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BIOMASS AND NUTRIENTS IN THE FOREST-FLOOR LITTER OF SECOND-GROWTH BRAZILIAN ATLANTIC FORESTS

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Resumo

Fitomassa e nutrientes na serapilheira acumulada de formações secundárias da Floresta Atlântica. O objetivo deste estudo foi avaliar a fitomassa e a composição química da serapilheira acumulada em três áreas da Floresta Ombrófila Densa Submontana, na Reserva Natural da Guaricica, Antonina, PR. As áreas selecionadas para o estudo encontram-se em diferentes estágios de sucessão secundária, aqui denominadas: estágio inicial (INI), estágio médio (MED) e estágio avançado (AVA). A serapilheira foi coletada em diferentes estações do ano (verão e inverno de 2013 e de 2014) e triada em frações: folhas inteiras (FR), folhas em algum estágio de decomposição (FD), miscelânea (MI) e galhos (GA). Após a triagem, a serapilheira foi seca em estufa, pesada e analisada quanto aos teores de C, N, P, K, Ca, Mg, e a quantidade acumulada de cada nutriente nas suas diferentes frações foi estimada. O acúmulo de fitomassa no INI foi inferior àquele no AVA. A fração FD apresentou maior acúmulo entre todas as frações. A concentração média de macronutrientes da serapilheira mostrou a seguinte sequência: C>N>Ca>Mg>K>P. A relação C/N foi maior no INI e MED em relação ao AVA. Maiores teores dos macronutrientes foram observados com frequência no AVA. Os aportes de C e da maioria dos nutrientes mostram-se crescentes do INI para o AVA, exceto Ca, cujo aporte variou pouco entre os diferentes estágios sucessionais.
Palavras-chave: ciclagem de nutrientes, serapilheira, ecologia florestal

Abstract

This study aimed to evaluate the biomass and chemical composition of the forest floor litter in three remnants of Submontane Dense Ombrophilous Forest located in the Guaricica Natural Reserve in the municipality of Antonina, state of Paraná, Brazil. The areas selected for this study are at different stages of secondary succession, here named initial stage (INI), intermediate stage (INT), and advanced stage (ADV). The litter was collected in different seasons of the year (summer and winter of 2013 and 2014) and sorted into fractions: whole leaves (WL), leaves under some stage of decomposition (DL), miscellaneous litter (ML), and branches (B). After sorting, the litter was oven-dried, weighed, and had the contents of C, N, P, K, Ca, and Mg measured. After that, the accumulated amount of each nutrient in the different litter fractions was estimated. Accumulation of biomass in the INI was lower than that in the ADV. The DL fraction showed the highest level of biomass accumulation among all fractions. The average concentration of macronutrients in the litter showed the following sequence: C>N>Ca>Mg>K>P. The C/N ratio was higher in the INI and INT compared with that in the ADV. Higher levels of macronutrients were frequently observed in the ADV. Inputs of C and of most nutrients increased from the INI to the ADV, except for Ca, whose input varied little throughout the different successional stages.
Keywords: nutrient cycling, litter, forest ecology

INTRODUCTION

The eastern coastal region of the state of Paraná, defined nearly entirely by the natural geographic barrier of Serra do Mar, is part of the Atlantic Forest biome (RODERJAN *et al.*, 2002). This biome is considered a global biodiversity hotspot, and approximately 28% of its vegetation cover still remains (REZENDE *et al.*, 2018). Most of these forest remnants are composed of highly fragmented second-growth forests under varying successional stages (ARROYO-RODRÍGUEZ e*t al.*, 2017) that have not yet been included in environmental protection areas, which increases their vulnerability to anthropic pressures (REZENDE *et al.*, 2018). Disturbances affect vegetation structure and productivity, which in turn interferes with ecological mechanisms and soil properties (RAJ; JHARIYA, 2021).

