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Original Article

Litterfall and Nutrient Dynamics in a Mature Atlantic Rainforest in Brazil

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ABSTRACT

We assessed litterfall and nutrient cycling in an old-growth Atlantic rainforest in southern Brazil. Plant litter collected monthly was separated into: leaves, twigs, reproductive organs, and fragments, and dried, weighed, and ground. Determination of carbon, nitrogen, phosphorus, potassium, calcium, magnesium, and sodium contents of different litter fractions was also performed. The total deposition was 8.44 Mg^{-1} ha^{-1} $year^{-1}$, with a higher proportion of leaves fraction. Litterfall predominated in spring and summer, coinciding with the highest average temperature and rainfall in the study area. For leaves, twigs and fragments, the elements sequence of concentration was C>N>Ca>K>Mg>P>Na; whereas for reproductive organs it was C>N>K>Ca>Mg>P>Na. A higher concentration of nutrients was observed in spring and summer for the leaves fraction. The quantitative transfer of nutrients by litterfall fractions to the forest soil followed the same sequence observed for the concentration of nutrients.

Keywords: biogeochemistry, Dense Ombrophilous Forest, nutrient deposition, litterfall.

1. INTRODUCTION

The Atlantic Rainforest is a lush biome of great importance once it hosts a significant portion of the Brazilian biological diversity, which is nationally and internationally recognized for its high biodiversity. It is also considered one of the most threatened biomes in the planet (Vandermeer & Perfecto, 2007). Although this biome coverage area is estimated at 1-1.5 million km^2, only 7-8% of the original forest cover still remains (Galindo-Leal & Câmara, 2005). The major remnants of this biome lie in the eastern costal region of Parana state (Roderjan & Kunyoshi, 1988), defined by the natural geographical barrier of the Serra do Mar, where the region of the Dense Ombrophilous Forest is located, which comprises forest formations of the Coastal Plain, the slopes of Serra do Mar, and part of the Ribeira River Valley (Roderjan et al., 2002).

As a result of a long historical period of degradation, the Atlantic Forest is currently highly fragmented into more than 245,000 fragments - 83% of them are less than 50 ha large, and many of its endemic species are considered endangered (Ribeiro et al., 2009). Because of the widespread loss of mature forests in the tropics, secondary forests will most likely play an important role in biodiversity conservation. It is expected that the conservation value of secondary forests grow over time as species from the remaining primary forest fragments accumulate. Studies have shown that both, primary and secondary forests, are important for the persistence of forest species in anthropogenic landscapes (Chazdon et al., 2009).

According to Bormann & Likens (1970), nutrients are distributed in four basic compartments in a forest ecosystem: the rock compartment, where nutrients are temporarily unavailable; the atmospheric compartment, where nutrients are under the form of gases and particulate matter; the nutrient compartment available in the soil solution or adsorbed on the surfaces of the organic mineral complex; and the organic compartment, composed of living organisms and their remains, in which the litterfall deposited on the forest floor is included. Litter deposition is the main organic matter and nutrients transfer path from plant shoots to the soil surface (Spain, 1984).

The litterfall-soil set represents not only a source of carbon and energy for soil organisms, but also the habitat that ensures their survival and reproduction (Britez, 1994). Nutrient cycling can be analyzed after separation of litterfall into different fractions, or by quantification of the nutrients that are stored in these compartments (Poggiani & Schumacher, 2000) and transferred to the forest soil.

Studies on litter production and nutrient cycling in the Atlantic Forest of Parana state have been developed for several forest phytophysiognomies, encompassing different soil conditions and successional stages of vegetation (Britez, 1994; Pinto & Marques, 2003; Martins, 2004; Protil, 2006; Rocha, 2006, Scheer, 2006; Pires et al., 2006; Dickow et al., 2012; Bianchin et al., 2016). However, despite the large number of studies on the topic, the vegetation of the Atlantic Rainforest in Parana state presents great diversity, and not all situations have been covered by the research conducted so far. In this context, the objective of this study was to evaluate the biomass and nutrients deposition by litterfall in forest plots representing an old-growth Submontane Dense Ombrophilous Forest.

