Savannas can Functionally Turn into Forests in the Amazonia/Cerrado Transition

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ABSTRACT – Adjacent forest formations are ecotones that can reveal changes in the vertical structure of tropical biomes *e.g.*, Cerrado (brazilian Savanna). Litterfall is a metric that shows some of these alterations. Thus, we investigated key functional aspects of a Cerradão (savanna forest) and a savanna (Dense Cerrado) in the Amazonia/Cerrado transition. We evaluated the litter layer, leaf decomposition, and root mat to verify to what extent these parameters are related to ecosystem functioning of the two distinct formations, savanna, and forest. The integrated litter layer/root mat system is the main pre-condition for ecosystem functioning and trophic balance of tropical forests on dystrophic soils. The litter layer, root mat, and leaf decomposition rates were very similar in both ecosystems, including carbon release from the litter layer, despite the differences in floristic and structure of both vegetations. These similarities indicate densification of the adjacent Cerrado with a pre-structuration of a forest-like ecosystem functioning, mainly due to the no fire event. Our findings suggest that savanna ecosystems on dystrophic soils of the Amazonia/Cerrado transition have high potential to establish the trophic functional conditions to support a forest community in the absence of fire and climate changes. As long as the current climate does not change to drier and hotter conditions (*e.g.*, increased El Niño anomalies), ecological succession can be triggered and savannas can functionally turn into forests, with an increase in carbon stocks of the ecosystem.

Keywords: Cerradão; Dense Cerrado; Marimon-Hay; decomposition constant *k*; root mat.

Savanas podem se Transformar Funcionalmente em Florestas na Transição Amazônia/Cerrado

RESUMO – As formações florestais adjacentes são zonas de ecótono que podem revelar mudanças na estrutura vertical de biomas tropicais, por exemplo, no Cerrado brasileiro. A produção de serapilheira é uma métrica que reflete essas alterações. Dessa maneira, investigamos os principais aspectos funcionais do Cerradão e Cerrado adjacentes na transição Amazônia/Cerrado. Avaliamos a camada de serapilheira, decomposição foliar e malha radicular com o objetivo de verificar até que ponto esses parâmetros estão relacionados ao funcionamento do ecossistema das duas formações distintas, floresta e savana. O sistema integrado de serapilheira/malha radicular é a principal pré-condição para o funcionamento do ecossistema e o equilíbrio trófico de florestas tropicais em solos distróficos. A camada de serapilheira, a malha radicular e as taxas de decomposição foliar foram semelhantes em ambos nos ecossistemas, incluindo a liberação de carbono da camada de serapilheira, apesar das diferenças florísticas e estruturais das vegetações. Essas semelhanças indicam uma densificação do cerrado adjacente com uma pré-estruturação do funcionamento de um ecossistema tipo floresta, principalmente devido à exclusão do fogo. Isso sugere que os ecossistemas de savana em solos distróficos de transição Amazônia/Cerrado apresentam alto potencial para estabelecer condições funcionais tróficas para sustentar uma comunidade florestal na ausência de fogo e mudanças climáticas. Contanto que o clima atual não mude para condições mais secas e quentes (por exemplo, aumento das anomalias do El Niño), a

sucessão ecológica pode ser desencadeada e as savanas podem se transformar funcionalmente em florestas, com um aumento nos estoques de carbono do ecossistema.

Palavras-chave: Cerradão; Cerrado denso; Marimon-Hay; constante *k* de decomposição; malha radicular.

Las Sabanas Pueden Convertirse Funcionalmente en Bosques en la Transición Amazonas/Cerrado