Litter, which comprises mainly leaves and fragments that fall from trees and are deposited on the forest floor (DICK; SCHUMACHER, 2020), can be separated into fractions, and their analysis can assist in understanding biogeochemical cycling in forests. Characteristics of the litter deposited on the soil vary according to the abiotic and biotic conditions of the forest site, such as climatic factors, soil fertility, floristic composition, and successional stages (MORFFI-MESTRE *et al.*, 2020). In addition, variations in litter accumulation on the ground indicate the local decomposition dynamic, and forest sites with greater litter accumulation tend to be

environments where the decomposition process is incomplete (TANNER *et al.*, 1998). Moreover, litter accumulation is also associated with successional stages of vegetation: forests at advanced stages of development present larger number of species and greater biomass, and thus greater litter production, whereas those at pioneer stages present less structural complexity and greater availability of light, resulting in smaller litter deposition (MACHADO *et al.*, 2015).

Quantification of the biomass accumulated on the soil and analysis of its chemical composition enables verification of its contribution to forest nutrient cycling and ecosystem productivity (ZHOU *et al.*, 2015). Some chemical elements remain immobilized for a longer time in the litter biomass, while others are released to the soil more rapidly. Thus, monitoring the chemical composition of the forest-floor litter enables a better understanding of the biogeochemistry in forest ecosystems.

In this context, this study aimed to contribute to the understanding of biogeochemical processes in the Atlantic Rainforest through assessment of litter accumulation and mineral nutrient cycling, at three successional stages, in two seasons, in forest remnants located in the municipality of Antonina, state of Paraná, Brazil.

MATERIAL AND METHODS

Study area

The study was conducted in the Guaricica Natural Reserve (GNR), located in the west-northwest portion of the Antonina Bay (25º 18' S; 48º 41' W) in the municipality of Antonina, coastal region of the state of Paraná (Figure 1). This is a private reserve owned by the Wildlife and Environmental Education Research Society (SPVS). According to IBGE (2012), the study area phytophysiognomy is Submontane Dense Ombrophilous Forest, located at an altitude ranging from 20 to 600 meters. According to the Köppen classification, climate in the region is mesothermal humid subtropical (Cfa), with mean temperatures of -3 ºC to 18 °C and >22 °C in the coolest and warmest months, respectively.

