

How long does it take to decompose all litter in Brazilian savanna forest?

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ECOLOGY

ABSTRACT

Background: Litter is an important component of ecosystems, and its characteristics (e.g., production, decomposition, and nutrient and carbon content) are relevant for the ecological maintenance of different ecosystems. Previous studies on decomposition patterns have focused only on short time periods. Furthermore, there is no information regarding the actual decomposition time of organic matter in the Brazilian savanna biome known as the Cerrado. Thus, analysis of the total decomposition time can provide reliable estimates for other models. This study aimed to evaluate total litter decomposition (100%) and its relationship with seasonality and floristic composition in the savanna forest (Cerradão) formation in central Brazil. Litter bags were randomly distributed over the soil, with 10 samples collected per quarter from August 2014 to May 2020. Single- and double-entry linear regression models were used to analyze the total litter decomposition.

Results: The half-life (time for which 50% of the litter was decomposed) occurred at 360 days, and 100% of litter decomposition occurred at 2.070 days. The single-entry model was more satisfactory for estimating the decomposition speed. There was a positive correlation between litter decomposition and precipitation, and the floristic composition helped to explain the litter decomposition trends.

Conclusion: Litter decomposition in the Cerradão is related to floristic diversity (quality of the material) and to the synergism of factors that occur mainly in the rainy season. Thus, the results of this study can contribute to conservation initiatives.

Keywords: Decomposition models, floristic diversity, seasonality, litter bags.

HIGHLIGHTS

In Cerrado vegetation, it takes over five years to decompose 100% of the litter.
Long-term studies can help to obtain answers about soil management practices.
The simple-entry model is suitable for estimating litter decomposition in the Cerrado.
Litter decomposition time is directly related to forest species.

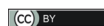
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INTRODUCTION

Savannas are naturally heterogeneous and have seasonal vegetation (Alencar *et al.*, 2020). In the Brazilian territory this type of tropical ecosystem is one of the most important environmental and economic regions, and its geographical expanse of 2 million km² therefore deserves attention. Its rich vegetation, characterized by numerous vegetation types, houses 12,000 species of plants and animals, 4,800 of which are endemic (Strassburg *et al.*, 2017).

The Cerrado, also known as the Brazilian savanna, is responsible for essential and mutually dependent ecological functions, such as the hydrological balance and biodiversity (Reis *et al.*, 2017). Despite the ecological relevance of the Cerrado, its conversion rate is unsustainable (Noojipady *et al.*, 2017), and the deforestation recorded in the biome is more intensive than that in the Legal Amazon (Reis *et al.*, 2017; Strassburg *et al.*, 2017). In this context, the implementation of conservation practices has become even more challenging. Furthermore, research conducted on the Cerrado should consider the characteristics and peculiarities of each of its phytophysiognomies (e.g., their carbon and nutrient cycles).

Therefore, it is important to study the role of litter production and decomposition time in order to determine the return of carbon and nutrients to the soil. Litter decomposition maintains nutrient cycling and the sustainability of forests by controlling the physical, chemical, and biological properties of the soil (Gatto *et al.*, 2014). Carbon fixation in the soil and wood residues is the main contributor to the potential of forests to combat global warming (Godoi *et al.*, 2016), as it contributes to the low emissions of N₂O and CH₄ (Oliveira *et al.*, 2021).

The distinctions between savanna (i.e., typical Cerrado) and savanna forest (i.e., Cerradão) can be observed in variations in litterfall, litter layer, and litter decomposition (Valadão *et al.*, 2016; Roquette, 2018; Valadão *et al.*, 2021). The release of nutrients that maintain vegetation in dystrophic tropical soils is quite important in the formation of the Cerrado (Carvalho *et al.*, 2019). In soil degradation and soil quality studies in forests, where vegetation has a longer life cycle compared to annual crops, it is important to consider indicators related to vegetation growth and development (Miranda *et al.*, 2020). Litterfall deposition is a constant variable that expresses the amount of organic matter, and this is the main factor that drives the Cerradão deciduous pattern (Giácomo *et al.*, 2012).