RESUMEN – Las formaciones forestales adyacentes son zonas de ecotono que pueden revelar cambios en la estructura vertical de biomas tropicales, por ejemplo, en el Cerrado (Sabana brasileña). La producción de hojarasca es una métrica que refleja estas alteraciones. Así, investigamos los principales aspectos funcionales del Cerradão (Bosque de la Sabana) y Cerrado denso (Sabana densa) adyacentes en la transición Amazonas/Cerrado. Evaluamos la capa de hojarasca, la descomposición de las hojas y la malla de la raíz para verificar hasta qué punto estos parámetros están relacionados con el funcionamiento del ecosistema de las dos formaciones diferentes, bosque y sabana. El sistema integrado de capa de hojarasca/malla de la raíz es la principal condición previa para el funcionamiento del ecosistema y el equilibrio trófico de los bosques tropicales en suelos distróficos. La capa de hojarasca, la malla de la raíz y las tasas de descomposición de las hojas fueron similares en ambos ecosistemas, incluyendo la liberación de carbono de la capa de hojarasca, a pesar de las diferencias florísticas y estructurales en las vegetaciones. Estas similitudes indican una densificación de la sabana adyacente con una preestructuración del funcionamiento de un ecosistema de tipo forestal, principalmente debido a la exclusión del fuego. Esto sugiere que los ecosistemas de sabana en suelos distróficos en la transición Amazonas/Cerrado tienen un alto potencial para establecer condiciones tróficas funcionales para sostener una comunidad forestal en ausencia de incendios y cambios climáticos. Desde que el clima actual no cambie a condiciones más secas y cálidas (por ejemplo, un aumento de las anomalías de El Niño), la sucesión ecológica puede desencadenarse y las sabanas pueden convertirse funcionalmente en bosques, con un aumento de las reservas de carbono del ecosistema.

Palabras clave: Cerradão (Bosque de la Sabana); Sabana densa; Marimon-Hay; constante de descomposición *k*; malla de la raíz.

Introduction

The integrated functional system, litter layer/root mat, is the most important pre-condition for ecosystem balance, nutrient balance and trophic maintenance of tropical forests on dystrophic soils (Vitousek & Sanford-Junior, 1986). For example, forests in the Amazonia/Cerrado transition (ACT) are functionally hyperdynamic, with high turnover (mortality vs recruitment) (Marimon *et al.*, 2014) and hypercycling of nutrients (Oliveira *et al.*, 2017), aspects close-related to litter layer/root mat system. Such a condition can favor the expansion of forests over savannas in the ACT under the current climate conditions (Passos *et al.*, 2018), increasing the stocks of carbon and nutrients in the ecosystem (Valadão *et al.*, 2016). On the other hand, this same hyperdynamic equilibrium may be the cause of the vulnerability of this vegetation in case of an increase in the frequency of drought and heat events (Peixoto *et al.*, 2018).

Deforestation and fires in the region of ACT known as Arc of Deforestation in the Brazilian agricultural frontier caused a major habitat fragmentation of the tropical world (Garcia *et al.*, 2019; Xu *et al.*, 2020). Therefore, to better understand the environmental dynamics and ecosystem functioning of the ACT is a key knowledge for conservation measures and protection of this unique ecoregion (Marimon *et al.*, 2014). The predominant ecotone vegetation in the ACT is the savanna forest *i.e.*, Cerradão (Ribeiro & Walter, 2008), vegetation composed of filtered set of species from savannas and forests, mostly occurring in the Southern and Southeastern Amazonia (Marques *et al.*, 2019). Dense Cerrado is an ecotone savanna under encroachment, due to the favorable current climate condition (Morandi *et al.*, 2015; Passos *et al.*, 2018). Despite the great relevance, there is a huge gap in the knowledge of the functionality of these savanna forest transitional and hyperdynamic ecosystem

that urgently need to be filled and improved across the ACT.

Cerradão has an accelerated dynamic compared to forests in the central Amazon, hyperdynamic condition similar to Dense Cerrado (Marimon *et al.*, 2014). Both phytophysiognomies mostly occur adjacent to each other (Marimon-Junior & Haridasan, 2005), and are distributed across all ~6,000km of the ACT (Marques *et al.*, 2019). The high mortality and recruitment rates of Cerradão also result in changes in the hierarchical ranking, such as the increase of forest species compared to Dense Cerrado (Franczak *et al.*, 2011). These variations observed in the tree community can alter the capacity for assimilation and release of carbon and nutrients in case of ecological succession (*i.e.* Dense Cerrado turning into Cerradão) (Peixoto *et al.*, 2018). Therefore, studies monitoring the litter layer, leaf decomposition and root mat also become relevant (Hobbie, 2015; Sitch *et al.*, 2015; Oliveira *et al.*, 2017).

Such compartments of the ecosystem may provide an overview about the functional conditions of each vegetation type. For example, litter layer is a powerful variable in the quantification of net primary production (NPP) (Malhi *et al.*, 2011), in addition to signaling consequences of the edge effect (Brasil *et al.*, 2013) and nutrient balance of the vegetation (Oliveira *et al.*, 2017). By monitoring leaf decomposition and root mat, the level of carbon fluxes (Sayer *et al.*, 2006), nutrient cycling and trophic balance of the ecosystem (Oliveira *et al.*, 2017) may be assessed.