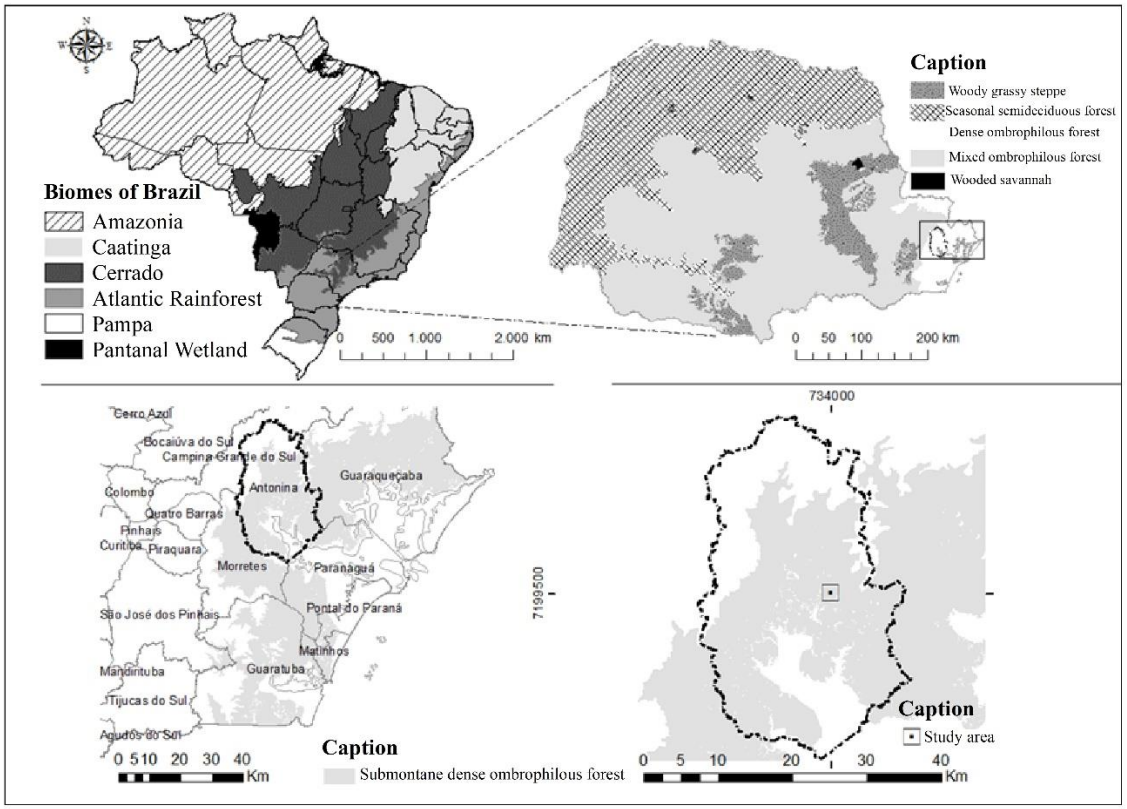


Figure 1. Study area located in the municipality of Antonina, state of Parana, Brazil.
Figura 1. Localização da área de estudo no município de Antonina, Paraná, Brasil.

Soils in the study plots were classified as Cambisols, which are composed of mineral material in an incipiently developed B horizon, and presenting great variation of physicochemical attributes (SANTOS et al., 2013). Based on the use history of this region, aerial photographs and field inspection, forests at three stages of secondary succession were selected, here named: INITIAL STAGE (INI) - with formations aged 20-25 years located in areas previously used as pasture, characterized mainly by the presence of pioneer tree species and a few

initial secondary species; INTERMEDIATE STAGE (INT) - with formations aged 45-60 years, representing areas of secondary forest with over 35 years after use as pasture, and that already present a great diversity of tree species; ADVANCED STAGE (ADV) - with formations that have undergone little change and have never been converted into another use, except the selective cutting of species of high commercial value (until the 1980s). Three (3) 1000 m² plots were established in forest remnants at each successional stage, totaling nine (9) plots, with 10 sampling subplots (10x10 m) allocated in each of them.

Collection and evaluation of the forest-floor litter

The forest-floor litter was randomly collected at five (5) points in each subplot using 45x45 cm (0.2025 m²) templates. The litter was collected during the Winter and Summer of 2013 and 2014. The samples were taken to the Biogeochemistry Laboratory at the Federal University of Paraná (UFPR) for sorting and drying. The litter was separated into the following fractions: WL - whole leaves with no sign of decay; DL - leaves under some stage of decomposition; ML - miscellaneous litter, considered as all unidentifiable material that passed through the 9 mm sieve; B - branches with diameter <2 cm. After separation, the samples were oven-dried at 60 °C under air circulation, where they remained until constant weight was reached, and were then weighed on a precision scale.

After that, the litter fraction samples were ground and the chemical analyses were performed, where the concentrations of carbon (C), nitrogen (N), phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) were obtained. Contents of C and N were determined by combustion in an Elementar Vario EL III analyzer. The other elements were determined, after dry digestion, as described in Martins and Reissmann (2007).

Statistical analysis

The data were statistically analyzed by multiple comparisons through application of the Kruskal-Wallis test at a 5% significance level ($p<0.05$) using the Action® software integrated with Excel EstatCamp (2014).

RESULTS

Total and per fraction biomass of forest-floor litter

Differences in total biomass were observed between the successional stages and seasons studied ($p\geq0.05$) (Table 1). The amount of litter accumulated in the initial stage (INI) was greater than those in the intermediate (INT) and advanced (ADV) stages, with a difference between the INI and the ADV stages. The greatest litter accumulation occurred in the Summer for all successional stages.

Table 1. Average values of forest-floor litter, annual and per season, at the three successional stages of the Submontane Dense Ombrophilous Forest, municipality of Antonina, state of Paraná, Brazil

Tabela 1. Valores médios de serapilheira acumulada, anuais e por estação, em três áreas secundárias de Floresta Ombrófila Densa Submontana, em Antonina, PR.

Successional stage	Forest-floor litter		
	Mean per season (kg ha^{-1})		Annual mean (kg ha^{-1} year^{-1})
Initial	Summer	5389.4 bc (8.3)	4728.6 b (21.3)
	Winter	4067.9 c (23.9)	
Intermediate	Summer	6.673.8 ab (16.1)	6023.5 ab (27.8)
	Winter	5373.3 bc (35.4)	
Advanced	Summer	6988.8 a (2.5)	6311.2 a (16.2)
	Winter	5633.6 ab (18.9)	

* Values followed by the same letter in the column do not differ statistically by the Kruskal-Wallis test at a 5% significance level; values in parentheses show the coefficient of variation (CV).

