where: NR% = nutrient retranslocation; SL = nutrient content in senescent leaves (g kg⁻¹); GL = nutrient

content in green leaves (g kg^{-1}). The more negative the NR% value, the higher the element internal retranslocation rate on the plant. On the other hand, positive or near zero NR% values indicated the absence of nutrient internal retranslocation with nutrient accumulation in senescent leaves.

Six simple soil samples per plot were collected using a screw auger at three depths: 0-5 cm, 5-10 cm and 10-30 cm. Sample points were randomly chosen, but the area where litter traps were installed was avoided. A bulked soil sample per plot was obtained by mixing the simple samples, which were air-dried, sieved (2.0 mm mesh) and subjected to chemical analyses (Empresa Brasileira de Pesquisa Agropecuária [Embrapa], 2009) that took place at the Soil and Plant Analysis Laboratory of the Embrapa Occidental Amazon. The results were subjected to an analysis of variance (ANOVA) and to the F test. The means were compared by the LSD test at 5% significance. Statistical analyses were performed using the software SAEG 5.0 (Statistical and Genetic Analysis System, Viçosa Federal University).

Results and discussion

According to the general means, the nutrient contents in both GL and SL leaves followed the same decreasing order: $\text{N} > \text{Ca} > \text{K} > \text{Mg} > \text{S} > \text{P}$ (Table 1). This pattern was also observed for other forest species (Table 2). There were small variations regarding the P and Mg contents in the GL among the forest species (0.90-1.00 and 1.38-2.05 g kg^{-1} , respectively) (Table 1). This may be

because there were no significant differences among the monospecific plantations in relation to the P and Mg availability in the soil (Table 3) as the foliar nutrient content may reflect the nutrient availability in the soil solutions (Aerts, 1996). However, the contents of N, K and Ca in the GL presented a wide variation among the forest species (N : 16.10-23.79 g kg^{-1} ; K : 3.17-11.33 g kg^{-1} ; Ca : 4.99-9.35 g kg^{-1}), although there were no differences among some plantations in relation to the availability of these nutrients in the soil. The contents of S also varied widely in GL (0.89-2.18 g kg^{-1}) (Table 1). There were no differences among the plantations regarding the pH, except for the *J. copaia* soil, which had a higher pH than *A. mangium* (0-5 cm) (Table 3).

A. mangium and *J. copaia* presented a higher N content in both GL and SL, with similar values for each (Table 1). For *J. copaia*, this result may be due to the higher availability of N found in the soil (0-5 cm) than for *D. odorata* and *P. decussata* (Table 3). There were no differences between the *A. mangium* and the other species regarding the N availability in the soil. However, the higher content of N in *A. mangium* leaves was expected because this species is from the Fabaceae (Leguminosae) family, which forms symbiosis with N-fixing bacteria (Schiavo & Martins, 2003). Thus, these plants have this nutritional benefit, which manifests in a higher N content in both green and senescent leaves.

Table 1. Mean nutrient content (standard deviation) in green leaves (GL) and senescent leaves (SL) and nutrient retranslocation (NR) in *Acacia mangium*, *Dipteryx odorata*, *Jacaranda copaia*, *Parkia decussata* and *Swietenia macrophylla*, distributed over different ecological groups (EG), P = pioneer, NP = non-pioneer species, and phenological groups (PG), ND = non-deciduous, D = semi-deciduous / deciduous species, at Itacoatiara-AM.