Cerradão and Dense Cerrado contain different floristic structure and composition, and in this way, the present study aimed to check if the parameters of litter layer, root mat, and decomposition rates also capture this distinction. Thus, we hypothesized that these parameters are able to capture the distinction between vegetation formations. This approach can assist in the understanding of future scenarios and provide support for choosing the best management practices in integral protection conservation units.

Material and Methods

Study area, soil and vegetation

The study was conducted in the Parque Municipal do Bacaba (PMB) *i.e.*, a wild city park Nova Xavantina, state of Mato Grosso, Brazil (14°42'02,3"S and 52°21'02,6"W). We investigated a Dense Cerrado (DC) (savanna formation) and an adjacent Cerradão (CD) ecotone forest in terms of the carbon cycle components. The soil of both vegetation types is dystrophic Latossolo Amarelo (Embrapa, 2018) (Oxisol) with similar base saturation, exchangeable Al and level of acidity (Marimon-Junior & Haridasan, 2005) (Table 1). The climate is AW (Köppen), with a dry period from April to September and a rainy period from October to March. The annual rainfall is 1,600mm and the average temperature is 24.4°C (Silva *et al.*, 2017).

The study areas belong to the set of permanent plots of the CNPq/PELD Project-Amazonia-Cerrado Transition (Mato Grosso State University), RAINFOR-Forest Inventory Network (University of Leeds) and the GEM-Plots (Global Ecosystem Monitoring) (University of Oxford), which investigate floristics, structure, phytosociology, carbon balance and functional aspects of ACT ecosystems, including trophic balance. Soil, floristic and phytosociological surveys were previously carried out by Marimon-Junior & Haridasan (2005), nutrient cycling by Oliveira *et al.* (2017) and carbon flows and ecosystem functionality by Valadão *et al.* (2016) and Peixoto *et al.* (2018). Floristics and phytosociology of vegetation are of dystrophic Cerradão (*sensu* Ratter *et al.*, 1973) and Typical Cerrado (*sensu* Ribeiro & Walter, 1998) (Marimon-Junior & Haridasan, 2005).

The Typical Cerrado vegetation type was reclassified in 2012 to Dense Cerrado (Morandi *et al.*, 2015). The floristic and phytosociology of vegetation was classified by Marimon-Junior & Haridasan (2005) as "dystrophic Cerradão" forest (*sensu* Ratter *et al.*, 1973) and "Cerrado *sensu stricto*" savanna (*sensu* Ribeiro & Walter, 1998). However the Typical Cerrado vegetation was reclassified in 2012 to Dense Cerrado (*sensu* Ribeiro & Walter, 1998) by Morandi *et al.* (2015). The main species in Importance Value Index – IVI, in the Cerradão are *Hirtela glandulosa* Spreng., *Tachigali vulgaris* L.G.Silva & H.C.Lima, *Xylopia aromatic* (Lam.) Mart., *Eriotheca gracilipes* (K. Schum.)A. Robyns and *Emmotum nitens* (Benth.) Miers and in the Dense Cerrado, *Qualea parviflora* Mart., *Davilla elliptica* A.St.-Hil., *Roupala montana* Aubl., *Syagrus flexuosa* (Mart.) Becc. and *Qualea grandiflora* Mart.

Table 1 – Chemical and physical properties of the soil at 0-10 and 10-20 cm depths (Marimon-Junior & Haridasan, 2005) in the Cerradão (CD) and Dense Cerrado (DC) in the Amazon-Cerrado transition zone in Nova Xavantina, state of Mato Grosso, Brazil. CEC = effective cation exchange capacity; V (%) = base saturation; SOM = soil organic matter.

	V (%)	pH (H₂O)	Sand	Silt	Clay	SOMS	N	P	Al	K	Ca	Mg	CEC
			%					mg kg⁻¹	cmol$_c$dm⁻³				
CD													
0-10	9.2	4.95	77.10	1.50	21.40	2.69	0.08	0.30	1.20	0.10	0.25	0.58	2.13
10-20	5.7	4.82	70.70	5.10	24.20	1.88	0.05	0.10	1.15	0.06	0.04	0.33	1.58
DC													
0-10	8.7	4.92	78.50	4.30	17.20	1.73	0.06	0.40	0.96	0.11	0.23	0.49	1.79
10-20	4.4	4.86	76.2	5.50	18.30	1.23	0.04	0.20	1.02	0.07	0.03	0.20	1.32

Litter layer, leaf decomposition and nutrient cycling

For volume, density and total biomass of the litter layer, we used Marimon Hay-collector (Marimon Junior & Hay, 2008). We collected 30 litter layer samples in each vegetation type monthly throughout 2013. Samples were oven-dried at 80°C to constant weight and weighed on a precision scale in the Laboratory of Plant Ecology of the Mato Grosso State University.