Cerrado areas have low decomposition rates (Souza *et al.*, 2016; Ribeiro *et al.*, 2018). This characteristic may be associated with low levels of shading and soil moisture as well as with the circulation of low concentrations of phosphorus and nitrogen, elements that favor leaf biomass decay, through the superficial organic soil layer of the soil (Jacobson and Bustamante, 2014). In addition, recent findings have indicated that the predicted conditions of climate change (rising

temperatures and changes in rainy periods) will slow down C and N cycling, an effect intensified by decreases in litter quality and decreases in fauna and edaphic microorganism (Prieto *et al.*, 2019).

Long-term evaluation of litter decomposition in natural ecosystems can provide better knowledge about the nutrient cycling in the soil (Lima *et al.*, 2015). This information can be used to inform strategies for the sustainable management of soil fertility in native degraded formations such as the Cerrado (Martins *et al.*, 2018; Fróes *et al.*, 2021). Therefore, this study aimed to evaluate the total litter decomposition in Cerradão (i.e., savanna forest) and verify the efficiency of two decomposition models. The study also investigated the influence of seasonality on the cycling of plant material in the soil.

MATERIAL AND METHODS

Study area

The study (Figure 1) area consists of approximately 4.0 ha of Cerradão (i.e., savanna forest). This vegetation type presents a medium-density woodland savanna with xeromorphic characteristics and a largely continuous canopy and tree cover of 50–90% (Ribeiro and Walter, 2008). Fire incidents occurred in the study area before 1996.

The soil in the experimental area was classified as clayey Oxisol (Typic Haplustox) (Soil Survey Staff, 2014). Chemical analysis was performed at the Embrapa Cerrado soil laboratory according to the methodology described by Embrapa (2017). The soil chemical properties (0–10 cm depth) are listed in Table 1. The soils in the studied areas were predominantly kaolinitic, and they had clay contents ≥ 63% and contained Fe and Al oxides (Table 1). According to Köppen's classification, the regional climate is rainy tropical, and it has two well-defined seasons: the dry season from May to September and the rainy season from October to April. The mean annual precipitation observed in the last 40 years was 1345.8 mm (Silva *et al.*, 2017). The precipitation and average temperature during the study period were 1192.34 mm per year and 21.68 °C, respectively (Figure. 2).

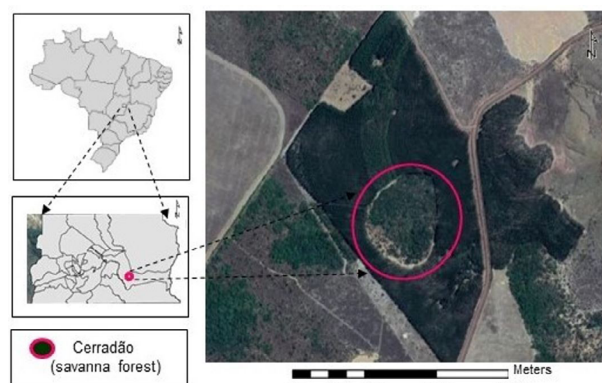


Figure 1. Study area in Distrito Federal, Brazil. Source: IBGE (2019).