2. MATERIAL AND METHODS

The study area is located in the Guaricica Natural Reserve (GNR), which is a private reserve of Natural Heritage owned by the Wildlife and Environmental Education Research Society (SPVS). It comprises a total area of 8600 hectares situated within the Environmental Protection Area (APA) of Guaraqueçaba, municipality of Antonina, north coast of Parana state, southern Brazil (Figure 1). The study area is composed of forests at different successional stages (Ferreti & Britez, 2005)

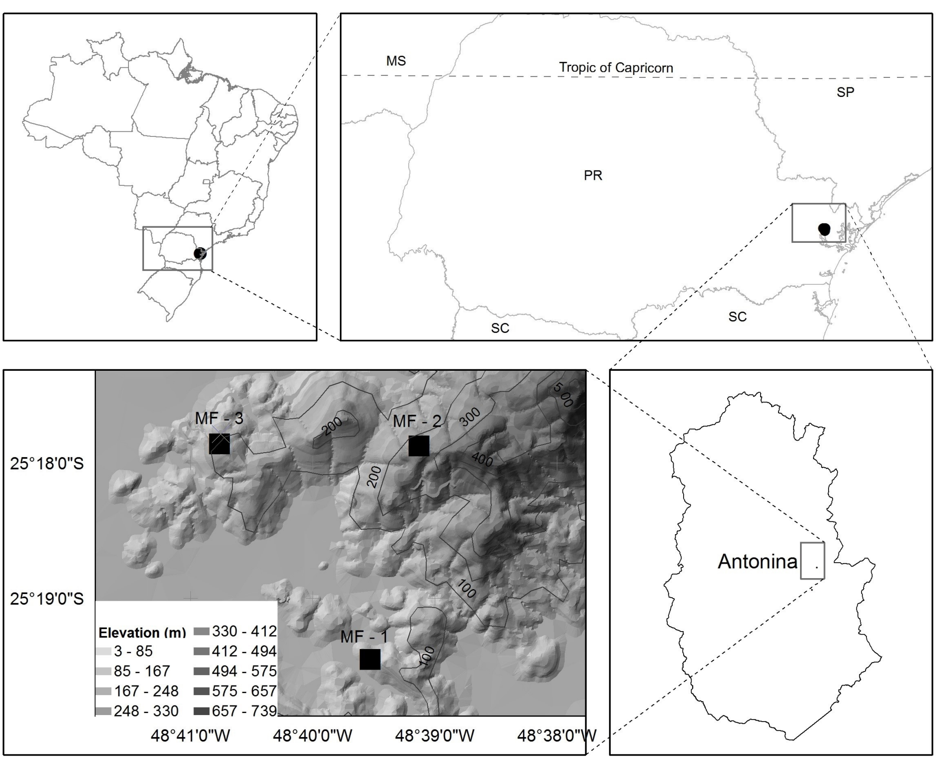

Figure 1. Spatial location of the three plots of Submontane Dense Ombrophilous Forest in Antonina, Parana state (PR), southern Brazil.

and, for this work, we selected three old-growth forests plots, with few disturbances or that had not suffered anthropogenic intervention for a long time, mentioned here as mature forests (Figure 1).

Climate in the region is humid subtropical mesothermal - Cfa according to the Köppen classification (Köppen, 1948), with mean temperatures below 18 °C and above 22 °C in the coolest and warmest months, respectively. Once the areas present low altitudes, there is no incidence of frost (IPARDES, 2001).

Analysis of the average climatic variables between 1999 and 2012 (Figure 2) shows that rainfall in the region varies at approximately 2550 mm per year. However, precipitation during the study period was greater than 3500 mm, a value within that (between 3300 and 3450 mm annually) considered normal for the region by Maack (2002).

The study area phytophysiognomy is Submontane Dense Ombrophilous Forest (IBGE, 2012), which according to Roderjan et al. (2002), comprises forests of the continental coastal plain with Quaternary sediments (colluvial deposits) and the beginning of the slopes of the Serra do Mar, located at an altitude ranging from 20 to 600 meters, with great diversity of species, most of them unique in this vegetation type.

