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## Nutrient fluxes in litterfall of a secondary successional alluvial rain forest in Southern Brazil

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**Abstract:** During forest succession, litterfall nutrient fluxes increase significantly. The higher inputs of organic matter and nutrients through litterfall affects positively soil fertility and the species composition, which are essential components in forest restoration and management programs. In the present study, the input of nutrients to the forest soil via litterfall components was estimated for two sites of different development stages, in an early successional alluvial rain forest in Brazil. Litterfall returned to the soil, in kg/ha, ca. 93 N, 79 Ca, 24 K, 15 Mg, 6 P, 1.7 Mn, 0.94 Fe, 0.18 Zn, 0.09 Cu and 11.2 Al, in the site where trees were more abundant and had higher values of basal area. In the other area, where trees were less abundant and values of basal area were comparatively low, litterfall returned <50% of those amounts to the forest soil, except for Al. The amount of Al that returned to the soil was similar in both areas due to the high contribution of *Tibouchina pulchra* (82% of Al returned). Comparatively, high proportion of three dominant native tree species (*Myrsine coriacea*, *T. pulchra* and *Cecropia pachystachya*) explained better litter nutrient use efficiency (mainly N and P) in the site with the least advanced successional stage. Although litterfall of these species show lower nutrient concentrations than the other tree species, their nutrient fluxes were high in both sites, indicating a certain independence from soil essential nutrients. Such feature of the native species is very advantageous and should be considered in forest restoration programs. Rev. Biol. Trop. 59 (4): 1869-1882. Epub 2011 December 01.

**Key words:** litter production, nutrient cycling, nutrient use efficiency, secondary succession, tropical rain forest.

The conversion of natural forests into agricultural and pasture areas disturbs natural nutrient cycling and soil organic matter content, resulting in loss of nutrients from the ecosystem. This phenomenon has been observed over the last few decades in large portions of the alluvial plains of the Brazilian Atlantic coast. Even though the Brazilian Forest Code (1965) and the National System of Conservation Units-SNUC (2000) now protect most of these areas, forests were severely damaged in the past, and most of the present vegetation is at an early to an intermediate stage of secondary succession. A successful management of

these areas, in order to achieve a fast natural recovery, requires a better understanding of secondary successional processes and related nutrient cycling.

The forest floor acts as an input-output system. Plant litter contributes significantly to soil organic matter and to mineralization through decomposition processes, maintaining site fertility and productivity (Prescott 2005). The reestablishment of this system is highly important during succession, particularly in tropical forests, where most available nutrients are generally bound to vegetation biomass or to the organic matter of the upper soil layers

(Brown & Lugo 1982, Ranger *et al.* 2003). The regeneration capacity of these ecosystems depends mainly on the soil degradation level.

Litterfall is an important indicator of primary productivity, nutrient fluxes and carbon transfer in forest ecosystems (Bray & Gorham 1964, Ranger *et al.* 2003). Nutrient-cycling pathways and nutrient-use efficiency are critical factors to consider the suitability of tree species to the different conditions present in forest stands undergoing restoration (Vitousek 1982, Lugo *et al.* 2004). The ratio between litterfall mass and litterfall nutrient content, or the inverse of nutrient concentrations in litterfall (Nutrient Use Efficiency-NUE, according to Vitousek 1982, 1984) can be used as an index of nutrient-use efficiency. Even though studies involving soil fertility or nutrient availability and other components of nutrient-use efficiency (Vitousek 1997), as well as potential and realized resorption (Killingbeck 1996) are available, the litterfall mass:litterfall nutrient content ratio is commonly used to compare ecosystems, sites and species (Silver 1994). This approach works best when the litterfall mass is a fixed proportion of ecosystem production (Vitousek 1982, Binkley *et al.* 2004).

Data on mineral cycling and secondary succession of alluvial plains in Brazilian Atlantic rain forests are scarce. Therefore, as part of a medium-term ecological study in an alluvial Atlantic rain forest, continuing the study by Scheer *et al.* (2009), this paper reports: (1) the role of common tree species in organic matter, nutrient (N, P, K, Ca, Mg, Fe, Mn, Cu, Zn) and Al mineralization through litterfall in a nine to ten year-old regenerating forest divided in two sites differing in tree abundance and values of basal area; (2) the differences in nutrient-use efficiency among species and between sites and its associated implications for succession; and (3) comparisons of observed nutrient fluxes to those of other tropical and subtropical forests.

## MATERIAL AND METHODS

**Study area:** The regenerating alluvial Atlantic rain forest (Floresta Ombrófila Densa,

according to the Brazilian official classification, Veloso *et al.* 1991) is located at Salto Morato Natural Reserve (RNSM) at an altitude of 20m.a.s.l., in Guaraqueçaba, Northeastern coast of Paraná state, Brazil (25°10'45" S - 48°17'48" W) (detailed location in Scheer *et al.* 2009). The vegetation of this area is typical of the alluvial plains along the Brazilian coastline. Soils within the study area are originally Cenozoic sediments from Serra do Morato (uplifted blocks of igneous and high-grade metamorphic rocks) and are predominantly medium-textured Fluvisols and Cambisols (World Reference Base for Soil Resources-FAO-WRB 1998) (Scheer *et al.* 2009). In the past, the area was used for water-buffalo grazing, but at about nine to ten years before this study, this activity was ceased, allowing vegetation to regenerate. The area (about 7ha), was stratified into two sites according to differences in tree abundance and values of basal areas in order to reduce sampling errors (Table 1). These variables were estimated in ten plots of 100m<sup>2</sup> (perimeter at breast height ≥10cm), each of them covering the whole area, which was randomly selected in a previous study (Gatti 2000).