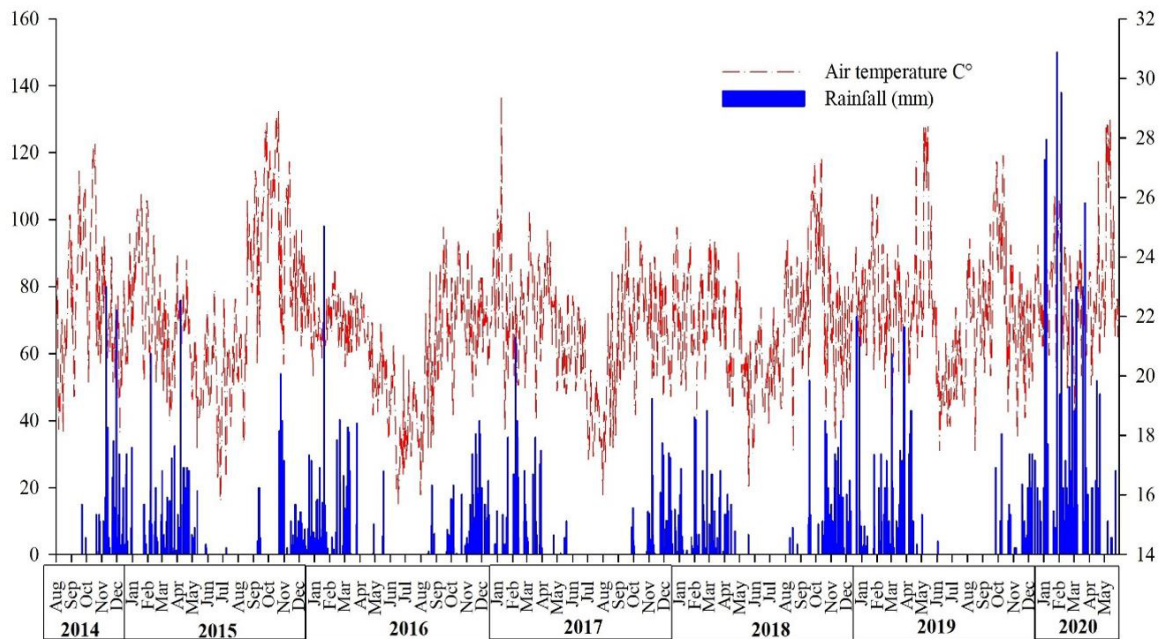


Figure 2. Precipitation (mm) and air temperature (°C) of Distrito Federal, Brazil, from August 2014 to May 2020.

Table 1. Soil chemical results (0–10 cm depth) of the study area in Distrito Federal, Brazil.

Variables	units	values
Organic matter	g kg ⁻¹	34.97
pH	H ₂ O	5.10
P ¹	mg dm ⁻³	1.52
Al	cmol _c dm ⁻³	2.29
Ca	cmol _c dm ⁻³	0.10
K	cmol _c dm ⁻³	0.53
Mg	cmol _c dm ⁻³	0.43
H+Al	cmol _c dm ⁻³	9.06
S ²	cmol _c dm ⁻³	1.06
CEC ³	cmol _c dm ⁻³	10.12
BS ⁴	%	10.47
Fe	mg L ⁻¹	141.67
Mn	mg L ⁻¹	10.67
B	mg L ⁻¹	0.50
Zn	mg L ⁻¹	0.48
Sand	%	13
Silt	%	27
Clay	%	63

1 Mehlich-1; 2 Sum of bases; 3 Cation Exchange Capacity; 4 Base saturation.

Litter decomposition analysis

To evaluate litter decomposition, 240 litter bags (20 × 30 cm, made of 2 mm nylon mesh) were randomly distributed on the forest floor, ensuring direct contact with the soil. The initial amount of litter per bag was 20 g (Santos and Whitford, 1981). Ten litter bags were collected every three months from August 2014 to May 2020 for analysis.

The litter was packed in labeled paper bags, sealed, and sent to the laboratory to determine the fresh weight. The material was dried to a constant weight in a forced air circulation oven (at 65 °C for 72 h) and then weighed again to determine the dry weight.

Litter decomposition per area was calculated based on the decomposition percentage, as proposed by Santos and Whitford (1981). The remaining litter rate was determined as the difference between the initial total litter mass (100%) and the rate for each assessment period.

Floristic inventory

To study the floristic composition, a forest inventory was carried out during the dry season (August 2015). The woody vegetation was sampled in 10 rectangular plots with dimensions of 20 × 50 m, totaling an area of 1 ha. The plots were allocated by an entirely randomized sampling method and were georeferenced using ArcGIS software, version 9.3.

The vegetation structure was characterized based on phytosociological parameters, specifically from indices expressing the horizontal vegetation structure. These included indices for absolute and relative density, dominance, frequency and relative-FR) and importance value index (IVI) (Mueller-Dombois and Ellenberg, 1974). All standing woody and shrub individuals with Db (diameter taken at 30 cm from ground level) equal to or greater than 5 cm (Felfili *et al.*, 2005) were inventoried, and their Db and total height were measured.