The decomposition rate was estimated using 20×24cm litter bags of 2mm nylon mesh. Each bag was filled with 10g dry freshly fallen leaves collected on the surface of the litter layer from each area. We distributed 75 litter bags in each area, which were collected at 15, 30, 60, 120, 240 and 365 days after the beginning of the experiment between 2011-2012 and 2012-2013 in both vegetation types. The material was separated from aggregate impurities, oven-dried at 65°C to constant weight and weighed on a precision scale.

The leaf material decay obtained by the litter bag method was calculated using the average biomass loss over time with the following equation: remaining mass (%) = (final mass/initial mass) × 100. The decomposition constant k was calculated using the equation based on Bocock & Gilbert (1957) and proposed by Olson (1963), where $X_t = X_0.e^{-kt}$, (Xt = dry weight of material remaining after t days and X_0 = dry weight of material at t = 0). Half-life time was calculated by means of the equation $t^{1/2} = \ln(2)/k$ (Olson, 1963).

Root mat

We collected 30 samples of root mesh in each area with tubular soil sample auger at 20cm of depth (Sayer *et al.*, 2006). Samples were taken in the dry and rainy period, in 2011 and 2013. In 2012, samples were taken only in the dry period. Fine roots were separated manually with tweezers, followed by washing in water. After oven-drying at 65°C, samples were weighed to obtain total biomass in kg ha⁻¹.

Carbon stock

Carbon stock (C) was calculated according to the methodology proposed by Higuchi *et al.* (1998), using linear and non-linear models to estimate different compartments *e.g.*, (stem, leaves, branches and roots) of harvested trees. For the litter layer and root biomass, the authors consider the percentages of 39 and 48.5% carbon, respectively, in relation to the total estimates.

Data analysis

Analysis of variance (ANOVA) was applied to compare litter layer parameters between months and leaf biomass decay in different periods. Significant differences between months or years were checked by Tukey's test. Independent t-test was used to establish comparisons between vegetation types, regarding the parameters of litter layer and organic carbon stock. The test was also applied to compare the root biomass in the CD and DC, and to compare the dry and rainy period. Parameters of the litter layer: biomass, volume and density were subjected to Spearman's correlation to assess whether formations show distinctions.

The residuals normality was checked by Shapiro-Wilk test and the homogeneity of variances by Levene test. When no homogeneity was found, data were transformed to Log10 (Zar, 2010). In cases where the assumptions were not met, Welch's ANOVA was applied for separate variances and Mann-Whitney with a significance level of 5% (Zar 2010), followed by Tukey's test. These analyses were performed in the software PAST 2.15.

Results

Litter Layer

The litter layer biomass estimated for the Cerradão (CD) (6.40 Mg ha^{-1}) was not different from the Dense Cerrado (DC) (5.99 Mg ha^{-1}) (Table 2). Similar condition was observed for litter layer volume and density, that is, vegetations were not significantly different from each other. The average of litter layer density was exactly the same for CD and DC (Table 2). Among all the parameters of the litter layer, only biomass did not show significant correlation between the formations (Table 3).

Table 2 – Average values of biomass (Mg ha^{-1}), volume (m^3 ha^{-1}) and density (g cm^{-3}) of the litter layer in Cerradão (CD) and Dense Cerrado (DC) in 2013 in the Amazonia-Cerrado transition, Nova Xavantina, state of Mato Grosso, Brazil.

	CD	DC	
Biomass (Mg ha^{-1})	6.54a	5.99b	(t=3.08; df=718; p<0.05)
Volume (m^3 ha^{-1})	156.55a	146.33a	(t=1.88; df=718; p=0.06)
Density (g cm^3)	0.049a	0.049a	(t=-0.10; df=718; p=0.91)

Means followed by different lowercase letters, in the same row, are significantly different by Tukey's test at 5% of probability.

Table 3 – Spearman correlation coefficient (rs) comparing monthly averages of volume, density and biomass of the litter layer between Cerradão and Dense Cerrado in 2013 in the Parque Municipal do Bacaba, Nova Xavantina, state of Mato Grosso, Brazil.