A comparative analysis of the litter accumulation dynamic in the seasons (summer and winter of 2013 and 2014) and the meteorological variables (Figure 2) shows that the greatest accumulation usually occurs in periods of lower temperature and rainfall, in winter.

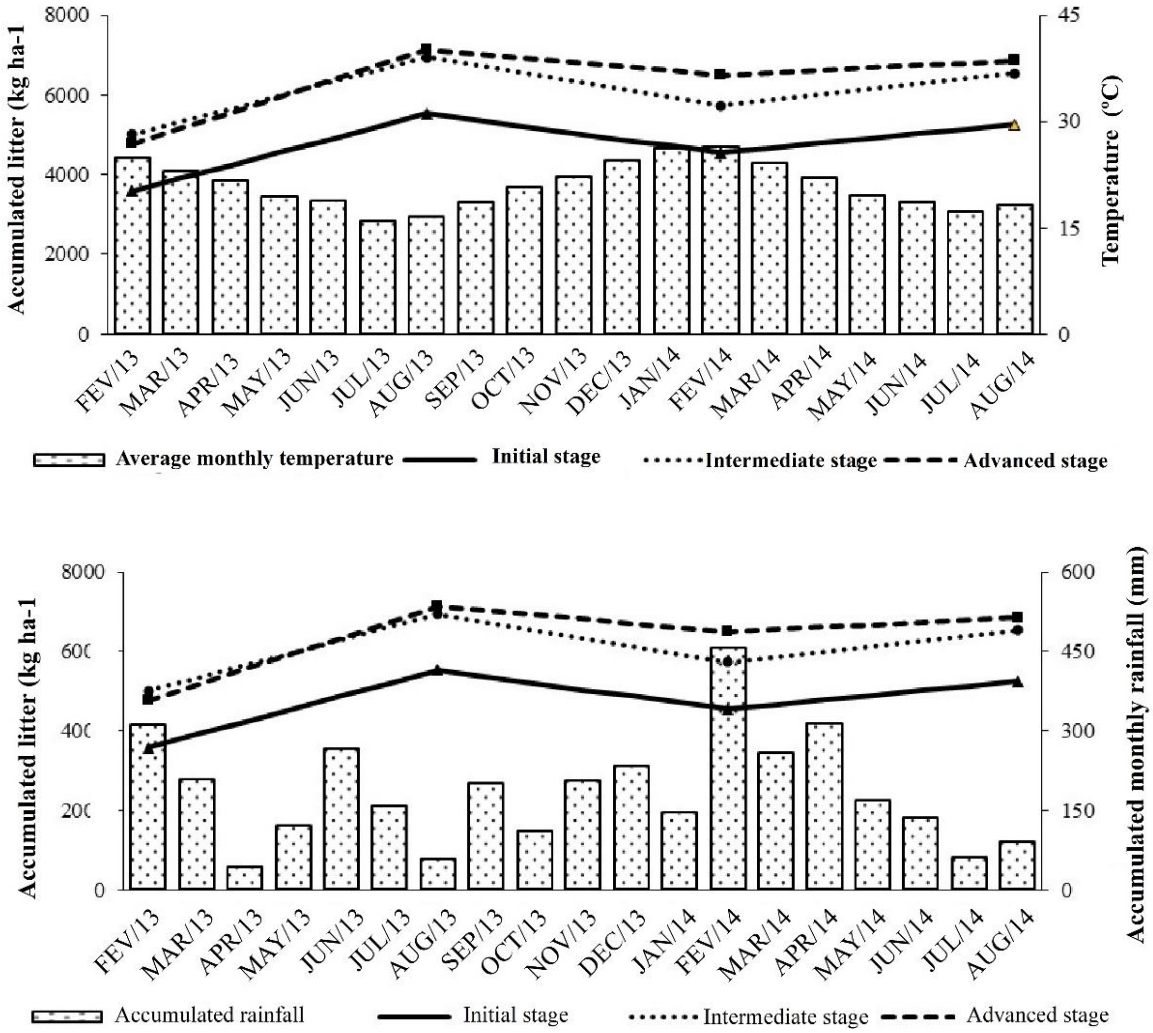


Figure 2. Comparison between the meteorological variables and the amount of forest-floor litter at three successional stages of the Submontane Dense Ombrophilous Forest, municipality of Antonina, state of Paraná, Brazil.