Data processing and analysis

To test models of the different parameters, we considered the constant k, obtained by means of a simple input exponential model (Olson, 1963) (Equation 1; hereafter referred to as the single-entry model), and a constant that

modeled the exponential sum of two parameters (Equation 2; hereafter referred to as the double-entry model), as proposed by Plante and Parton (2007). The k_A and k_B constants were obtained using Sigma Plot software for Windows 12.5 to analyze the data on the litter contained in the litter bags over the 2070 days evaluated.

$$X_t = X_0 e^{-k_A t} \tag{1}$$

$$y = A e^{-k_A t} + B e^{-k_B t} \tag{2}$$

where X_t is the dry weight of the material remaining after t days, X_0 is the dry weight of the material when $t = 0$, y is the amount of remaining dry matter (g) after t days, A and B are constants, k_A is the short-term decomposition constant, and k_B is the recalcitrant decomposition constant. The time required for the disappearance of 50% of the litter (half-life; Olson, 1963) assumes that the decomposition speed of the litter decreases exponentially with time (Equation 3). The time required for the disappearance of 95% of the litter was obtained according to Equation 4.

$$t^{1/2} = \ln(2) / k \tag{3}$$

$$t^{0.95} = 3/k \tag{4}$$

The quantitative litter decomposition was tested for normality (Shapiro-Wilk), and was then analyzed by analysis of variance (ANOVA). The distinct collection periods were considered categorical variables, and the mean of the ten litter bags was the quantitative variable. The means were compared by the Tukey test ($p < 0.05$) using SISVAR version 5.6 to detect possible differences between the sampling periods regarding seasonality and time. The data on the remaining litter mass and qualitative variables were compared between all sampling periods (0, 90, 180, 270, 360, 450, 540, 630, 720, 810, 900, 1080, 1170, 1260, 1350, 1440, 1530, 1620, 1710, 1800, 1890, 1980, and 2070 days) and were analyzed by regression analysis for each area over time. To evaluate the correlation between litter decomposition and precipitation, Pearson correlation analysis was performed using Sigma Plot for Windows 12.5.

RESULTS

Litter decomposition

The litter decomposition in the Cerradão (savanna forest) was more pronounced in the first year, during which 50% of the material decomposed (Fig. 3). The decomposition of 75% of the material occurred between 720 and 810 days. At 2070 days (5 years and 9 months), 100% of the litter had decomposed. After 180 days, it was possible to observe a large part of the leaf structure. This structure was fragmented after 360 days; at 1710 days, only the midrib structure and thin branches could be observed, and this material was mixed with the soil (Figure 3). The litter bags initially contained 20 g of litter material, and their losses were significant after 180 days (Table 2). From days 900 to 1980, the biomass was constant, and it reached zero 90 days after the last collection day (i.e., day 2070).

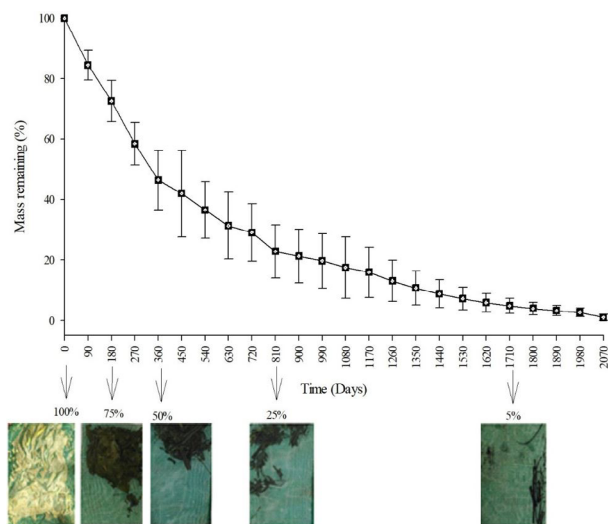


Figure 3. Percentage of the remaining litter mass during decomposition over 2070 days ($n = 10$) in savanna forest. Images below the graph show the appearance of the litter remaining in the litter bag.

Table 2. Mean remaining mass (g) over a 2070-day period in savanna forest, Distrito Federal, Brazil.

Days	Remaining mass (g)	
0	20	a
90	16.9	ab
180	14.5	bc
270	11.7	cd
360	9.3	de
450	8.4	def
540	7.3	def
630	6.3	defg
720	5.8	efghi
810	4.6	efghi
900	4.3	efghij
990	3.9	efghij
1,080	3.5	efghij
1,170	3.2	efghij
1,260	2.6	fghij
1,350	2.1	fghij
1,440	1.8	fghij
1,530	1.4	ghij
1,620	1.2	ghij
1,710	1.0	hij
1,800	0.8	hij
1,890	0.7	ij
1,980	0.5	j
2,070	0.0	l

* Different letters indicate significant differences ($p < 0.05$) between the litter collections.