	CD x DC		
	Rs	*t*	*p*
Biomass	0.4196	1.4617	0.1744
Volume	0.9650	11.6424	<0.0001
Density	0.8811	5.921	<0.0002

Leaf decomposition

Between 2011 and 2012, in CD, the biomass decay differs from zero time after 120 days. In DC, this difference was detected earlier, after 60 days (Table 4). In the second period (2012-2013), the decomposition was similar in both formations. In both formation and year interval, after 120 days the leaf biomass decay did not differ from 365 days (Table 4).

Table 4 – Average weight (g) and percentage of leaf biomass decay in Cerradão and Dense Cerrado in the Parque Municipal do Bacaba, Nova Xavantina, state of Mato Grosso, Brazil.

Days	2011-2012		2012-2013	
	CD	DC	CD	DC
0	10 (100%)a	10 (100%)a	10 (%)a	10 (%)a
30	9.41 (94.1%)a	9.52 (95.2%)ab	8.82 (88.2 %)ab	9.06 (90.6 %)ab
60	8.61 (86.1%)ab	8.28 (82.8%)bc	7.97 (79.7 %)bc	8.30 (83.0 %)bc
120	7.47 (74.7%)bc	7.18 (71.8%)cd	7.31 (73.1 %)cd	7.42 (74.2 %)cd
240	5.89 (58.9%)c	6.45 (64.5%)ce	5.19 (51.9 %)ce	6.58 (65.8 %)ce
365	5.05 (50.5%)c	5.30 (53.0%)de	5.47 (54.7 %)de	6.37 (63.7 %)de
	F. Welch$_{(5. 33.8)}$=89.9; $p<0.01$	F. Welch$_{(5. 33.6)}$=52.9; $p<0.01$	F. Welch$_{(5. 34.2)}$=97.7; $p<0.01$	F. Welch$_{(5. 33.3)}$=23.7; $p<0.01$

Means followed by different lowercase letters, in the same column, are significantly different by Tukey's test at 5% of probability.

In the first period (2011-2012), the remaining leaf biomass was 50.0% and 53.0%, in CD and DC. In the second period (2012-2013), this percentage was 54.7% in CD and 63.7 in the DC, and this difference was significant ($p>0.05$). The estimate of biomass decay was 1.03 Mg ha^{-1} in CD, and 0.98 Mg ha^{-1} between 2011 and 2012. In the second period, this estimate was 0.94 Mg ha^{-1} in CD, and 0.75 Mg ha^{-1} in DC.

The *k* constant calculated by litter bag sampling was 0.0019, with a half-life ($T^{1/2}$) of 365 days in Cerradão, and for Dense Cerrado, this constant was 0.0016 with a $T^{1/2}$ = 433 days, in 2011-2012. For the second period (2012-2013), the constant and half-life values were 0.0015 and 462 days in the CD, and 0.001 and 693 days in the DC.