The structural data of the study plots (Table 1) show that the areas exhibit high floristic diversity, given the high values of the Shannon Diversity and Pielou Equitability Indices.

Soils in the study plots were classified as Typic Tb dystrophic Haplic Cambisol (Inceptisol) (Santos et al., 2013). According to IBGE (2007), these soils are relatively young from the pedogenetic standpoint, usually shallow, with good drainage, presenting a poorly developed B horizon (Bi, incipient), of various colors, often stony, gravelly, and even rocky.

For the study of litter deposition we allocated 25 litter traps made of PVC, 1 m² large, with 2 mm nylon mesh, distributed in each of the three plots of 1.0 ha, in a systematic and uniform manner. Litterfall was collected monthly from October 2009 to September 2010. The samples were taken to a laboratory where they were separated into fractions as described by Dickow et al. (2012): varied leaves; twigs and thin branches (with diameter up to 2 cm); reproductive organs, which correspond to flowers, fruits and seeds; and debris or fragments, which correspond to material not included in the other fractions. After fractions' separation, the samples were dried at 60 °C and then weighed on a precision scale to quantify the litterfall biomass. Equation 1 was used to estimate the annual litterfall production in an area equivalent to one hectare (Lopes et al., 2002).

$$ALP = \frac{\sum MLP \times 10.000}{AT} \quad (1)$$

where: ALP = annual litterfall production (kg ha^{-1} year^{-1}); MLP = mean monthly litterfall production (kg ha^{-1} month^{-1}); AT = area of the trap (m^2).

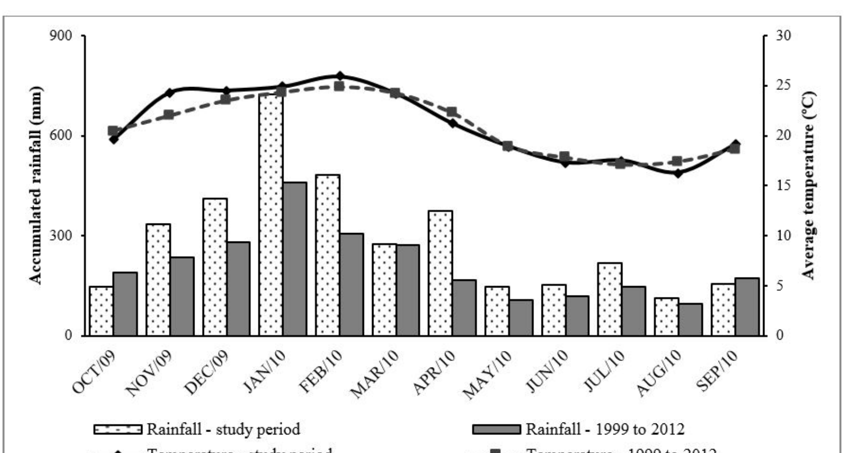

Figure 2. Monthly accumulated rainfall and average temperature during the study period and between 1999 and 2012 - data obtained from the SIMEPAR weather station in Antonina, Parana state.

Table 1. Phytosociological and structural information on the fragments of mature forest in Submontane Dense Ombrophilous Forest in Antonina, Parana state, southern Brazil.