The single- and double-entry decomposition models showed regression indexes ≥ 0.99 and significance at 1% for the monitored periods. The disappearance of 50% of the litter material occurred at 360 days, and the disappearance of 95% took 1710 days (Table 3). Both models were satisfactory for estimating shorter periods than longer periods, as the obtained values were closer to the observed data. The number of days estimated by the models (i.e., Olson and Plant and Parton) has no difference for short periods (i.e., 4 periods) to longer periods (i.e., 8 periods) a simple entry model is indicated. After 5 years and 9 months, six dry periods and six rainy periods were recorded. Pearson's linear correlation showed a significant positive correlation between the rainy season and litter decomposition; this pattern was not observed for the dry season (Table 4).

Table 3. Leaf decomposition parameters obtained through exponential regression using four and eight collection periods in savanna forest, Distrito Federal, Brazil.

	Four periods		
	Olson (1963)	Plante and Parton (2007)	
Equation	$X_i = 20.08e^{-0.0019}$	$y = 9.2e^{-0.0019} + 10.87e^{-0.0019}$	
k^*	0.0019	0.0019	0.0019
Time $1/2^*$ (days)	365	365	365
Time 0.95^* (days)	1,579	1,579	1,579
	Eight periods		
	Olson (1963)	Plante and Parton (2007)	
Equation	$X_i = 20.09e^{-0.0019}$	$y = 18.52e^{-0.0019} + 1.67e^{-1.35E^{-12}}$	
k^*	0.0019	0.0022	1.351E-12
Time $1/2^*$ (days)	365	315	513,062,309,815
Time 0.95^* (days)	1,579	1,364	2,220,577,350,111

* k = constant; Time $1/2^*$ = time to decompose 50% of litter; Time 0.95^* = time to decompose 95% of litter.

Table 4. Pearson's linear correlation coefficient (P) and p-value (p) for litter decomposition during the dry and rainy periods in savanna forest, Distrito Federal, Brazil.

	P	p
Dry season litter loss	-0.1228	0.8440
Rainy season litter loss	0.7996	<0.0005

* k = constant; Time $1/2^*$ = time to decompose 50% of litter; Time 0.95^* = time to decompose 95% of litter.

Floristic composition

The forest inventory data confirmed the description of Cerradão (i.e., savanna forest formation) and showed a density of 1858 ind. ha⁻¹ with Db ≥ 5 cm, including 83 species and 41 botanical families. The largest number of species was from the family Melastomataceae with 520 individuals. *Miconia pohliana*, which belongs to this family, showed the highest IVI (Table 5). The 20 species with the highest IVI represented 84% of the sampled species.

DISCUSSION

Decomposition pattern in the Cerradão

In the forested savanna environment of the Cerradão with Oxisol soil, the highest rate of litter decay occurred in the first year (Figure 3). Rapid decomposition occurred in the first few months, which can be explained by the fragmentation of litter by physical agents, soil fauna, and the release of soluble compounds, such as sugars, starches, and proteins, which are quickly used by decomposers (Ribeiro *et al.*, 2018). After this period, a decrease in the decomposition speed was observed because the most resistant structures, called recalcitrants, remained.

The model estimations exhibited a decomposition constant ($k \leq 0.0022$ (Table 3). Although the double-entry model by Plante and Parton (2007) allows for measuring different decomposition dynamics, indicating quantitative biomass models, and describing the biological processes of the system, Olson's (1963) single-entry model was the most suitable for the studied Cerradão vegetation, as it presented a lower underestimation of litter decomposition.

In the Cerrado biome of Brazil, hot weather conditions and good water availability contribute to decomposition at the beginning of the rainy season. As in the present study, research has shown that higher rates of litter decomposition in Cerrado phytophysognomies occur after the first rains (Souza *et al.*, 2016). Seasonality is an important factor that alters the density and diversity of edaphic macrofauna. Batista *et al.* (2014) observed a lower density of edaphic macrofauna individuals in the dry season of the Cerradão, whereas in the rainy season, the total density was more than twice that observed in the dry season.