**Site 1:** Most advanced vegetation (Table 1). Located at about 100m from an advanced secondary successional stage of a lower montane rain forest, a major propagule source. At the time this study was performed, the canopy was dominated by *Myrsine coriacea* (Sw.) R. Br. ex Roem. and Schult., Myrsinaceae; *Senna multijuga* (Rich.) H. S. Irwin and Barneby, Fabaceae; *Cecropia pachystachya* Trécul, Urticaceae; and *Tibouchina pulchra* Cogn., Melastomataceae. *Citharexylum myrianthum* Cham. (Verbenaceae), a species from a previous secondary forest, was scattered throughout the site. *Piper aduncum* L. and *Boehmeria caudata* Sw. are frequent species among shrubs. In the herbaceous stratum, *Cyrtocymura scorpioides* (Lam.) H. Rob. and *Manettia congesta* (Vell.) K. Schum. were widespread. *Hieronyma alchorneoides* Allemão and *Vochysia bifalcata* Warm seedlings, species that would probably

TABLE 1  
Stand characteristics and soil properties of the study sites

Parameters*	Site 1 (most advanced)	Site 2 (least advanced)
Age (years)	9-10	9-10
Mean tree height (m)	8	6
Number of tree species	36	24
Stand density (trees/ha, PBH $\geq$ 10cm)	2820	1130
Basal area (m <sup>2</sup> /ha)	22.2	6.7
Dominant early successional tree species (% of basal area)		
Vegetation		
<i>Myrsine coriacea</i>	14	22
<i>Cecropia pachystachya</i>	11	22
<i>Tibouchina pulchra</i>	5	20
<i>Senna multijuga</i>	10	9
<i>Psidium guajava</i>	4	7
<i>Alchornea glandulosa</i>	2	1
<i>Citharexylum myrianthum</i>	28	4
Other species	26	15
Soils*	Medium textured Fluvisols and Cambisols	
Soil (upper layers; 0 – 20 cm depth)		
pH (CaCl <sub>2</sub> )	4.2	4.1
P (mg/kg)	0.4	0.4
Na <sup>+</sup> (cmol <sub>c</sub> /kg)	0.07	0.06
K <sup>+</sup> (cmol <sub>c</sub> /kg)	0.12	0.09
Ca <sup>2+</sup> (cmol <sub>c</sub> /kg)	1.33	1.38
Mg <sup>2+</sup> (cmol <sub>c</sub> /kg)	0.86	0.94
Al <sup>3+</sup> (cmol <sub>c</sub> /kg)	1.92	1.91
H+Al <sup>3+</sup> (cmol <sub>c</sub> /kg)	8.27	9.93
S (cmol <sub>c</sub> /kg)	2.4	2.5
CEC (cmol <sub>c</sub> /kg)	10.7	12.4
BS%	22.6	20.2
OM (g/kg)	49.4	45.1

S=sum of bases (Na<sup>+</sup>+Ca<sup>2+</sup>+Mg<sup>2+</sup>+K<sup>+</sup>), CEC=cation-exchange capacity (S+(H+Al<sup>3+</sup>)), BS=base saturation (100\*S/ CEC), OM=organic matter.

\* Vegetation and Soil data (n=10) from Gatti (2000) and Scheer (2006).

dominate the community in the next successional stage were also observed.

**Site 2:** Least advanced vegetation (Table 1). This site holds partially the same species as site 1. However, the trees were more sparsely distributed, rarely forming a continuous canopy. Shrubs such as *Vernonanthura beyrichii* (Less.) H. Rob. and *Solanum fastigiatum* Willd. were frequent. *Cyrtocymura scorpioides*, *Paspalum wettsteinii* Hack. and

*Brachiaria mutica* (Forsk.) Stapf. dominate the herbaceous community.

Even though both sites (same age) were at a similar successional stage before early grazing activities and were growing on soils with similar chemical conditions (Table 1), some possible reasons to explain present differences in tree abundance and values of basal area are: (1) site 2 is farther from the secondary forest than site 1 (about 100m) and is about 50m closer to a rural road, indicating lower possibility

of receiving propagules from the secondary forest; (2) before forest regeneration, the water buffalo grazing was more intense in site 2 than in site 1, and invasion of *Brachiaria* spp. (alien invasive species) from neighboring areas with hydromorphic Histosols might have happened, delaying the successional process.

**Climate:** The daily mean temperature during the coldest month is 18°C and the mean temperature during the warmest month is about 22°C, with hot and wet summers (January-March) and a less pronounced dry season. The mean annual rainfall is 2 403mm (Scheer 2008). During the period of this study, annual average rainfall in the study area was 2 676mm, with no differences between years ( $p < 0.01$ ). The highest rainfall rates occurred in February 2002 (about 572mm) and the lowest ones in June 2002 (47mm) (Scheer 2009, Scheer *et al.* 2009). The climate of this region is considered subtropical or transitional tropical (Maack 1968).

**Litterfall collection and partition:** For each site, thirty 0.5m<sup>2</sup> circular fixed litter traps were placed in 10 (100m<sup>2</sup>) plots (three traps per plot). Litterfall was collected fortnightly from September 2001 to September 2003. On a monthly basis (28 days) the material (total fine above-ground litterfall) from three traps of each plot was then pooled together to form one sample ( $n = 10$  per site). After air-drying, each sample was divided into four fractions: leaves; reproductive parts; twigs  $\leq 2$ cm in diameter; and miscellaneous material composed by small leaf, bark, twig and insect fragments. Leaves were then split into eight subfractions, summing up 11 subfractions. Seven of the leaf subfractions were composed of the most abundant tree species (*M. coriacea*; *S. multijuga*; *C. pachystachya*; *T. pulchra*; *Alchornea glandulosa* Poepp. And Endl., Euphorbiaceae; *C. myrianthum* and *Psidium guajava* L., Myrtaceae) and one was composed of leaves from all other tree species in the community. Each fraction was dried at 65°C to a constant weight, and then ground and homogenized. The seven

studied species of site 1 comprised about 60% of the total tree abundance and 90% of the total value of basal area. The corresponding values for site 2 were 74% and 85% (Table 1).