MF-1			MF-2			MF-3		
Species	**NI***	**IV****	**Species**	**NI**	**IV**	**Species**	**NI**	**IV**
Virola bicuhyba	43	5.9	*Eugenia multicostata*	15	7.8	*Vochysia bifalcata*	28	6.6
Psychotria nuda	141	5.4	*Ocotea catharinensis*	64	5.6	*Hyeronima alchorneoides*	94	6.2
Sloanea guianensis	74	5.3	*Myrceugenia myrcioides*	119	5.5	*Sloanea guianensis*	114	6.0
Mollinedia schottiana	80	3.9	*Psychotria nuda*	132	5.4	*Myrceugenia myrcioides*	93	5.0
Myrceugenia myrcioides	75	3.8	*Brosimum lactescens*	53	4.4	*Euterpe edulis*	112	4.7
Marlierea obscura	61	3.5	*Euterpe edulis*	58	2.9	*Psychotria nuda*	113	4.1
Brosimum lactescens	55	3.5	*Alchornea* sp.	35	2.9	*Cupania oblongifolia*	79	4.0
Guapira opposita	69	3.2	*Sloanea guianensis*	27	2.4	*Pera glabrata*	63	3.8
Euterpe edulis	64	3.0	*Virola bicuhyba*	27	2.4	*Virola bicuhyba*	27	3.3
Coussarea contracta	57	2.6	*Mollinedia schotiana*	41	2.1	*Zollernia* sp.	64	3.0
Other species	807	59.9	Other species	934	60.7	Other species	884	53.3
Total	**1526**	**100**	**Total**	**1464**	**100**	**Total**	**1671**	**100**
Number of species		146	Number of species		132	Number of species		114
Total basal area (m^2 ha^{-1})		35.3	Total basal area (m^2 ha^{-1})		52.9	Total basal area (m^2 ha^{-1})		34.9
Shannon Diversity Index (H')		4.06	Shannon Diversity Index (H')		4.14	Shannon Diversity Index (H')		3.87
Pielou Equability Index (J)		0.82	Equability Pielou Index (J)		0.85	Equability Pielou Index (J)		0.82

*NI = number of individuals per hectare; **IV = Importance Value (%). The data herein calculated (NI and IV) refer to the vegetation survey, where only individuals with diameter at breast height (DBH) greater than 10 cm were sampled.

To perform the chemical analyses, the material deposited monthly from each fraction was homogenized and ground in a Wiley slicer, with three repetitions for each season, corresponding to the monthly collections. The composition of samples corresponding to each repetition followed the procedure described by Bianchin (2013). Contents of C and N were determined by dry combustion in an Elementar Vario EL III CNHOS analyzer. The concentrations of P, Ca, Mg, K, and Na were obtained after dry digestion according to the methodology described by Martins & Reissmann (2007). Levels of Ca and Mg were determined using an AA-6200 Shimadzu atomic absorption spectrophotometer, the contents of K and Na were formulated using a Digimed NK 2000 flame photometer, and the levels of P were obtained by colorimetry in a 1240-Mini UV/VIS Shimadzu spectrophotometer.

To evaluate the differences in litterfall production and nutrients concentration between fractions, data were submitted to analysis of variance (ANOVA), and the means were later compared by the Tukey test at 5% probability level. The Pearson's correlation coefficient was used to verify the correlation between litter deposition and the meteorological variables, and the Student t test was applied at 5 and 1% probability levels to assess the significance of the correlation.

3. RESULTS AND DISCUSSION

The annual litterfall production (Table 2) was estimated at 8.4 Mg ha^{-1} $year^{-1}$. Leaves fraction was statistically superior to the other fractions, followed by fragments and twigs, and finally, reproductive organs, with the lowest deposition in all seasons.

The references found in the specific literature with respect to annual amount of litterfall vary according to forest formation. According to Golley et al. (1978), litterfall contribution in tropical forests worldwide ranges from 4 to 25 Mg ha^{-1} $year^{-1}$. Greater depositions tend to occur in forests at advanced stages of development (Pinto et al., 2008; Calvi et al., 2009; Menezes et al., 2010). In some cases, greater deposition was observed in advanced secondary forests compared with mature forests (Aryal et al., 2015). Still for areas of secondary Atlantic Forest, values higher than those found in this study were reported by Abreu et al. (2010) in Rio de Janeiro (9.8 Mg ha^{-1} $year^{-1}$).

The leaves fraction accounted for 73% of the total litter production, which shows the importance of this fraction to nutrient cycling in these ecosystems. The fractions twigs and fragments were at an intermediate position (12 and 13%, respectively), and the fraction reproductive organs was the least representative (3%). Several studies at the Atlantic Forest demonstrate that leaves are abundant in the plant litter deposited in secondary formations of both ombrophillous (Varjabedian & Pagano, 1988; Gama-Rodrigues & Barros, 2002; Pinto & Marques, 2003; Toledo & Pereira, 2004; Pires et al., 2006; Menezes et al., 2010; Dickow et al., 2012; Bianchin et al., 2016) and deciduous (Pezzatto & Wisniewski, 2006; Schumacher et al., 2011; Machado et al., 2015) forests.