A direct relationship was observed between precipitation and litter decomposition (Table 4). The observed decomposition can be strong interactions with the precipitation in native forests in the Cerrado and the ability of native forests to retain water in the soil (Scalon *et al.*, 2014; Ribeiro *et al.*, 2018). The amount of water in the leaves is directly proportional to their palatability to decomposers; consequently, a decrease in the percentage of water observed in the dry season makes the leaves less palatable, which is another factor that contributes to the reduction of litter decomposition during the dry season (Agrawal and Fishbein, 2006). The physical properties related to litter decomposition and a reduction in the mean precipitation of 8.4% in the Cerrado (125.8 mm) shows that there has been climate variability in the biome in recent years (Campos and Chaves, 2020). These oscillations may alter the dynamics of litter and nutrient cycling in the soil.

Table 5. Phytosociological parameters of woody species (diameter 30 cm from ground [Dg] \geq 5 cm) in savanna forest, Distrito Federal, Brazil.

Species	Family	DA	DR	FA	FR	DoA	DoR	IVI
<i>Miconia pohliana</i> Cogn.	Melastomataceae	290	15.61	100	2.92	3.12	18.45	36.98
<i>Qualea grandiflora</i> Mart.	Vochysiaceae	161	8.67	100	2.92	2.59	15.31	26.90
<i>Xylopia aromatica</i> (Lam.) Mart.	Annonaceae	171	9.20	100	2.92	1.41	8.32	20.45
<i>Miconia albicans</i> (Sw.) Triana	Malastomataceae	230	12.38	100	2.92	0.83	4.92	20.22
<i>Alibertia edulis</i> (Rich.) A. Rich. ex DC.	Apiaceae	137	7.37	100	2.92	0.42	2.50	12.80
Kielmeyera cf. coriacea	Calophyllaceae	121	6.51	100	2.92	0.54	3.21	12.65
<i>Qualea cf. parviflora</i> Mart	Vochysiaceae	24	1.29	80	2.34	1.05	6.20	9.83
<i>Emmotum cf. nitens</i> (Benth.) Miers	Icacinaceae	45	2.42	100	2.92	0.70	4.15	9.50
<i>Xylopia brasiliensis</i> var. <i>brasiliensis</i> Spreng.	Annonaceae	76	4.09	100	2.92	0.37	2.19	9.20
<i>Astronium fraxinifolium</i> Schott	Anacardiaceae	56	3.01	100	2.92	0.48	2.86	8.80
<i>Curatella americana</i> L.	Dilleniaceae	34	1.83	90	2.63	0.62	3.69	8.15
<i>Amaioua guianensis</i> Aubl.	Rubiaceae	31	1.67	90	2.63	0.51	3.04	7.34
<i>Rudgea viburnoides</i> (Cham.) Benth.	Rubiaceae	40	2.15	100	2.92	0.30	1.76	6.84
<i>Byrsonima pachyphylla</i> A. Juss.	Malpighiaceae	32	1.72	100	2.92	0.21	1.24	5.89
<i>Terminalia argentea</i> Mart.	Combretaceae	23	1.24	70	2.05	0.42	2.47	5.76
<i>Eriotheca pubescens</i> (Mart. & Zucc.) Schott & Endl.	Bombacaceae	12	0.65	70	2.05	0.33	1.97	4.66
<i>Davila elliptica</i> A.St.-Hil.	Dilleniaceae	24	1.29	80	2.34	0.17	0.99	4.62
<i>Simarouba versicolor</i> A.St.-Hil.	Simaroubaceae	20	1.08	80	2.34	0.19	1.13	4.55
<i>Schefflera macrocarpa</i> (Cham. & Schlecht.) Frodin	Araliaceae	16	0.86	80	2.34	0.18	1.04	4.24
<i>Piptocarpha rotundifolia</i> subsp. <i>Hatschbachii</i> G. Lom. Smith	Asteraceae	19	1.02	70	2.05	0.12	0.71	3.78

DA, absolute density ($N\ ha^{-1}$); DR, relative density (%); FA, absolute frequency (%); FR, relative frequency (%); DoA, absolute dominance ($m^2\ ha^{-1}$); DoR, relative dominance (%); and IVI, importance value index (%). Species are listed in decreasing order of IVI. and cellulose, which makes the leaves less attractive to shredders (Reis et al., 2019).