Species	EG	PG	N			P			K			Ca			Mg			S		
			GL	SL	NR	GL	SL	NR	GL	SL	NR	GL	SL	NR	GL	SL	NR	GL	SL	NR
			(g kg^{-1})	(g kg^{-1})	%	(g kg^{-1})	(g kg^{-1})	%	(g kg^{-1})	(g kg^{-1})	%	(g kg^{-1})	(g kg^{-1})	%	(g kg^{-1})	(g kg^{-1})	%	(g kg^{-1})	(g kg^{-1})	%
<i>A. mangium</i>	P	ND	23.79 (0.38)	14.64 (0.80)	-38.46 (0.09)	0.94 (0.08)	0.24 (0.08)	-74.47 (1.01)	7.28 (0.90)	3.01 (0.90)	-58.65 (1.61)	5.17 (0.91)	5.89 (0.39)	13.93 (0.16)	1.89 (0.16)	1.85 (0.16)	-2.12 (0.28)	1.21 (0.09)	0.75 (0.09)	-38.02 (0.09)
<i>D. odorata</i>	NP	ND	18.01 (3.28)	10.29 (0.60)	-42.87 (0.05)	0.90 (0.08)	0.28 (0.08)	-68.89 (0.80)	4.01 (0.51)	1.31 (0.51)	-67.33 (1.21)	6.13 (2.37)	11.07 (0.22)	80.59 (0.28)	1.38 (0.28)	1.79 (0.28)	29.71 (0.24)	1.05 (0.05)	1.02 (0.05)	-2.86 (0.05)
<i>J. copaia</i>	P	D	23.49 (2.48)	17.71 (1.76)	-24.61 (0.06)	1.00 (0.04)	0.43 (0.04)	-57.00 (0.11)	3.17 (0.11)	0.71 (0.11)	-77.60 (0.77)	4.99 (0.35)	5.58 (0.35)	11.82 (0.06)	2.05 (0.47)	1.71 (0.47)	-16.59 (0.08)	0.89 (0.06)	0.82 (0.06)	-7.87 (0.06)
<i>P. decussata</i>	P	ND	17.20 (1.43)	14.30 (2.78)	-16.86 (0.20)	0.79 (0.09)	0.37 (0.09)	-53.19 (0.90)	4.13 (0.65)	1.20 (0.65)	-70.94 (3.18)	8.26 (0.37)	7.78 (0.37)	-5.81 (0.15)	1.40 (0.15)	0.92 (0.15)	-34.29 (0.39)	1.55 (0.17)	1.39 (0.17)	-10.32 (0.17)
<i>S. macrophylla</i>	NP	D	16.10 (0.64)	8.17 (1.36)	-49.25 (0.02)	0.90 (0.05)	0.46 (0.05)	-48.89 (3.62)	11.33 (3.04)	6.80 (3.04)	-39.98 (0.95)	9.35 (2.50)	10.81 (0.95)	15.61 (0.19)	1.54 (0.19)	1.78 (0.19)	15.58 (0.34)	2.18 (0.20)	1.66 (0.20)	-23.85 (0.20)
P MEAN			21.49 (3.72)	15.55 (1.88)	-26.24 (0.11)	0.91 (0.10)	0.35 (0.10)	-60.17 (2.15)	4.86 (1.21)	1.64 (1.21)	-68.68 (1.84)	6.14 (1.19)	6.42 (0.34)	13.88 (0.50)	1.78 (0.50)	1.49 (0.50)	-16.99 (0.33)	1.22 (0.35)	0.99 (0.35)	-16.27 (0.35)
NP MEAN			17.06 (1.35)	9.23 (1.50)	-45.64 (0.00)	0.90 (0.13)	0.37 (0.13)	-59.09 (5.18)	7.67 (3.88)	4.06 (3.88)	-55.22 (2.28)	7.74 (0.18)	10.94 (0.18)	48.83 (0.11)	1.46 (0.01)	1.79 (0.01)	24.51 (0.80)	1.62 (0.80)	1.34 (0.45)	-11.70 (0.45)
ND MEAN			19.67 (3.59)	13.08 (2.57)	-32.04 (0.13)	0.88 (0.09)	0.30 (0.09)	-64.04 (1.79)	5.14 (1.07)	1.84 (1.07)	-65.62 (2.33)	6.52 (2.61)	8.25 (0.35)	36.80 (0.49)	1.56 (0.35)	1.52 (0.49)	-0.77 (0.35)	1.27 (0.35)	1.05 (0.29)	-14.06 (0.29)
D MEAN			19.79 (4.36)	12.94 (8.97)	-36.93 (0.07)	0.95 (0.22)	0.44 (0.22)	-53.29 (5.02)	7.25 (0.37)	3.75 (0.37)	-59.81 (2.51)	7.17 (2.81)	8.20 (2.81)	14.46 (0.34)	1.79 (0.93)	1.74 (0.93)	0.16 (0.74)	1.53 (0.41)	1.24 (0.41)	-15.01 (0.41)
GENERAL MEAN			19.72 (3.65)	13.02 (3.78)	-34.00 (0.08)	0.91 (0.09)	0.36 (0.09)	-59.74 (3.37)	5.98 (2.50)	2.61 (2.50)	-63.30 (1.94)	6.78 (2.62)	8.23 (0.30)	27.86 (0.39)	1.65 (0.39)	1.61 (0.39)	-0.39 (0.51)	1.38 (0.39)	1.13 (0.39)	-14.44 (0.39)