**Chemical analyses:** Every third month, the 11 subfractions were pooled together by category in order to form a seasonal sample for each year (two years=eight sampling periods). The seasonal sample was then divided into two subsamples for analysis as follows:

**Nutrient content of total litterfall:** The first subsample of each seasonal sample was grouped to determine the nutrient concentration of total litterfall per plot in each site ( $n = 10$  per site).

**Nutrient content of litterfall components:** Even though nutrient concentrations of leaf litter mass often varied between sites for a given species, the second subsample of each fraction from site 1 was combined with the corresponding material from site 2. This resulted in 11 combined samples of litter components for each of the eight sampling periods (eight replications per each litter component).

In the present study, the total above-ground fine litterfall fluxes were calculated as the sum of the litterfall components (using the concentrations of each fraction).

Chemical analyses were carried out at the Biogeochemistry Laboratory of the Federal University of Paraná, Brazil. The N (Kjeldahl method), K, Ca, Mg, Fe, Mn, Cu, Zn and Al analyses were performed according to Martins & Reissmann (2007), using a Perkin-Elmer 2380 atomic absorption spectrophotometer. Potassium was determined by emission and P was analyzed by colorimetry with a UV/VIS 554 Perkin-Elmer spectrophotometer (ammonium vanadate-molybdate method).

Carbon concentrations of total leaf litter (using a Leco CN-2000 dry combustion analyzer) and of the remaining dry mass after one year of decomposition (experiment carried out during the same period of this study, data from Scheer 2008) were used to estimate the

amount of this element on the forest floor. The nutrient content of litterfall was determined as the product between nutrient concentration and litterfall mass.

Standard errors were calculated for each mineral element concentration. Data were ln-transformed whenever necessary to satisfy assumptions of normality and equality of variance. A paired t-test was performed to test whether there were differences in annual mean concentrations in total litterfall between sites, and a repeated-measure ANOVA (rm-ANOVA) was performed to test differences of mineral element concentration among fractions. "Season" was assigned as the within-subject factor and "fractions" was assigned as the between-subject factor. Because the data did not satisfy the assumption of sphericity (Mauchly's test), the degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity. Differences in between-subject factors were further evaluated using Duncan test. Data were explored using the software SPSS 13.0 (Statistical Package for Social Sciences) for Windows.

## RESULTS

**Amount of litterfall:** The total annual amount of litterfall in site 1 was  $6.4 \pm 1.2 \text{ mg/ha}$  (95% confidence interval) and only  $3.0 \pm 1.0 \text{ mg/ha}$  in site 2. The highest amount of litterfall was

observed at the beginning of the rainy season, which occurred three months before the annual peaks of rainfall and temperatures (Scheer *et al.* 2009).

In the plots of site 1, leaf litter comprised 69% of total litterfall whereas in site 2 leaf litter contribution was ca. 80%. Total litterfall in site 2 showed a higher (56%) relative contribution of the three dominant species listed in Table 1 than in site 1 (22%).

Based on data published by Scheer (2008), the carbon concentration in total leaf litterfall was 440g/kg in samples collected from the same area. After one year of decomposition, the carbon concentration in the remaining dry mass (about 50%) was 340g/kg (Scheer 2008). Therefore, the annual amount of carbon from litterfall origin on the forest floor was 2.81Mg/ha in site 1. After one year decomposing, only 1 090kgC/ha remained as litter standing crop. The corresponding values for site 2 were 1 320kgC/ha/yr and 510kgC/ha, respectively.

**Mineral elements in litterfall:** Average concentrations of N, P, K, Ca, Mg, Cu and Zn in total litterfall of site 1 (higher basal area and tree abundance) were significantly higher than that of site 2, while Al concentrations of site 2 were higher (Table 2). N and Ca had the highest concentrations of all the elements in almost all the litter components, followed by K, Mg,

TABLE 2  
Annual average concentration of nutrients and aluminum in total litterfall of two sites in a secondary alluvial Atlantic rain forest (mean $\pm$ SE; n=8)

		Site 1			Site 2			<i>p</i> value (paired <i>t</i> -test)
N		14.45	$\pm$	1.09	11.58	$\pm$	0.39	<0.05
P		0.96	$\pm$	0.04	0.78	$\pm$	0.07	<0.05
K	(g/kg)	4.38	$\pm$	0.15	3.85	$\pm$	0.23	<0.05
Ca		14.87	$\pm$	0.24	13.68	$\pm$	0.37	<0.01
Mg		2.64	$\pm$	0.22	2.35	$\pm$	0.17	<0.01
Fe		141.8	$\pm$	7.1	138.0	$\pm$	8.0	=0.61
Mn		275.9	$\pm$	13.9	246.4	$\pm$	13.7	=0.09
Cu	(mg/kg)	12.4	$\pm$	0.3	11.2	$\pm$	1.2	<0.01
Zn		25.9	$\pm$	0.9	18.3	$\pm$	0.5	<0.01
Al		1910.9	$\pm$	164.1	3070.6	$\pm$	243.3	<0.01

and P (Table 3). The gradient in micronutrient concentration was as follow:  $Mn > Fe > Zn > Cu$  (Table 3).