This larger proportion of leaves in the litterfall is a behavior that has been extensively reported in the literature on litter deposition in many forest ecosystems (Moraes et al., 1999; Britez et al., 1992; Figueiredo et al., 2003; Pinto et al., 2008). It occurs, in part, due to the fact that leaves are the physiologically active organs responsible for photosynthesis (Epstein & Bloom, 2006), that is, for the incorporation of carbon by plants; but they are also responsible for the transfer of this carbon and nutrients to forest soils, thus contributing to maintain and even enrich their fertility.

The largest litterfall occurred in the warmer seasons (spring and summer) both for total litter and fractions (Table 2). The lowest values for the coefficient of variation (CV) of the fractions in these seasons indicate a more continuous and homogeneous deposition in these periods, and a more heterogeneous contribution in autumn and winter, as observed in other studies on Dense Ombrophilous Forest on the coast of Parana state (Pinto & Marques, 2003; Dickow et al., 2012; Bianchin et al., 2016). In constantly humid forests, such as the Atlantic Forest, the largest litterfall usually coincides with the period of greatest rainfall (Jackson, 1978; Cunha et al., 1993; Moraes et al., 1999; Pinto & Marques, 2003; Schumacher et al., 2003; Dickow et al., 2012); in the case of the Atlantic Forest of Parana state, it is also the period with the highest temperatures.

The descending macronutrients, carbon, and sodium sequence of concentration was C>N>Ca>K>Mg>P>Na for the fractions leaves, twigs and fragments, whereas for the fraction reproductive organs the sequence was C>N>K>Ca>Mg>P>Na. No differences in the concentration of the elements were identified between the fractions analyzed (Table 3).

The N values were relatively high and close to those observed in forests at advanced stage of secondary succession by Pinto & Marques (2003) in Lowland Dense Ombrophilous Forest, and by Bianchin (2013) in Submontane Dense Ombrophilous Forest. In the specific case of Submontane Dense Ombrophilous Forest, the latter author associated the high levels of N with the high population density of understory species, such as *Psychotria nuda*, which stores a high

Table 2. Mean litter deposition per season, per fraction, and total in mature Submontane Dense Ombrophilous Forest in Antonina, Parana state.

Fraction	Spring		Summer		Autumn		Winter		Total Annual Litterfall
	Litterfall (kg ha^{-1})	CV* (%)	Litterfall (kg ha^{-1})	CV (%)	Litterfall (kg ha^{-1})	CV (%)	Litterfall (kg ha^{-1})	CV (%)	kg ha^{-1} yr^{-1}
Leaves	2467.7 Aa	16.1	1666.3 Aba	27.0	850.6 Ba	32.7	1165.6 Aba	68.6	6150.21 a
Twigs	252.6 Ab	6.7	342.2 Ab	7.8	158.6 Ab	52.3	226.1 Ab	55.2	979.47 b
Reproductive Organs	50.1 Ac	56.1	96.5 Ac	49.0	45.8 Ab	77.9	45.2 Ac	42.3	237.55 c
Fragments	333.4 Ab	15.6	390.0 Ab	5.1	136.5 Bb	31.2	209.0 ABb	58.5	1068.96 b
Total by season	**3103.96 A**	-	**2495.05 AB**	-	**1191.30 B**	-	**1645.89 AB**	-	**8436.20**

Values followed by the same uppercase letter in the line or the same lowercase letter in the column do not differ statistically by the Tukey test at 5% probability level. *CV = coefficient of variation.

Table 3. Annual mean concentrations of carbon, macronutrients, and sodium in the fractions of litterfall in mature Submontane Dense Ombrophilous Forest in Antonina, Parana state.

Fraction	C	N	P	K	Ca	Mg	Na
	.... g kg^{-1}						
Leaves	455.7 a	19.0 a	1.16 a	2.18 a	3.83 a	1.69 a	0.51 a
Twigs	447.5 a	16.5 a	0.63 a	1.94 a	3.05 a	1.51 a	0.58 a
Reproductive Organs	471.1 a	19.1 a	1.03 a	4.04 a	2.59 a	1.53 a	0.53 a
Fragments	450.4 a	19.4a	0.91 a	2.18 a	3.77 a	1.73 a	0.44 a

Means followed by the same letter do not differ statistically by the Tukey test at 5% significance level.

content of this nutrient in its tissues, what would explain the high levels of N found in the litterfall of these environments. In this study plots, this species was also present, although not always with the highest indices of Importance Value (Table 1).