this may be the case with *A. mangium* (Tables 1 and 3). The GL of *A. mangium* presented high N content, whereas the GL of *S. macrophylla* presented high contents of both K and S compared with other forest species from another works (Table 2). The GL of *J. copaia* also had relatively high contents of N, P and Mg.

On the other hand, the GL results presented low N contents for *P. decussata* and *S. macrophylla*; low P contents for *D. odorata*, *P. decussata* and *S. macrophylla*; low K contents for *A. mangium*, *D. odorata*, *J. copaia* and *P. decussata*; low S contents for *A. mangium*, *D. odorata* and *J. copaia*; and low Ca and Mg contents of for all evaluated species (Table 2). The low macronutrient content in the GL of *P. decussata* and *D. odorata* indicates macronutrients to be the most limiting nutrient in the studied area. This is more evident when the species does not have high nutrient retranslocation rates, as observed with the low retranslocation of N in *P. decussata*. In fact, the soil under this species presented low N, K and Ca contents compared with the soil under the other forest species studied.

Nutrient retranslocation followed the decreasing order: K > P > N > Mg > S (Table 1). This pattern is very similar to the ones found by different studies in relation to 15 other tree species, which differ in only the rank of K (P > K > N > Mg > S) (Table 2). The method used to estimate nutrient retranslocation had not considered the intensively leached quantities of K, which may have influenced the first position of K among the other nutrients in relation to the retranslocation in this work. Internal retranslocation rates of N, P, and K occurred in all studied species, with high variation (N: from -16.86 to -49.25% / mean value = -34.41%; P: from -48.89 to -74.47% / mean value = -60.48%; K: from -39.98 to -77.60% / mean value = -62.90%) (Table 1). Internal retranslocation was a function of two

factors: the low availability of these nutrients in all forest plantations soils (Table 3), which is frequently observed in most tropical soils, especially for N and P (Kobe, Lepczyk, & Iyer, 2005), and the high mobility of these nutrients in plant organisms.

Considering the available results of nutrient N, P and K retranslocation, of 18 forest species, N and P were both internally redistributed in 94% of the species and K in 89% (Table 2). It is believed that the rates of N retranslocation were lower than those of P and K because of the N input in the soil-plant system by rainfall. Forti and Moreira-Nordemann (1991) estimated that the deposition of N-NH₄⁺ via rainfall was approximately 0.15 kg ha⁻¹ over 40 days in the rainy season and 0.34 kg ha⁻¹ N over 60 days in the dry season in a Dense Upland Rain Forest in the Ducke Reserve, Brazilian Amazon.

The internal retranslocation rate of N for *A. mangium* was intermediate and higher than that of *J. copaia* and *P. decussata* (Table 1). Lower values for *A. mangium* were expected due to the association of this species with N-fixing bacteria. This pattern of low rates of N internal retranslocation occurred for *Acacia mearnsii* De Wild (Caldeira et al., 1999), a Fabaceae species that also forms symbiosis with N-fixing bacteria (Vargas et al., 2007). Among the species presented in Table 2 with N retranslocation results, symbiosis was also confirmed for the Fabaceae species *Cedrelinga catenaeformis* Ducke and *Dialium guianensis* (Aubl.) Sandwith. (Magalhães, Magalhães, Oliveira, & Dobereiner, 1982). No information was found regarding this aspect for the Fabaceae species *Andira anthelmintica* Benth. The remaining 13 species form the non-Fabaceae group. The mean rate of N retranslocation (-27.80%) for Fabaceae was close to the non-Fabaceae group (-29.05%).