The total annual amounts of mineral elements returned to the forest floor from site 1 were (in kg/ha): 93 N, 79 Ca, 24 K, 15 Mg, 6 P, 1.7 Mn, 0.94 Fe, 0.18 Zn, 0.09 Cu and 11.2 Al. Except for Al, less than half of these amounts were added to the forest floor in site 2, (Table 4). Leaf litter contributed with 75% of macronutrients, 67% of micronutrients and 81% of Al in site 1; for site 2, these values were 81%, 75% and 93%, respectively (Table 4). The input of macronutrients and micronutrients via litterfall of the three main tree species was respectively ca. 27% and 21% in site 1 and 54% and 45% in site 2.

Specific results for nutrient concentrations and fluxes via litterfall components (Table 3 and 4) as well as comparisons with other forests (Table 5) are discussed below.

## DISCUSSION

**Nutrient concentrations in total litterfall:** The concentrations of most of the studied elements were significantly higher in total litterfall of site 1 than in site 2. This can be explained by the fact that total litterfall of site 2 was dominated by the three species with comparatively large basal areas and low levels of nutrients. Lower nutrient availability in soil can lead to high nutrient-use efficiencies (Vitousek 1982, Gallardo *et al.* 1999, Dent *et al.* 2006). A decrease in the efficiency of nutrient use (considered as the inverse of nutrient concentrations in litterfall) can occur along the process of forest regeneration, improving soil fertility for late successional species (Vitousek 1982). In fact, it has been reported for more advanced stages of succession or across gradients of forest productivity, that biomass increments become driven by woody biomass, diluting the proportion of leaves in litterfall (Bray & Gorham 1964, Rodin & Basilevich 1967, Vitousek & Reiners 1975, Binkley *et al.* 2004). Therefore, we should not expect the N use efficiency to decline as N supply increases (Binkley *et*

*al.* 2004). In the second year studied (from the 9<sup>th</sup> to the 10<sup>th</sup> year of forest regeneration), the least advanced vegetation (site 2) had a higher increase in biomass and nutrient rates than that of the most advanced vegetation (site 1) (Gatti *et al.* unpublished data).

Aluminum concentrations in site 2 were significantly higher than in site 1 due to the higher contribution of *T. pulchra* ( $p < 0.01$ ), an Al-accumulating species. No clear evidence of seasonality for nutrient or Al concentrations was found (data not presented), a pattern also observed for other Brazilian Atlantic rain forests (Domingos *et al.* 1997). However, some studies (Sampaio *et al.* 1988, Domingos *et al.* 1990) observed higher K, Mg, Na, Mn, and B concentrations in dryer months, which can be partially related to a lower degree of leaching from litter traps.

**Macronutrient concentrations in components of litterfall:** There was neither a significant difference between mineral element concentrations among seasons nor an interaction between the factors "Season" and "Fractions" (rm-ANOVA,  $p > 0.05$ ). Concentrations of N and P within miscellaneous materials were significantly higher than in leaf litter of selected species, probably due to the decomposition of animal material (e.g. excrement and arthropod fragments), as well as leaf fragments (Domingos *et al.* 1997). Among leaf litter fractions, significantly higher N concentrations were observed in *A. glandulosa* and *S. multijuga*. These species probably exhibit a more efficient N uptake from soil or a greater demand for this element. This could indicate that these species do not have a high nutrient use efficiency (NUE), or during the studied years they presented low resorption, as suggested by Killinbeck (1996). The average N concentrations were at intermediate ranges comparing to data from the literature (10 to 20g/kg dry weight or 100 to 20 NUE respectively). This range was observed in Amazonian and slope Atlantic rain forests. Higher N concentrations (between 20 and 35g/kg) were observed in Brazilian deciduous and semideciduous forests that generally occur on



TABLE 3  
Annual average concentration of nutrients and aluminum in litterfall components (material of both sites together) in a secondary alluvial Atlantic rain forest (mean±SE; n=8)

Fraction	g/kg						mg/kg													
	N	P	K	Ca	Mg	Fe	Mn	Cu	Zn	Al										
Twigs	8.1±0.7	f	0.4±0.1	f	2.4±0.2	e	9.0±0.5	c	1.7±0.1	cd	95±10	c	274±26	b	15±1	ab	35±2	a	696±105	d
Reprod. Parts	17.2±1.3	bcd	1.8±0.1	bcd	6.7±0.5	a	7.1±0.4	c	2.1±0.2	bcd	114±11	bc	140±13	c	14±1	abc	23±2	bcd	929±93	cd
Miscellaneous	25.1±2.1	a	1.8±0.1	a	4.2±0.2	c	13.9±0.7	b	2.6±0.2	bcd	313±90	a	275±17	b	16±2	ab	39±2	a	2 901±252	b
Leaves																				
Other species	17.5±1.0	bcd	1.2±0.1	bcd	4.2±0.2	c	15.0±0.5	ab	3.2±0.2	b	166±22	b	427±51	a	16±1	ab	34±3	a	1 701±138	c
<i>M. coriacea</i>	14.4±1.2	cde	0.8±0.1	cde	4.2±0.2	c	8.9±0.1	c	1.7±0.1	cd	149±17	b	125±14	c	10±1	de	19±1	d	491±66	d
<i>A. glandulosa</i>	20.9±2.0	ab	1.0±0.1	b	4.0±0.2	cd	14.8±1.3	b	2.2±0.3	bcd	145±15	b	411±60	a	12±1	bcd	27±3	bc	507±80	d
<i>P. guajava</i>	15.2±0.9	cde	1.1±0.0	cde	6.0±0.4	ab	12.6±0.4	b	3.0±0.2	b	135±23	bc	267±35	b	18±1	a	27±2	b	439±81	d
<i>S. multijuga</i>	18.0±1.1	bc	1.0±0.0	bc	3.4±0.1	d	12.3±1.2	b	2.1±0.2	bcd	138±5	b	256±30	b	11±1	cde	21±2	cd	441±62	d
<i>C. pachystachya</i>	11.8±0.8	ef	0.7±0.0	e	5.4±0.5	b	14.2±0.4	b	2.7±0.2	bc	115±8	bc	259±14	b	7±1	e	15±1	e	338±85	d
<i>T. pulchra</i>	13.2±1.2	de	0.7±0.1	de	2.5±0.1	e	17.5±0.8	a	1.4±0.1	d	133±11	bc	66±5	d	8±1	de	13±1	e	14 008 ±416	a
<i>C. myrianthum</i>	13.8±0.9	de	1.1±0.0	cde	3.1±0.2	d	15.2±0.9	ab	3.7±0.4	a	135±11	bc	206±64	bc	18±2	a	26±3	b	424±116	d