Figura 2. Comparação entre as variáveis meteorológicas e a quantidade de serapilheira acumulada nos três estágios de sucessão de Floresta Ombrófila Densa Submontana, em Antonina, PR.

The amount of biomass accumulated in the litter fractions showed the following descending sequence: DL>ML>B>WL (Table 2 and Figure 3). The behavior of the DL fraction was similar to that of the total biomass, revealing that the accumulation pattern of the latter was determined by the former.

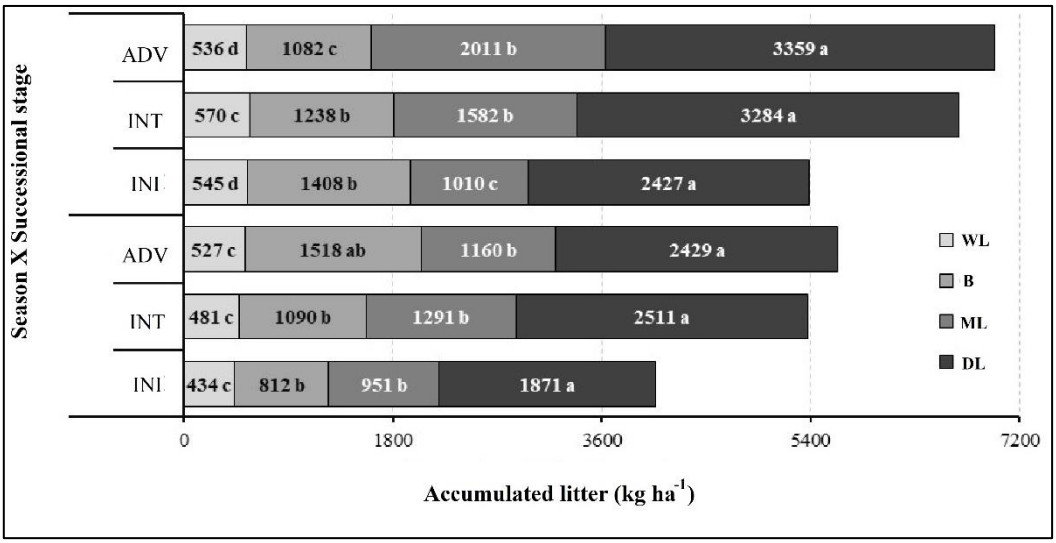
Comparison between the stages of secondary succession (Table 2) evidenced that litter accumulation was smaller in the ML and DL fractions in the INI in summer, whereas litter accumulation was smaller in the B fraction in the same stage in winter. Regarding the WL fraction, no difference was identified between successional stages both in summer and winter.

Table 2. Forest-floor litter fractions by season at three successional stages of the Submontane Dense Ombrophilous Forest, municipality of Antonina, state of Paraná, Brazil

Tabela 2. Frações de serapilheira acumulada por estação do ano, em três estágios de sucessão de Floresta Ombrófila Densa Submontana, em Antonina, PR

Successional stage	DL	ML	B	WL
Forest-floor litter - Summer (kg ha^{-1})				
Initial	2426.50 b (18.24)	1010.26 c (37.17)	1407.64 a (23.04)	544.99 a (14.48)
Intermediate	3283.82 ab (32.06)	1581.96 b (14.86)	1238.16 a (32.81)	569.83 a (32.61)
Advanced	3359.47 a (11.19)	2010.93 a (11.19)	1082.06 a (19.33)	536.31 a (12.97)
Forest-floor litter - Winter (kg ha^{-1})				
Initial	1871.18 a (44.56)	951.28 a (46.45)	811.51 b (12.87)	433.91 a (17.77)
Intermediate	2510.55 a (43.74)	1291.26 a (70.81)	1090.17 ab (39.14)	481.27 a (18.8)
Advanced	2428.94 a (37.78)	1159.82 a (34.02)	1517.79 a (31.04)	527.02 a (28.99)

* Values followed by the same letter in the column do not differ statistically by the Kruskal-Wallis test at a 5% significance level; values in parentheses show the CV. *Captions*: WL - whole leaves with no sign of decay; DL - leaves under some stage of decomposition; ML - miscellaneous litter, considered as all unidentifiable material that passed through the 9 mm sieve; B - branches with diameter <2 cm.