Table 3. Soil chemical attributes (0-5, 5-10, 10-30 cm)* in monospecific plantations of *Acacia mangium*, *Dipteryx odorata*, *Jacaranda copaia*, *Parkia decussata* and *Swietenia macrophylla*, at Itacoatiara-AM.

Species	pH	N	P	K	Ca	Mg
	(H ₂ O)	(g kg ⁻¹)	(mg dm ⁻³)	(mg dm ⁻³)	(cmol. dm ⁻³)	(cmol. dm ⁻³)
0-5 cm						
<i>A. mangium</i>	4.17±0.27b	1.93±0.27bc	3.67±0.58a	24.00±5.57b	0.51±0.15bc	0.29±0.11a
<i>D. odorata</i>	4.50±0.19ab	1.88±0.09c	5.00±1.00a	30.33±5.51ab	0.65±0.25ab	0.36±0.07a
<i>J. copaia</i>	4.66±0.14a	2.28±0.15ab	4.33±0.58a	28.00±1.00ab	1.00±0.37a	0.41±0.21a
<i>P. decussata</i>	4.34±0.04ab	1.69±0.21c	4.33±0.58a	21.33±3.21b	0.19±0.07cd	0.25±0.05a
<i>S. macrophylla</i>	4.38±0.04ab	1.96±0.20bc	5.00±1.00a	35.00±4.00a	0.32±0.09bc	0.31±0.09a
5-10 cm						
<i>A. mangium</i>	4.14±0.23a	1.26±0.23a	3.33±0.58a	16.67±4.04a	0.24±0.10bc	0.18±0.07a
<i>D. odorata</i>	4.45±0.25a	1.30±0.27a	3.67±0.58a	21.00±1.00a	0.44±0.24ab	0.28±0.11a
<i>J. copaia</i>	4.51±0.16a	1.59±0.18a	4.00±0.00a	22.67±2.52a	0.57±0.18a	0.29±0.15a
<i>P. decussata</i>	4.26±0.07a	1.07±0.25a	3.67±1.15a	17.33±4.04a	0.11±0.01cd	0.16±0.04a
<i>S. macrophylla</i>	4.29±0.06a	1.63±0.26a	4.33±0.58a	23.33±3.21a	0.21±0.12bc	0.21±0.11a
10-30 cm						
<i>A. mangium</i>	4.33±0.11a	0.90±0.06a	1.33±0.58a	6.67±0.58a	0.06±0.04a	0.08±0.03a
<i>D. odorata</i>	4.50±0.22a	0.97±0.08a	1.67±0.58a	9.00±1.00a	0.20±0.14a	0.16±0.07a
<i>J. copaia</i>	4.48±0.16a	1.05±0.13a	1.67±0.58a	12.67±4.51a	0.26±0.15a	0.17±0.10a
<i>P. decussata</i>	4.37±0.08a	0.85±0.09a	1.67±0.58a	11.33±4.73a	0.08±0.01a	0.11±0.03a
<i>S. macrophylla</i>	4.31±0.08a	0.96±0.10a	2.00±0.00a	15.33±3.06a	0.09±0.03a	0.09±0.03a

*Means values±standard deviation followed by different letters in the column, in the same depth, are different (LSD test; p < 0.05).

According to the results in Table 2, high retranslocation rates ($>$ general mean) of P and N, the most limiting nutrients regarding availability to plants in tropical soils, occurred in *A. mangium*, *D. odorata* and *S. macrophylla*. Species that have nutrient retranslocation from dead leaves to other tissues before their abscission have a higher capacity to store them in their organism, which minimize losses and results in a litterfall with low nutrient content that slowly decomposes and mineralizes (Aerts & Chapin, 2000). Thus, the nutrient content in the green leaves of these species may be relatively higher, not reflecting the limited availability in the soil (Aerts & Chapin, 2000). Although high retranslocation rates of P were observed in *P. decussata* and *J. copaia*, these species performed low retranslocation rates of N. Therefore, *A. mangium*, *D. odorata* and *S. macrophylla* may be considered more suitable for cultivation in ecosystems with edaphoclimatic conditions similar to the studied area.