Averages followed by the same letter within a column do not differ significantly at  $p \leq 0.05$  by the Duncan's test.  
Leaves of the seven individual species plus leaves of other species in the community represent leaf litter.



TABLE 4  
Annual average of litterfall (n=10), nutrients and aluminum (kg/ha/yr) content in litterfall components  
at two sites in a secondary alluvial Atlantic rain forest

Fraction	Litterfall	N	P	K	Ca	Mg	Fe	Mn	Cu	Zn	Al
Twigs	1 396	10.47	0.46	3.12	11.98	2.12	0.129	0.369	0.021	0.050	0.855
Reproductive parts	285	4.96	0.49	1.85	1.98	0.61	0.034	0.040	0.004	0.006	0.255
Miscellaneous	326	7.90	0.56	1.33	4.39	0.84	0.109	0.086	0.005	0.013	0.998
Leaves											
Other species including*	1 965	24.20	1.53	5.87	20.24	3.75	0.255	0.590	0.021	0.047	2.674
<i>Myrsine coriacea</i>	658	9.49	0.51	2.71	5.83	1.09	0.101	0.085	0.007	0.013	0.300
<i>Alchornea glandulosa</i>	244	5.62	0.25	0.94	3.99	0.55	0.035	0.114	0.003	0.007	0.113
<i>Psidium guajava</i>	318	4.92	0.34	1.86	4.12	1.00	0.049	0.101	0.006	0.009	0.139
<i>Senna multijuga</i>	408	7.23	0.38	1.37	4.77	0.83	0.057	0.099	0.004	0.008	0.170
<i>Cecropia pachystachya</i>	391	4.76	0.28	2.00	5.51	1.02	0.045	0.102	0.003	0.006	0.131
<i>Tibouchina pulchra</i>	376	5.10	0.27	0.94	6.55	0.53	0.051	0.025	0.003	0.005	5.308
Total of the 6 species	2 395	37.12	2.03	9.82	30.77	5.02	0.338	0.526	0.026	0.048	6.154
<i>Citharexylum myrianthum</i> *	(616)	8.05	0.65	2.02	9.80	2.48	0.080	0.102	0.012	0.018	0.219
Total leaf litterfall	4 360	61.32	3.56	15.69	51.01	8.77	0.59	1.12	0.05	0.10	8.82
TOTAL**	6 367	92.72	5.71	24.02	79.19	14.83	0.944	1.713	0.089	0.183	11.163
Twigs	335	2.63	0.11	0.75	2.86	0.53	0.030	0.093	0.005	0.012	0.233
Reproductive parts	184	3.42	0.34	1.23	1.30	0.42	0.020	0.027	0.003	0.004	0.157
Miscellaneous	93	2.19	0.16	0.38	1.25	0.25	0.032	0.025	0.001	0.004	0.277
Leaves											
Other species including*	455	4.60	0.29	1.14	3.79	0.64	0.05	0.12	0.00	0.01	0.540
<i>Myrsine coriacea</i>	288	4.19	0.22	1.18	2.54	0.48	0.044	0.037	0.003	0.006	0.130
<i>Alchornea glandulosa</i>	10	0.21	0.01	0.03	0.15	0.02	0.001	0.005	0.000	0.000	0.004
<i>Psidium guajava</i>	76	1.19	0.08	0.44	0.99	0.25	0.012	0.027	0.001	0.002	0.032
<i>Senna multijuga</i>	159	2.78	0.15	0.53	1.94	0.34	0.022	0.041	0.002	0.003	0.072
<i>Cecropia pachystachya</i>	844	10.26	0.61	4.55	12.04	2.24	0.100	0.221	0.006	0.014	0.241
<i>Tibouchina pulchra</i>	567	7.83	0.41	1.41	9.76	0.79	0.077	0.037	0.005	0.007	7.923
Total of the 6 species	1 944	26.46	1.48	8.14	27.42	4.12	0.26	0.37	0.02	0.03	8.379
<i>Citharexylum myrianthum</i> *	(204)	2.69	0.21	0.66	3.26	0.82	0.027	0.036	0.004	0.006	0.076
Total leaf litterfall	2 399	31.06	1.77	9.28	31.21	4.76	0.30	0.49	0.02	0.04	8.92
TOTAL**	3 011	41.99	2.60	12.30	39.87	6.78	0.412	0.670	0.035	0.067	9.688

\* Leaf litter of *Citharexylum myrianthum* were sampled separately only in the second year.

\*\* Fluxes calculated as the sum of the litterfall components (using the concentrations of each fraction).