*Values with same letter in the line (bar) do not differ statistically by the Kruskal-Wallis test at a 5% significance level. *Captions*: WL - whole leaves with no sign of decay; DL - leaves under some stage of decomposition; ML - miscellaneous litter, considered as all unidentifiable material that passed through 9 mm sieve; B the 9 mm sieve; B - branches with diameter <2 cm; ADV - Advanced stage; INT - Intermediate stage; INI - Initial stage.

Figure 3. Biomass in the forest-floor fractions by season at three successional stages of the Submontane Dense Ombrophilous Forest, municipality of Antonina, state of Paraná, Brazil.

Figura 3. Fitomassa nas frações de serapilheira acumulada, por estação do ano, em três estágios de sucessão de Floresta Ombrófila Densa Submontana, em Antonina, PR.

Contents of C and macronutrients in forest-floor litter

The predominant sequence of macronutrients was C>N>Ca>Mg>K>P for all litter fractions (Table 3). The highest mean levels of C were found in the B and WL litter fractions (432.25 and 429.38 g kg^{-1}, respectively), while the lowest mean level was observed in the ML fraction (295.28 g kg^{-1}). For N, the DL and WL fractions presented the greatest mean values (16.45 and 15.96 g kg^{-1}, respectively), whereas the B fraction showed the smallest value (12.19 g kg^{-1}). Concerning P, the highest mean levels were observed in the DL and ML fractions (0.68 and 0.67 g kg^{-1}, respectively), and the lowest level was found in the B fraction (0.50 g kg $^{-1}$). Regarding K, the WL and DL fractions showed the greatest values (1.87 and 1.43 g kg^{-1}, respectively), while the ML fraction presented the smallest value (1.01 g kg^{-1}). Similar patterns were verified for Ca, with the highest mean levels in

the WL and DL fractions (7.34 and 7.14 g kg^{-1}, respectively) and the lowest level in the ML fraction (5.43 g kg^{-1}), and for Mg, with the greatest mean values in the WL and DL fractions (1.87 and 1.84 g kg^{-1}, respectively) and the smallest value in the ML fraction (1.41 g kg^{-1}). For the C/N ratio, the highest (36.42 g kg^{-1}) and lowest (20.50 g kg^{-1}) mean levels were observed in the B and ML litter fractions, respectively.

Table 3. Average concentrations of C and macronutrients in the forest-floor litter at three successional stages of the Submontane Dense Ombrophilous Forest, municipality of Antonina, state of Paraná, Brazil
Tabela 3. Teores médios de carbono e macronutrientes na serapilheira acumulada, em três estágios de sucessão de Floresta Ombrófila Densa Submontana, em Antonina, PR

Litter fraction	Successional stage	C	N	P	K	Ca	Mg	C/N ratio
		.....(g kg^{-1})						
DL	**Initial**	371.40	15.02	0.65	1.59	8.21	1.77	25.14
	Intermediate	383.76	16.44	0.58	1.27	6.20	1.91	23.61
	Advanced	404.74	17.90	0.80	1.43	7.00	1.83	22.70
	Mean	**386.63**	**16.45**	**0.68**	**1.43**	**7.14**	**1.84**	**23.84**
ML	**Initial**	286.38	13.41	0.68	1.26	7.34	1.41	21.59
	Intermediate	302.05	14.49	0.53	0.76	4.37	1.46	20.92
	Advanced	297.40	15.66	0.79	1.01	4.59	1.37	19.00
	Mean	**295.28**	**14.52**	**0.67**	**1.01**	**5.43**	**1.41**	**20.50**
B	**Initial**	426.35	11.07	0.59	1.07	7.68	1.34	40.00
	Intermediate	435.38	12.22	0.37	1.12	5.37	1.64	36.45
	Advanced	435.03	13.29	0.53	1.03	6.24	1.56	32.80
	Mean	**432.25**	**12.19**	**0.50**	**1.07**	**6.43**	**1.51**	**36.42**
WL	**Initial**	425.64	14.37	0.54	2.06	8.67	1.82	30.79
	Intermediate	427.33	15.20	0.49	1.69	6.46	1.91	28.68
	Advanced	435.17	18.31	0.69	1.86	6.88	1.87	23.93
	Mean	**429.38**	**15.96**	**0.57**	**1.87**	**7.34**	**1.87**	**27.80**