Role of biodiversity in litter decomposition

In addition to the influence of water availability, the characteristics of the substrate also influence the decomposition rate (Castanho and Oliveira, 2008). The microbial communities in the litter and soil are the functional links between the tree species of the ecosystem, and they can alter the rates of soil processes that are essential for nutrient cycling (Prescott and Gray, 2013). The speed of decomposition is also related to the structural characteristics of the native forest species in the Cerrado (Table 5), and it may vary due to the litter palatability and food preferences of the edaphic fauna species. In particular, the food preferences of shredders are related to the quality of leaves that have been conditioned by fungi and bacteria; these leaves generally have greater palatability (Graça and Cressa, 2010). In Cerrado species, this conditioning is associated with high concentrations of chemical elements that limit palatability, such as high contents of lignin and cellulose, which makes the leaves less attractive to shredders (Reis et al., 2019).

The palatability index for native vegetation can be considered an indicator of the litter decomposition rate. For example, the growth process of *Xylopia aromatica*, the species with the third highest IVI (Table 5), promotes the reduction of nutritional quality and the increase of chemical

and physical defenses; therefore, when the leaves mature, they lose the characteristics that make them palatable (Varanda et al., 2008). Silva (2009) categorized fragments as having poor palatability when they had an index < -0.2 , and as having high palatability with an index > 0.2 . *Qualea grandiflora*, the species with the second-largest IVI (Table 5) has a palatability index of 0.12 for leaf-cutting ants (e.g., *Atta laevigata*), while *Miconia albicans* has an index of -0.03 and *Qualea multiflora* has an index of -0.51 (Silva et al., 2009).

Litter decomposition, organic matter, and nutrient cycling are interrelated and involve associations between macrofauna, mesofauna, and soil microorganisms (Korasaki et al., 2013). "Ecosystem engineers" such as ants, beetles, termites, and earthworms cause intense movement of the soil (Brown and Domínguez, 2010). Although decomposition and cycling are specific functions of microorganisms, macrofauna facilitate the execution of these processes by grinding debris and dispersing microbial propagules (Prescott and Gray, 2013).

Leaf size also influences decomposition according to the amount of surface area available for microbial colonization, which increases the litter palatability for crushers. Among the species cataloged in the floristic inventory, 79% have leaves ≥ 15 cm in length and ≥ 5 cm in width (Lorenzi, 2016; Palmia et al., 2019). When evaluating different leaf sizes, it was observed that the largest ones

showed greater respiration and biomass loss. However, Rezende *et al.* (2018) found that small litter fragments exhibit a greater release of soluble compounds and faster degradation than larger fragments.

Cerradão is a vegetation type that is similar to *Cerrado lato sensu* (Ribeiro and Walter, 2008). However, some functional traits represented by the species and the soil cause the Cerradão to be more complex. Thus, litter decomposition in forest formations depends not only on the flora, but also on a set of factors and their interactions. This pattern can be explained by the different nutritional needs of each species for nutrient absorption, resorption, storage, and loss (González, 2012).

There have been several studies on litter decomposition in native formation areas in Brazil, but most of these studies have only analyzed decomposition over a short time period. Such study designs can result in the development of incorrect models for estimating the true rate of decomposition.

CONCLUSIONS

Total litter decomposition occurred after 5 years and 9 months. Compared to the model proposed by Plante and Parton (2007), the model proposed by Olson (1963) presented better estimates of the total and half-life decomposition of Cerradão in the Cerrado biome. Seasonality influenced decomposition during the rainy period. The floristic structure of the vegetation, although complex, helps to explain the decomposition through the particularity of each species. The biological and environmental diversity of the vegetation makes the system more complex, as litter decomposition in forest environments depends not only by the flora composition.

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AUTHORSHIP CONTRIBUTION

Project Idea: FPR

Database: FPR, ADO, AG

Processing: FPR

Analysis: FPR

Writing: FPR, ADO, APB, MIR, MSSC, IMLJ, MBXV, AG

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