The twigs fraction is generally characterized by high concentrations of Ca (Britez et al., 1992; Villela & Proctor, 1999), because it is a structural element, whereas the reproductive organs fraction exhibits higher contents of P and K (Britez et al., 1992; Britez, 1994; Moraes et al., 1999; Villela & Proctor, 1999; Martins, 2004; Bianchin, 2013). As the levels of nutrients in litterfall result from various biotic and abiotic factors, depending on the characteristics of each ecosystem, a given factor may prevail over the others (Calvi et al., 2009) and influence nutrients concentration in each litter fraction.

Contents of P, K, Ca, Mg, and Na were similar to those found by Bianchin (2013) in Parana state; close to the values obtained by Martins (2010) in the coast of Sao Paulo state; and in the specific case of calcium, similar to the levels reported by Sampaio et al. (1988) in tropical rainforest in northeastern Brazil. In contrast, Dickow (2010), in other plots of the same reserve, obtained Ca values approximately two times higher than those observed in this study.

The seasons did not affect the levels of C and macronutrients in the fractions twigs, reproductive organs, and fragments (Table 4). With regard to the leaves fraction, differences were observed only for the contents of C, K, and Na: higher concentrations of C were noted in spring and autumn, whereas greater values of K and Na were found in spring.

The annual amount of carbon, macronutrients, and sodium transferred to the soil by the litter fractions (Table 5) was proportional to the amount of litterfall; the leaves fraction was responsible for the largest return of nutrients to the forest soil due to its higher biomass contribution (6.1 Mg ha^{-1} yr^{-1}). The reproductive organs fraction transferred the smallest quantities of nutrients owing to the small amount of biomass deposited by this fraction (Table 2). The descending order of transfer of macronutrients and carbon via total contribution of litterfall was C>N>Ca>K>Mg>P>Na for all fractions investigated. The transfer of nutrients to the soil via litterfall is variable, especially in tropical forests, and it depends on the functional characteristics of each element in the metabolism of plants, on soil characteristics, climate, nutritional status, phenology, successional stage, and on the presence or absence of nutrient-retention mechanisms (Golley et al., 1978; Vitousek & Sanford, 1986).

Table 4. Contents of carbon, macronutrients, and sodium in the fractions of litterfall by season of the year in mature Submontane Dense Ombrophilous Forest in Antonina, Parana state.

Fractions	Seasons	C	N	P	K	Ca	Mg	Na
		g kg^{-1}						
Leaves	Spring	441.7 a	20.3 a	1.0 a	2.9 a	4.3 a	2.1 a	0.8 a
	Summer	469.8 a	18.9 a	1.2 a	1.7 b	4.1 a	1.7 a	0.3 b
	Autumn	458.4 ab	17.2 a	1.1 a	1.8 b	3.7 a	1.5 a	0.5 ab
	Winter	453.0 ab	19.7 a	1.3 a	2.4 ab	3.3 a	1.5 a	0.6 ab
Twigs	Spring	429.0 a	14.6 a	0.5 a	2.2 a	2.8 a	1.5 a	0.6 a
	Summer	457.4 a	19.5 a	0.7 a	1.7 a	3.3 a	1.7 a	0.4 a
	Autumn	449.6 a	16.2 a	0.5 a	1.8 a	3.3 a	1.4 a	0.8 a
	Winter	454.2 a	15.7 a	0.8 a	2.1 a	3.6 a	1.5 a	0.5 a
Reproductive Organs	Spring	474.4 a	17.7 a	1.2 a	4.3 a	2.3 a	1.8 a	0.6 a
	Summer	485.8 a	19.5 a	1.0 a	4.2 a	2.5 a	1.1 a	0.5 a
	Autumn	466.8 a	19.9 a	0.9 a	3.8 a	3.0 a	1.7 a	0.7 a
	Winter	457.4 a	19.3 a	1.1 a	3.9 a	2.6 a	1.6 a	0.4 a
Fragments	Spring	462.3 a	25.1 a	1.0 a	2.3 a	4.4 a	1.8 a	0.5 a
	Summer	445.4 a	18.8 a	1.0 a	2.2 a	3.8 a	1.7 a	0.4 a
	Autumn	453.6 a	19.0 a	0.7 a	2.1 a	3.8 a	1.9 a	0.4 a
	Winter	440.3 a	19.6 a	1.0 a	2.2 a	3.1 a	1.5 a	0.5 a