Biomass loss over the sampling period followed a similar trend of decay in both vegetation types, although CD showed a more accentuated regression curve (Figure 1A) compared to DC (Figure 1B), and was highly correlated both in the first (rs = 1.00, $p <0.01$) and in the second period (rs = 0.90, $p <0.05$).
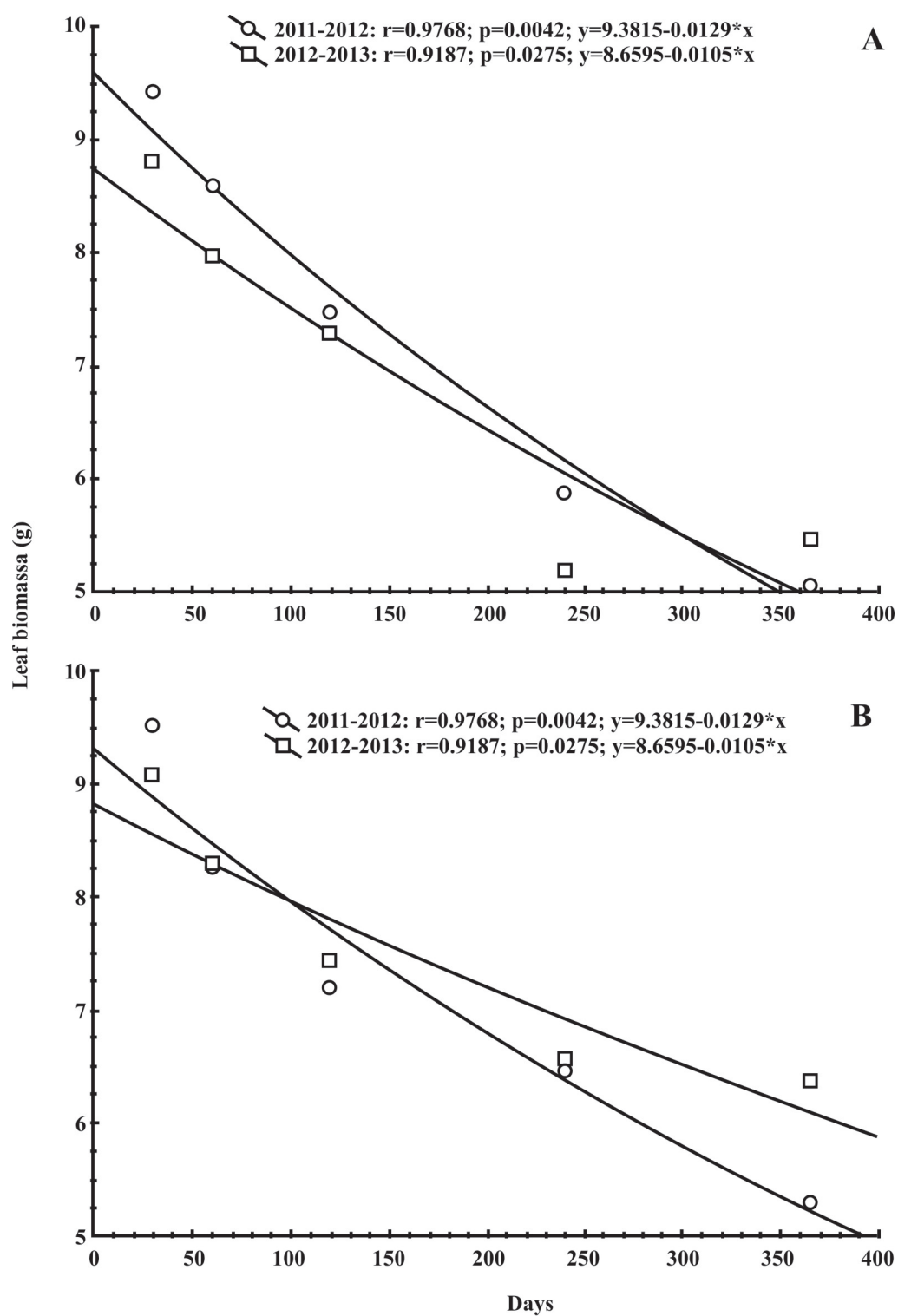
Figure 1 – Exponential regression of leaf biomass (g) over the days in 2011-2012 and 2012-2013 in Cerradão (A) and in Dense Cerrado (B).

Root mesh

Cerradão showed the highest amount of root biomass in the dry period in 2011 and 2012 and only in the rainy period in 2013. However, in 2012, in the dry period, the Dense Cerrado showed a higher average value compared to the Cerradão (Table 5).

Although there were up and downward variations in root mesh estimates in the dry and rainy periods, differences were detected between the periods in 2011, with higher averages in the rainy period in both vegetation types. However, in 2013 the average was higher in the dry period, with a significant difference only for the CD (Table 5). Estimates for the three years of collection showed an increase of root mesh during the dry period in DC (Table 5).

Table 5 – Average weight of root biomass in the Cerradão and Dense Cerrado in dry and rainy periods in 2011, 2012 and 2013 in the Parque Municipal do Bacaba, Nova Xavantina, state of Mato Grosso, Brazil.

	2011		2012*		2013	
	CD	**DC**	**CD**	**DC**	**CD**	**DC**
	--- kg ha⁻¹ ---					
Rainy	329.63aAa	316.32aAa	-	-	268.73bAa	346.92aAb
Dry	199.03bBa	115.84bCb	131.51Cb	174.64Ba	494.33aAa	404.51aAa

Means followed by different lowercase letters, in the same column, are significantly different (between dry and rainy periods); uppercase letters for comparison between years, and subscript lowercase letters for comparison between vegetation types, in the same row. * Only in the dry period.