Leaves of the seven individual species plus leaves of other species represent total leaf litter.

TABLE 5  
Total litterfall and nutrient fluxes in some tropical and subtropical forests

Forest type/site		Soil Information (FAO-WRB)	Litterfall kg/ha/yr	kg/ha/yr									
				N	P	K	Ca	Mg	Fe	Mn	Cu	Zn	Al
ATLANTIC DENSE RAIN FORESTS													
Restinga <sup>1</sup>		Podzols	3 900	28	1	7	30	11	0.5	1.5	0.0	0.1	1.3
Restinga <sup>2</sup>	Between beach ridge	Podzols	7 673	82	2	28	51	1	0.8	1.1	0.1	0.1	3.9
Restinga <sup>2</sup>	On beach ridge	Podzols	5 235	39	1	17	35	13	0.4	1.1	0.0	0.1	1.6
Restinga <sup>3</sup>	On beach ridge	Podzols	5 080	57	4	12	65	16	0.9	0.8	0.0	0.2	—
Alluvial	SITE 1 – This study	Fluvisols	6 367	93	6	24	79	15	0.9	1.7	0.09	0.18	11.2
Alluvial	SITE 2 – This study	Fluvisols	3 011	42	3	12	40	7	0.4	0.7	0.04	0.07	9.7
Lower Montane <sup>1</sup>	—	—	6 300	102	4	20	60	19	1.2	4.6	0.1	0.2	5.3
Lower Montane <sup>4</sup>	Affected by pollution	Ferral./Cambi.	1 803	46	2	6	22	3	4.9	1.2	0.0	0.1	1.7
Lower Montane <sup>4</sup>	Affected by pollution	Ferral./Cambi.	3 810	82	3	10	39	5	7.2	1.9	0.1	0.3	3.0
Lower Montane <sup>5</sup>	Affected by pollution	Ferral./Cambi.	5 289	135	7	18	80	7	21.4	1.7	0.0	0.3	33.0
Lower Montane <sup>5</sup>	Mid successional	Ferral./Cambi.	5 682	128	3	14	56	13	3.7	3.5	0.1	0.3	10.1
Lower Montane <sup>5</sup>	Mid successional	Ferral./Cambi.	4 460	98	2	11	30	9	2.4	2.4	0.1	0.2	5.9
AMAZONIAN DENSE RAIN FORESTS													
Terra firme <sup>6</sup>	—	—	7 400	106	2	13	18	13	1.2	0.7	0.0	0.1	—
Terra firme <sup>7</sup>	Forest	Ferralsols	6 657	126	3	26	49	14	1.4	4.2	0.1	0.1	—
MIXED RAIN FORESTS (ARAUCARIA MOIST FORESTS)													
Alluvial <sup>8</sup>	Late successional	Fluvisols	9 400	199	18	42	132	21	—	—	—	—	—
Montane <sup>9</sup>	—	Acri. and Ferral.	6 527	89	6	32	63	16	—	—	—	—	—
SEMIDECIDUOUS FORESTS/SAVANNAS													
Coastal <sup>10</sup>	Late successional	Acri. and Ferral.	8 340	—	3	23	49	14	1.3	0.4	0.4	0.4	—
Upper Montane <sup>11</sup>	—	—	6 700	128	3	26	66	13	1.9	3.7	0.5	0.5	10.1
Montane <sup>12</sup>	—	Ferralsols	8 643	198	7	48	149	27	4.9	2.8	0.3	0.3	9.2
Montane <sup>11</sup>	—	Ferralsols	8 600	174	5	40	146	20	1.7	3.7	0.3	0.3	4.0
Montane <sup>13</sup>	—	—	8 800	203	6	44	109	24	2.9	8.7	0.2	0.2	9.3
Montane <sup>14*</sup>	—	—	—	184	5	39	148	20	3.7	8.7	0.2	0.2	9.3
Montane <sup>15</sup>	—	—	11 600	230	7	82	210	30	8.8	1.4	0.6	0.6	—
Montane <sup>16</sup>	Late successional	—	9 014	161	9	69	217	36	4.9	2.5	0.4	0.4	4.8
Montane <sup>17</sup>	Late successional	—	12 970	219	6	67	108	38	10.6	7.7	0.8	0.8	—
Montane <sup>17</sup>	Mid successional	—	10 460	166	5	50	89	29	10.0	6.7	0.7	0.7	—
Montane <sup>18</sup>	—	Ferralsols	7 770	118	4	35	32	24	18.3	5.3	0.2	0.2	—
Tall Savanna <sup>19</sup>	—	Ferralsols	7 800	64	5	12	27	11	—	—	—	—	—
Savanna <sup>19</sup>	—	Ferralsols	2 100	18	1	3	7	3	—	—	—	—	—
Savanna/Riparian <sup>20*</sup>	—	—	—	107	5	29	52	17	3.6	2.5	0.2	0.2	20.1

References: <sup>1</sup>Moraes *et al.* (1999); <sup>2</sup>Britez (1994); <sup>3</sup>Pires (2001); <sup>4</sup>Domingos *et al.* (2000); <sup>5</sup>Leitão-Filho *et al.* (1993); <sup>6</sup>Klinge & Rodrigues (1968); <sup>7</sup>Scott *et al.* (1992); <sup>8</sup>Sousa (2003); <sup>9</sup>Britez *et al.* (1992); <sup>10</sup>Sampaio *et al.* (1988); <sup>11</sup>Morellato (1992)/1987\*; <sup>12</sup>Pagano (1989); <sup>13</sup>Cesar (1993); <sup>14</sup>Schlittler (1990)\*; <sup>15</sup>Diniz (1987); <sup>16</sup>Santos (1989); <sup>17</sup>Toledo *et al.* (2002); <sup>18</sup>Dias & Oliveira-Filho (1997); <sup>19</sup>Peres *et al.* (1983); <sup>20</sup>Delitti (1984)\*. \* Listed by Britez (1994).

more eutrophic soils, alluvial *Araucaria* moist forests, and Atlantic rain forests affected by pollutants. Forests over sandy soils, such as “restingas”, “cerrados” (savannas), and the transition formations between “Caatinga” and Amazon biomes, had a lower range (5 to 8g/kg), even though some species can present very high concentrations in leaf litter (Pinto & Marques 2003).