Internal retranslocation of S occurred in all studied species, with a high variation (rate ranging from -2.86 to -38.02% / mean value = -16.58%), and the retranslocation of Mg occurred in *A. mangium*, *J. copaia* and *P. decussata* (from -2.12 to -34.29% / mean value = -1.54%). The retranslocation of Ca was observed only in *P. decussata*, and the rate was considered very low (inferior than 6%), which may be due to the variation in the plant nutrient absorption capability (Table 1). According to the results of Ca, Mg and S available in Table 2, the retranslocation of S was observed in 64% of the forest species, whereas the retranslocation of Mg and Ca were observed in 53 and 22% of the species, respectively. Among the macronutrients, Mg and Ca are less mobile in plant organisms due to their structural role in cementing the middle lamella of the cell wall (Larcher, 2000; Malavolta, 2006; Almeida et al., 2014).

There was a trend of a higher N content in GL (21% higher) and SL (41%) in the pioneer species than in the non-pioneer group (Table 1). The opposite pattern, higher contents in the leaves of non-pioneer species group, tended to occur for the K, Ca and S contents in GL (37; 21; 25%, respectively) and SL (60; 41; 26%, respectively). There was not a clear pattern regarding the P and Mg contents in leaves because the differences between the ecological groups were low (less than 20%).

The general mean obtained for all of the species in Table 2, including the species evaluated in this study (39 species total: 16 pioneer species and 23 non-pioneer species), shows that the pattern of

Ca and S contents in GL (56 and 36% higher in non-pioneer species) were sustained. However, the contents of K and Mg were higher in GL from pioneer species (26 and 22%, respectively), whereas the differences between the ecological groups regarding N contents were low (5%).

This divergence occurred due to the wide variation among the species from the same ecological group regarding the N content in GL (pioneer species: 11.10-25.60 g kg⁻¹; non-pioneer species: 11.20-31.10 g kg⁻¹), K (pioneer species: 2.40-22.66 g kg⁻¹; non-pioneer species: 3.56-16.98 g kg⁻¹) and Mg (pioneer species: 1.40-11.14 g kg⁻¹; non-pioneer species: 1.10-4.20 g kg⁻¹). Pioneer species commonly present a higher Mg content in green leaves than non-pioneer species (Boeger et al., 2005) because they have higher photosynthetic activity due to the increased exposure to solar radiation, which increases Mg requirement, an essential element for photosynthesis (Larcher, 2000). Moreover, species in the early stages of succession usually present larger amounts of tissue with secondary walls in the leaves, where Mg accumulates, than do plants that feature the more advanced stages of succession (Boeger & Wisniewski, 2003). *P. decussata* was the only pioneer species that did not fit this pattern.

The species evaluated in an Atlantic Forest fragment in the advanced stage of regeneration presented higher foliar contents of N, P and K, whereas no differences were found among the species present in three different successional stages regarding the Ca content in green leaves, according to Boeger, Wisniewski and Reissmann (2005). These authors argued that this result was probably a reflection of the gradual increase of the litter layer thickness throughout the forest regeneration development, which was responsible for the increases in soil nutrients. However, comparing that study to the species in Table 2 has limitations because in that study some groups of pioneer and non-pioneer species occurred in two or three different successional stages, and the nutrient contents were calculated as a general mean for all species in the forest fragments.

The values of the P retranslocation rates were similar between the groups of pioneer and non-pioneer species studied (Table 1). However, non-pioneer species did not retranslocate Mg and had higher rates of N retranslocation, whereas pioneer species retranslocated Mg and had higher rates of K and S retranslocation. There was no retranslocation of Ca in any ecological groups. A global analysis including the studied species and species from other studies showed that the rates of K, S, P and N

internal retranslocation was 69, 48, 30 and 24% higher in pioneer species, which also retranslocated Mg, whereas non-pioneer species did not retranslocate this nutrient (Table 2).