Carbon stock

Estimates of the organic carbon stock for both vegetation types confirm the differences between CD and DC in most of the compartments analyzed. The total organic carbon stock, considering all compartments, also showed a difference between vegetation types. The root mesh was the only variable with no differences between the formations (Table 6).

Table 6 – Organic carbon stock in the litterfall, litter layer and root mesh (Mg ha⁻¹) in Cerradão and Dense Cerrado in 2013 in the Parque Municipal do Bacaba, Nova Xavantina, state of Mato Grosso, Brazil.

	CD	DC	
Litterfall *	3.4a	1.65b	(t=2.86; df=22; p<0.01)
Litter layer	2.55a	2.33b	(t=3.08; df=22; p<0.05)
Root mesh	0.15a	0.14a	(t=1.58; df=58; p=0.11)
Total	6.1a	4.1b	(t=2.10; df=22; p=0.05)

Means followed by different letters, in the same row, are significantly different. *Valadão *et al*. (2016).

Discussion

Litter Layer

The parameter litter layer did not reflect the difference between CD and DC as it did for litterfall (Valadão *et al*., 2016). This difference between litter layer and litterfall between vegetation types may be the result of the densification that occurs in the Dense Cerrado. This condition was quite evident by the increase in IVI – Importance Value Index for Cerradão species in the Parque Municipal do Bacaba (Franczak *et al*., 2011).

The key species on the CD, *Tachigali vulgaris*, in a study by Morandi *et al*. (2015) demonstrated a rapidly colonization of the DC formation adjacent to the CD in the PMB. Such alteration can be associated, in large part, with the exclusion of fire and the history of increased rainfall in the entire Amazon Basin (Neves *et al*., 2018).

Even presenting a forest structure, the Cerradão has a higher degree of leaf senescence compared to transition forests between Amazonia and Cerrado. This pattern makes the CD a hyperdynamic vegetation, where turnover rates (mortality × recruitment) are among the highest for tropical forests (Marimon *et al*., 2014). High turnover rates in the CD are largely determined by the dominance of *T. vulgaris*, a pioneer species with a short life and fast growth, which causes the constant opening of clearings in Cerradão and consequently increase the input of nutrients into the soil (Franczak *et al*., 2011; Marimon *et al*., 2014; Oliveira *et al*., 2017).

Leaf decay

The *k* values were higher compared to a study conducted by Souza *et al*. (2016) in a Dense Cerrado, in which the authors reported a coefficient of 0.0007. On the other hand, the *k* values were lower compared to Ribeiro *et al*. (2018), in Cerradão with a coefficient of 0.0021. In the present study, the results showed that CD and DC are efficient in assimilating and decomposing the carbon material deposited on the soil. According to Olson (1963), the *k* coefficient measures the efficiency of decomposing organisms, such as fungi, bacteria and certain decomposing animals. Thus, the higher the *k*, the greater the amounts of mineralized carbon, organic matter available in the soil, and the greater the biogeochemical dynamics (Ribeiro *et al*., 2018).

Comparing the biomass decay in percentage Ribeiro *et al*. (2018) found a loss of 54% litter in a Cerradão, in the Distrito Federal, Brazil, and Souza *et al*. (2016) found a loss of 30% in a Dense Cerrado, also in the Distrito Federal. Both studies reported the trend of decay verified in the present study, where CD had more biomass loss than DC. The greater loss in Cerrado areas can be explained by the availability of water and biodiversity, which leads to greater fragmentation of plant material, accelerating the physical and biochemical transformation of organic matter (Oliveira *et al*., 2017).

Biomass decay was similar between the savanna and forest vegetation types. However, the half-life ($T^{1/2}$) and *k* rate indicated greater carbon assimilation capacity in the Cerradão. This may be associated with lower levels of shading and soil moisture and mainly with low concentrations of phosphorus and nitrogen circulating on the soil top organic layer, elements that favor the decay of leaf biomass (Jacobson & Bustamante, 2014).

Root mesh

The lack of a pattern to define the distinction between the vegetation types, years interval, and periods *e.g*., dry and rainy denotes the inherent heterogeneity of vegetation roots, which requires a more extensive sampling method (Sochacki *et al*., 2017). Results observed in 2011 were similar to the study of Sayer *et al*. (2006), in Panama tropical forests with a reduction in the dry seasib. However, this pattern was not found in the following years of data collection.