The fundamental metabolic processes involving carbohydrates in flowering, fruiting and seed formation have a relevant contribution for the significantly higher levels of P and K in the fraction comprising the reproductive parts (Mengel & Kirkby 1982). The lowest concentrations of P among the studied fractions were observed in the twig fraction. Among the studied species, significantly lower P concentrations were observed in *T. pulchra*, *C. pachystachya* and *M. coriacea*. P concentrations were similar to other Atlantic rain forests and in *Araucaria* moist forests (0.6 to 1g/kg). Forests growing on more eutrophic soils have demonstrated higher levels of P in litterfall, generally above 1g/kg. Values ranging from 0.2 and 0.5g/kg were reported for “restinga” and Amazonian “Terra Firme” forests, indicating that P is a limiting element in these tropical ecosystems (Vitousek 1984). The low P concentrations found in this study indicate high P use efficiency. The K concentrations (about 4g/kg) were slightly higher than in other Atlantic rain forests (Pinto & Marques 2003) and lower than most of the other forests (Britez *et al.* 1992, Dias & Oliveira-Filho 1997).

The highest Ca and Mg concentrations were observed in leaf litter. Concentrations of Ca in leaf litter of *T. pulchra* were significantly higher than in leaf litter of other species. *C. myrianthum* leaf litter had the highest Mg concentrations. Ca concentrations were intermediate compared to other Atlantic rain forests and to *Araucaria* forests (Britez *et al.* 1992, Sousa 2003) where values range between 9 and 17g/kg of dry weight (Leitão-Filho *et al.* 1993, Pinto & Marques 2003). Brazilian semi-deciduous forests contained higher Ca concentrations, (13 to 40g/kg). In oligotrophic soils,

the reported values were between 3 and 9g/kg, suggesting high Ca use efficiency. Similar values have been reported in deciduous forests in Southeastern Brazil (Pagano 1989, Santos 1989). The Mg concentrations obtained in the present study (about 2.5g/kg) were similar to those reported in other studies (Britez *et al.* 1992, Britez 1994).

**Micronutrient and aluminum concentrations in components of litterfall:** Higher Fe concentrations in leaves than in twigs and reproductive parts can be explained by its lower Fe mobility between different plant organs and its presence in the chlorophyll structure as Mg (Mengel & Kirkby 1982). Concentrations of Mn in *T. pulchra* leaf litter were significantly lower than in other species. The lowest levels of Cu were found in *C. pachystachya*, while the lowest levels of Zn were observed for both *T. pulchra* and *C. pachystachya*. Concentrations of Mn in the leaf litter of other species (all leaves except that of selected species) and *A. glandulosa* were significantly higher than that observed for other species studied. The highest Cu concentrations were observed in *P. guajava* and *C. myrianthum* leaf litter. Micronutrients are not often quantified in litterfall studies (Moraes *et al.* 1999) and the few data available (e.g. Fe and Mn) are quite variable. However, the resulting gradient in micronutrient concentration observed here (Mn>Fe>Zn>Cu) was also observed in podzols of Atlantic rain forests (Britez 1994, Moraes *et al.* 1999) and in Amazonian forests (Klinge & Rodrigues 1968).

Aluminum concentrations (2 500mg/kg in average) were higher in the studied sites compared to other forests due to the presence of *T. pulchra*, and were lower than Atlantic rain forests affected by air pollution (Leitão-Filho *et al.* 1993) where this species can also be found. *T. pulchra* has about 35 times more Al than other species (14 000mg/kg of dry matter). These plants have a high capacity for Al uptake and accumulation and are very well adapted to high Al availability in acid soils, which are common in Atlantic rain forests (Domingos *et al.* 2003). A possible mechanism

for detoxification of Al consists of: Al uptake through Al-F (fluoride) or Al-citrate complexes and storage in large intercellular spaces in the leaf apoplast, together with Si (silicon) or Al-oxalate complexes (Mengel & Kirkby 1982, Klumpp *et al.* 1996, Britez 2001, Jansen *et al.* 2002, Domingos *et al.* 2003). Other species in this forest community may have mechanisms that facilitate Al exclusion. Membrane impermeability of toxic forms, exudation of chelant organic acids and carboxylate complexes in rizosphere can prevent Al-toxicity in aerial plant parts (Mengel & Kirkby 1982, Klumpp *et al.* 1996, Jansen *et al.* 2002). Al availability may stimulate the growth of some species of *Tibouchina* (Jansen *et al.* 2002). As already mentioned, *T. pulchra* also contained high levels of Ca in leaf litter. The Ca-H or Ca-Al exchange reactions in the upper soil layers provide an efficient buffer for soil acidity (Ranger *et al.* 2003). *T. pulchra* was a very common pioneer species, mainly in site 2 (about 20% of basal area, 1.4m<sup>2</sup>/ha). Further investigations are needed to characterize the precise role of *T. pulchra* in the Al cycle during succession and its influence in other species of the forest community.