*Values with same letter in the line (bar) do not differ statistically by the Kruskal-Wallis test at a 5% significance level. *Captions*: WL - whole leaves with no sign of decay; DL - leaves under some stage of decomposition; ML - miscellaneous litter, considered as all unidentifiable material that passed through 9 mm sieve; B the 9 mm sieve; B - branches with diameter <2 cm.

Inputs of C and macronutrients via forest-floor litter

Regarding the annual amount of macronutrients and C in the forest-floor litter (Figure 4), there is a tendency of increased inputs as secondary succession advances, with the greatest inputs of all macronutrients occurring in the ADV stage. Carbon input varied between 1747 and 2416 kg ha^{-1}, whereas N input ranged from 65.7 to 101.1 kg ha^{-1}, throughout the successional stages. Regarding Ca, input varied between 35.6 and 39.3 kg ha^{-1}, while Mg input ranged from 7.7 to 10.9 kg ha^{-1}. The inputs of K and P were the smallest: from 6.6 to 8.4 kg ha^{-1} and 2.9 to 4.8 kg ha^{-1}, respectively. Nutrient input was not affected by season ($p \geq 0.05$).

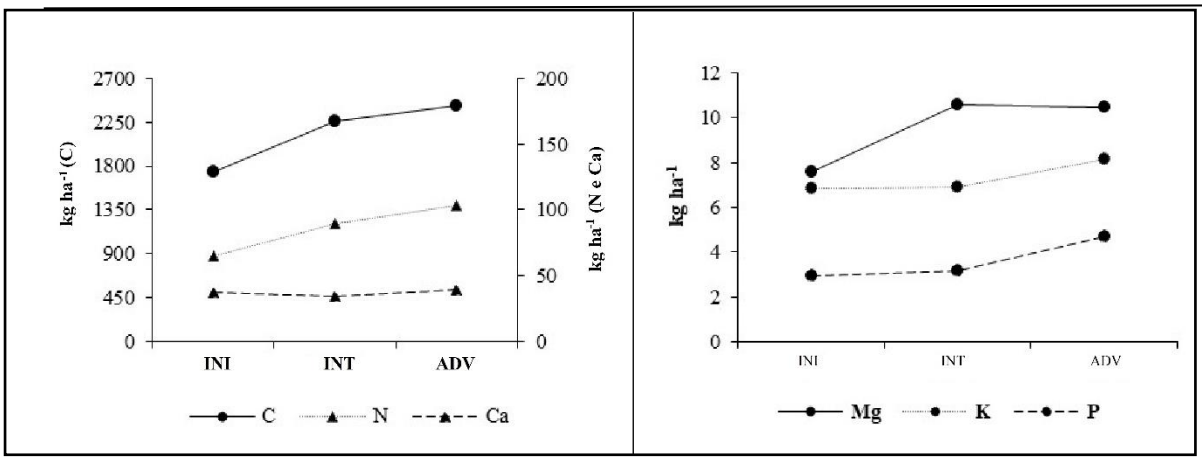


Figure 4. Macronutrients and carbon (kg ha^{-1}) in the forest-floor litter at three successional stages of the Submontane Dense Ombrophilous Forest, municipality of Antonina, state of Paraná, Brazil.

Figura 3. Quantidade de macronutrientes e carbono (kg ha^{-1}) na serapilheira acumulada, em três estágios de sucessão de Floresta Ombrófila Densa Submontana, em Antonina, PR.