Means followed by the same letter (for columns within each fraction) do not differ statistically by the Tukey test at 5% significance level.

Table 5. Annual contribution of carbon, macronutrients, and sodium per fraction and total of litterfall in mature Submontane Dense Ombrophilous Forest in Antonina, Parana state; and transfer of nutrients for total litterfall reported by other studies in mature or advanced-stage forests of the Atlantic Rainforest.

Fraction	Litterfall ($Mg\ ha^{-1}\ yr^{-1}$)	C	N	P	K	Ca	Mg	Na
		....................................kg ha^{-1} $year^{-1}$....................................						
Leaves	6.15	2785.5 a	121.48 a	6.50 a	14.17 a	24.02 a	11.49 a	3.17 a
Twigs	0.98	438.6 b	16.68 b	0.65 b	1.85 b	3.36 b	1.66 b	0.51 b
Reproductive Organs	0.24	112.5 c	4.48 c	0.24 b	0.90 c	0.71 c	0.41 b	0.13 c
Fragments	1.07	482.9 b	21.72 b	1.00 b	2.32 b	4.17 b	1.91 ab	0.47 b
Total Annual (this study)	**8.44**	**3819.2**	**164.36**	**8.40**	**19.24**	**32.26**	**15.47**	**4.28**
Rocha (2006)	6.90	-	66.3	3.7	11.1	66.1	13.8	3.4
Pereira et al. (2008)	7.90	-	122.0	2.0	32.1	-	-	-
Calvi et al. (2009)	2.93	-	40.2	2.3	10.8	-	-	-
Dickow (2010)	5.32	-	95.3	4.1	15.4	30.3	9.3	3.1
Bianchin (2013)	8.09	3667.1	152.6	5.3	14.3	42.5	24.9	6.1

Means followed by the same letter (for columns within each fraction) do not differ statistically by the Tukey test at 5% significance level.

The nutrients flux, especially N and P, was relatively high when compared to the results of other studies conducted in the same region, in areas of forests at advanced stage of secondary succession (Rocha, 2006; Dickow, 2010; Bianchin, 2013) and other areas of secondary Atlantic Forest (Pereira et al., 2008; Calvi et al., 2009). In the case of P, the contribution observed was much higher than the values reported in other studies, and was close to those obtained by Bianchin (2013). The larger deposition of biomass observed in the study area compared with those of other secondary forests, as well as the higher concentration of these elements in the litter, explain the relatively high nutrient transfer values in these mature forests.

The return of K was considered intermediate: higher than those found by Rocha (2006), Calvi et al. (2009), Dickow (2010), and Bianchin (2013), but lower than those reported by Pereira et al. (2008). The return of Ca, Mg, and Na were intermediate compared with those of the other studies in Table 5, even when they were compared with relatively nearby areas, such as in the studies by Rocha (2006), Dickow (2010), and Bianchin (2013), mainly due to the low levels of nutrients in the litter fractions of this study.

4. CONCLUSIONS

Total annual litterfall was higher than that observed in other secondary forests at advanced stages of the study area.

The leaves fraction was the most representative proportionally to the total litter deposition.

The largest litter depositions occur in spring and summer - warmer periods with higher rainfall.

For most of the fractions analyzed, the descending concentration order of elements was C>N>Ca>K>Mg>P>Na.

Annual transfer of nutrients by litterfall followed the same order observed for the nutrients concentration in the different litter fractions, which indicates that the quantity of deposited biomass was a determining factor for the amount of nutrients transferred to the forest soil.

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