Nutrient retranslocation is a function of the continuous growth of new tissues (Fife & Nambiar, 1997) and their higher metabolic transpiration (Malavolta, 2006). The slow-growing non-pioneer species absorb the soil nutrients more slowly, which minimizes the nutritional depletion of soils (Chapin, 1980). Therefore, it is believed that non-pioneer species, which have a slow growth rate compared with that of the pioneer species, would probably be more suited to low-fertility soils. When the soil nutrient availability is insufficient for plant growth, such elements are mobilized from the senescent leaves to growing regions such as meristems and young leaves to supply the demand for continuous growth (Chapin, 1980). Thus, under the same edaphic condition of low fertility, the rates of internal nutrient retranslocation are higher in pioneer than in non-pioneer species.

In this work, the differences between phenological groups were low (less than 20%) regarding the contents of N, Ca, Mg and S in GL and SL and the contents of P in GL (Table 1). On the other hand, the deciduous species tended to present a higher K content in GL (29% higher) and SL (51%) and a higher P content in SL (33%), than the non-deciduous species. Considering the results in Table 2 (a total of 39 species which accounted by 26 evergreen and 13 deciduous, including the species in this work), the differences between the phenological groups regarding contents of N, P, K and S in both GL and SL, and Mg in SL were low (less than 20%). However, contents of Ca were 20% higher in GL of deciduous species, whereas contents of Mg 23% higher in GL of non-deciduous species.

According to some authors, non-deciduous plants usually present lower foliar macronutrient contents than deciduous species (Aerts, 1996; Aerts & Chapin, 2000; Franco et al., 2005). This is a consequence of some strategies that minimize the nutritional demand and increase nutrient conservation by non-deciduous species, such as low growth rates and higher leaf longevity, allowing them to colonize low-fertility soils (Chapin, 1980; Araújo & Haridasan, 2007). However, this pattern is not a definite rule because a global analysis of the data from 92 studies conducted in different ecosystems indicated that there are no significant differences between deciduous and non-deciduous species regarding the N and P contents in green and senescent leaves (Kobe et al., 2005). This result may be expected due to the influence of different factors,

such as variations even between species from the same phenological group (Wright & Westoby, 2003), phylogeny (plant family) (Villar, Robledo, Jong, & Poorter, 2006) and environment conditions (Franco et al., 2005; Araújo & Haridasan, 2007).

This work demonstrated that non-deciduous species presented higher retranslocation rates of P and K and performed Mg retranslocation, whereas deciduous species did not retranslocate Mg, and the retranslocation rates of N and S were virtually identical to those of the non-deciduous species, because the differences between the phenological groups were less than 20% (Table 1). As expected, there was no evidence of Ca retranslocation in any of the phenological groups.

High rates of transpiration may increase nutrient absorption and retranslocation (Kerbaudy, 2004). In Amazonia, the average precipitation and temperature are high. Thus, the leaf abscission performed by the deciduous species to avoid high rates of transpiration in higher temperature periods probably influenced the lower foliar retranslocation of the mobile nutrients P and K. This is the reason why deciduous plants generally present higher nutrients contents in senescent leaves (Aerts & Chapin, 2000; Franco et al., 2005; Araújo & Haridasan, 2007). A global analysis of all species in Table 2 indicated that higher rates of N retranslocation occurred for the non-deciduous species (22% higher), whereas the higher rates of S and K retranslocation were observed for the deciduous species (94 and 44% higher, respectively). The rates of both P and Mg retranslocation were virtually identical between the phenological groups (differences < 20%). Although the non-deciduous species presented lower contents of some nutrients in senescent leaves, this fact does not necessarily indicate that these species perform a more efficient nutrient retranslocation than the deciduous species because this ability depends more on the species (Aerts, 1996).

Conclusion

Pioneer species presented higher foliar contents of N, whereas higher foliar contents of K, Ca and S were found in the non-pioneer species. The differences between the ecological groups regarding P and Mg contents were low.

Deciduous species presented higher foliar contents of K and P, although the foliar contents of N, Ca, Mg and S were virtually identical between the phenological groups.

The retranslocation of foliar nutrients in pioneer and non-deciduous species was higher than in non-pioneer and deciduous species.

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