The response time of plants as a function of soil moisture (Speleta & Clark, 2007) is a factor that can influence the root biomass quantification. In the rainy period, the phenological activity of roots becomes more intense, when the soil moisture increases (Andrade *et al*., 2020). Thus, the greater production of the superficial root mat seems to be related to the length of the rainy period and the total volume of rain at the end of this period (Oliveira *et al*., 2005; Barbosa *et al*., 2012).

The larger volume of roots in the dry period may also be associated with the allocation of carbohydrates (Hoffmann *et al*., 2004). When comparing compartments that best estimate NPP *i.e*., Net Primary Production, in humid tropical forests, Malhi *et al*. (2011) considered the root

biomass a weak predictor comparing to the litterfall. This condition can be explained by the tradeoff between investment in root system and diameter increase in arboreal communities in tropical forests (Malhi *et al.*, 2011).

The displacement of NPP to roots in drought periods can relieve prolonged water stress, thereby increasing nutrient uptake and carbon assimilation (Doughty *et al.*, 2015). Also, the distribution of fine roots in tropical forests is usually proportional to the amount of litter available on the soil surface, which in the transition forest is greater during the dry period (Sayer *et al.*, 2006).

The significant increase in root biomass of the Dense Cerrado during the sampling period may be an indication that the DC is in the process of densification of vegetation. One of the main conditions for the transformation of the Dense Cerrado (savanna vegetation) into the Cerradão (forest vegetation) is the exclusion of fire (Hoffmann *et al.*, 2012b). In this case, periods of more than seven years contribute for the Dense Cerrado to present forest characteristics (Hoffmann *et al.*, 2012b) and, consequently, increase in the superficial root mat.

This effect of densification of the DC in the Parque Municipal do Bacaba can be evidenced in the alterations in the importance value index of the tree component of this formation. Typical heliophyte species of Dense Cerrado, such as *Eriotheca gracilipes* (K. Schum.) A. Robyns lost positions in the hierarchical ranking in a six-year period in the DC, according to studies by Franczak *et al.* (2011). The same study also highlighted the increase of semi-deciduous species from shaded environments, such as *Chaetocarpus echinocarpus* (Baill.) Ducke in the same area. Recently, Morandi *et al.* (2015) verified a large number of *T. vulgaris*, a typical forest species of Cerradão, fully established in the DC.

Carbon stock

The distinctions between Cerradão and Dense Cerrado in the compartments were also confirmed regarding the organic carbon stock. These differences between the vegetation types are important findings in initiatives for the management and conservation of sites vulnerable to suppression of natural vegetation, as is the case of areas of the Amazon Forest adjacent to the Cerrado Biome.

The distinction between CD and DC was not so evident for organic carbon and litter layer compared to the litterfall, as reported by Valadão *et al.* (2016). Our study showed that carbon estimates of the litterfall produced and the respective litter layer provided a greater input of C into the cycling system via litterfall. Tree species have a predominant influence on carbon stocks, mainly due to the faster decomposition rates and the higher amounts of organic matter added to the soil through litterfall deposition (Jobbágy & Jackson, 2000).

The amount of carbon added to the soil by litterfall is also related to the high rates of mortality and recruitment in transition forests on the southern edge of the Amazon (Marimon *et al.*, 2013). This dynamic in the carbon balance indicates a mix of difference residues that accumulate in forests and results in differences in the decay time.

The compartments of root mesh and litter layer showed that CD and DC have similarities regarding the accumulation of biomass and amounts of carbon. The explanation may lie in the fact that the Dense Cerrado is in a forward successional process, tending to show more forest characteristics, by a significant increase in the basal area of *Tachigali vulgaris* (Morandi *et al.*, 2015).

This pattern is related to the exclusion of fire for periods longer than seven years (Hoffmann *et al.*, 2012a). The establishment and later maturity of forest species can result in the exclusion of grasses, the main fuel material for the savanna formation (Hoffmann *et al.*, 2012b). The closing of the canopy can cause drastic changes, since heliophyte species tend to show slower growth in densely shaded places (Hoffmann *et al.*, 2012a). Thus, at each density cycle, positive feedback is formed with a progressive reduction in the combustible material, an increase in the relative humidity of the air and a reduction in the internal temperature of the ecosystem.

Conclusion

Litter layer and leaf decay were able to capture the distinction between the vegetation types; however, the root mat did not show this capacity. Even so, there is a possibility that an adjacent vegetation type, *e.g.*, Typical Cerrado species, changes the structure and dynamics of

vegetation and exposes to vulnerabilities to local extinction.

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