**Litterfall mineral element fluxes:** The quantity of nutrients and organic matter returned to the forest floor are very important factors in successional stages of vegetation for the restoration of soil organic resulting in higher availability of nutrients in this compartment. The sum of macronutrient fluxes in litterfall reached 217kg/ha/yr in site 1 and 104kg/ha/yr in site 2. Values ranging from 150 to 280kg/ha/yr were measured in many Amazonian and Atlantic rain forests and *Araucaria* moist forests. Semi-deciduous forests showed the highest values, ranging from 215 to 645kg/ha/yr. Macronutrient fluxes ranging from 75 to 180kg/ha/yr were reported for forests over sandy (oligotrophic) soils, “cerrados”, lowland and “restinga” forests. Therefore, even though the studied area is a regenerating forest (nine to ten years old), it produces substantial amounts of nutrients in litterfall, what indicates high productivity.

Oligodominance, which is very common in the earlier stages of secondary succession, can explain the major contributions of *C. pachystachya* and *T. pulchra* in total litterfall from site 2, where the least advanced vegetation dominated (site 2) as well as its lower proportion of twigs in litterfall. *M. coriacea* leaf litter was responsible for the highest annual amount of N and K deposition in site 1, while *C. myrianthum* was responsible for the greatest annual amount of P, Ca and Mg. *C. pachystachya* and *T. pulchra* showed the highest annual contribution of all analyzed macro and micronutrients in site 2 due to their higher leaf litter mass.

*M. coriacea* leaf litter contributed to the highest annual input of Fe to the forest soil, while *A. glandulosa* contributed to the highest annual input of Mn, and *C. myrianthum* to the highest annual additions of Cu and Zn in site 1.

*T. pulchra* contributed with up to 24% of leaf fall and 82% of Al returned to soil through litterfall in site 2. The Al flux at this site was similar to that of site 1. In a “restinga” forest near the study area, Britez (2001) noticed that *Faramea marginata* (Rubiaceae), an Al-accumulating species, contributed approximately with 60% of the total Al input thought total litterfall, although it contributed with only 2% of total leaf litter. Determining how Al is deposited on the soil surface will help to understand whether it will be available to plants in litter standing crops or not.

**The role of potential species in soil restoration along succession:** The lowest N, P, Mn, Zn and Cu concentrations were observed in leaf litter of *M. coriacea*, *T. pulchra* and *C. pachystachya*. These species had greatest importance in arboreal community structure (Gatti *et al.* unpublished data), litter production, carbon and nutrient transfer in both sites, showing relative high efficiency in the use of those nutrients. In similar areas in Southern and Southeastern Brazil, *C. pachystachya* is generally the first arboreal species to colonize the land after grazing or agriculture have stopped. The lowest N concentrations in leaf litter indicated

that *C. pachystachya* seems to tolerate better N degraded soils, emphasizing its importance in the early stages of secondary succession. As previously stated, this species was responsible for 24% of N returned to the soil through litterfall in site 2 (10.3kg/ha/yr), and for only 5% of the N input in site 1 (most advanced vegetation) (4.8kg/ha/yr). A similar pattern for P seems to occur with *C. pachystachya* and *T. pulchra*. *M. coriacea* and *S. multijuga* had the highest Ca use efficiency or presented a lower demand for this nutrient in their leaves. In other words, they produced considerable amounts of litter with low levels of Ca. *T. pulchra* has a high capacity of Al uptake and accumulation and is very well adapted to high Al availability in common acid soils, mainly in degraded sites of the Atlantic rain forest.

Finally, during secondary succession, each group of species seems to perform a different role in restoring the original characteristics of the soil surface horizons, such as increasing organic matter and nutrient availability and alleviation of toxicity for plants. Such features should be considered in forest restoration programs.

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#### RESUMEN

Durante la sucesión secundaria forestal, el flujo de nutrientes en la hojarasca se incrementa significativamente. Los altos ingresos de materia orgánica y nutrientes a través de la hojarasca afecta positivamente la fertilidad del suelo y la composición de especies, las cuales son componentes esenciales para programas de restauración forestal y de manejo. En el presente estudio, el ingreso de nutrientes a través de la hojarasca y sus componentes fueron estimados para dos sitios de una selva lluviosa atlántica aluvial en sucesión temprana. La cantidad anual de elementos que ingresan al suelo desde la vegetación más desarrollada (sitios con alta área basal y abundancia de árboles) fueron (en kg/ha): 93 N, 79 Ca, 24 K, 15 Mg, 6 P, 1.7 Mn, 0.94 Fe, 0.18 Zn, 0.09 Cu y 11.2 Al. Menos de la mitad de esas cantidades fueron aportadas por la vegetación menos desarrollada, excepto para el Al. La cantidad de Al aportada a este sitio fue similar a la contribución de la vegetación más desarrollada, debido a la contribución de: *Tibouchina pulchra* (82% de todo el Al aportado). La eficiencia en el uso de nutrientes de la hojarasca (principalmente de N y P) de la vegetación menos desarrollada fue superior a la eficiencia de una más desarrollada, debido a la alta proporción de tres especies nativas dominantes (*Myrsine coriacea*, *Tibouchina pulchra* y *Cecropia pachystachya*) en la primera. Si bien la hojarasca de esas especies presenta menor concentración de nutrientes que las otras especies arbóreas, el flujo de nutrientes fue mayor (para ambos sitios), marcando una cierta independencia de los nutrientes esenciales del suelo. Las cantidades de esas especies deberían ser consideradas con mayor atención para su uso en programas de restauración forestal.

**Palabras clave:** producción de hojarasca, ciclo de nutrientes, eficiencia en el uso de nutrientes, sucesión secundaria, selva lluviosa tropical.

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