DISCUSSION

The INI areas accumulated less litter than INT and ADV areas. The same behavior has been observed in several studies carried out in the Atlantic Rainforest, evidencing a tendency of greater litter accumulation as secondary succession progresses (PINTO; MARQUES 2003; DICKOW *et al.*, 2012). As forests mature, there are changes in their vegetation structure, with an increase in species richness, size and canopy density, thus increasing litter production (ALONSO *et al.*, 2015).

Although the amount of litter that accumulates on the soil varies greatly throughout the year because of the heterogeneity of species and local characteristics of climate and relief (MORFFI-MESTRE *et al.*, 2020), the average litter values found in this study agree with those reported by Rocha (2006), who obtained annual values of accumulated biomass between 13.6 and 40.3 Mg ha^{-1} in a Submontane Dense Ombrophilous Forest, and by Caldeira *et al.* (2008), who observed values from 4.5 to 5.3 Mg ha^{-1} in a forest remnant in the municipality of Blumenau, state of Santa Catarina, Brazil. The significant accumulation in the ML fraction, which represents material under the most advanced stage of fragmentation, but not in the humic form, suggests that total litter decomposition in these sites takes more than a year.

It has been proven that climatic variables as precipitation and temperature influence the litter dynamic (SETA *et al.*, 2018). The greater amount of litter accumulated in Summer is the result of the greater deposition that normally occurs at this season (CALDEIRA *et al.*, 2008), when rainfall and winds are more intense and frequent, driving the fall of senescent leaves and even live leaves. In addition, in hot periods, plants have greater metabolic activity, thus producing new shoots and releasing old leaves (BRUN *et al.*, 200). This behavior is evidenced by the greater accumulation in the WL fraction in Summer compared with that in Winter.

The same elements of plant leaves are found in the litter, although in very different concentrations and proportions in the different litter fractions. Variations depend on the composition of forest species existing at the site (MORFFI-MESTRE *et al.*, 2020), which explains the lower nutrient levels verified in the INI - a fact already observed in previous studies (PINTO; MARQUES, 2003). Differences between forest species may be associated with their nutritional composition (PINTO; MARQUES, 2003), but also result from differences in their decay rates (ROCHA, 2006).

Another factor that influences the variation of nutrient contents in the forest-floor litter is the mobility of elements, such as K, which is intensely subject to leaching, and thus little accumulated in the litter fractions. Contrarily, Ca has little mobility in plant tissues, which results in higher levels in litter than in live leaves (CALDEIRA *et al.*, 2008). The slightly lower concentrations of C found in the ML fraction result from the more advanced decomposition process of this fraction, which disagrees with the findings by Woiciechowski and Marques (2017), who reported small variations in C levels between the fractions evaluated. Concentration of N is smaller in woody fractions than in leaf fractions, as it is part of chlorophyll and other compounds in the active metabolism of plants, which are more concentrated in photosynthetic organs (BREDEMEIER; MUNDSTOCK, 2000). Increased N contents in leaf fractions as secondary succession advances is related to the presence of forest species with higher leaf contents in this element, as previously reported by Pinto and Marques (2003) in other typologies of the Atlantic Rainforest.

The C/N ratio is directly associated with litter quality, decomposition, and nutrient release (PALM *et al.*, 2001). The slightly greater values found in the B fraction indicate more difficult decomposition, while the smaller values observed in the ML fraction are associated with easier decomposition and nutrient release (FERREIRA *et al.*, 2014), and thus more subject to mineralization (HEINRICHS *et al.*, 2001). These results demonstrate how the different litter components contribute to the biogeochemical cycling on forest soil surface, in addition to being excellent indicators of these processes.

CONCLUSIONS

- This study showed how forest age (size, leaf area) influences the accumulation of litter on the soil, as a result of the increase in biomass that occurs throughout the successional cycle.
- Changes in the stages of secondary succession were reflected in changes in the chemical composition of the litter and in the amounts of different fractions, as a result of changes in the floristic composition throughout these stages.
- The season of the year is an important factor to be considered in studies addressing litter, as it strongly influences both the amount of biomass accumulated on the soil and the proportions of different litter fractions.

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