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Original article

Belowground biomass seasonal variation in two Neotropical savannahs (Brazilian Cerrados) with different fire histories

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Abstract – The belowground biomass of two types of ecosystems, frequently burned open savannah (Campo Cerrado) and protected-from-fire closed savannah (Cerradão), was sampled every two months during a one year period, in three soil layers (0–12, 13–24, 25–36 cm). Living organs were separated by flotation and sieving. Belowground biomass showed significant seasonal variation, values being higher during the rainy season and lower during the dry period. Fire, and soil depth also had significant effects on belowground biomass. Biomass values were significantly higher in Cerradão for all months and in all soil layers. Belowground biomass was correlated significantly with climatic variables related to the water availability of the year sampled. Cerradão belowground biomass showed a higher correlation with climatic parameters than Campo Cerrado. The cerrados belowground biomass must be taken in consideration in the studies of fire effects, land use change and global carbon storage and release capacity.

belowground biomass / Brazil / cerrado / fire / roots / tropical savannah

Résumé – Variation saisonnière de la biomasse souterraine dans deux savanes tropicales (Cerrados brésiliens) ; l'une protégée et l'autre soumise à des incendies fréquents. La biomasse souterraine de deux types d'écosystème, savane ouverte fréquemment brûlée (Campo cerrado) et savane fermée protégée du feu (Cerradão), a été échantillonnée tous les deux mois pendant un an, en trois couches de sol (0–12, 13–24 et 25–36 cm). Les matières vivantes ont été séparées par flottation et tamisage. La biomasse souterraine a présenté une variation saisonnière significative, avec des valeurs plus élevées pendant la saison des pluies et plus petites pendant la saison sèche. Les résultats indiquent que l'époque de l'année, le régime du feu et la profondeur du sol ont des effets significatifs sur la biomasse souterraine. Les estimations de la biomasse ont été significativement plus élevées au Cerradão pour tous les mois et toutes les couches du sol. La biomasse souterraine présente une corrélation significative avec les variables climatiques en relation avec la disponibilité en eau de l'année d'échantillonnage. Au Cerradão, la corrélation a été plus élevée qu'au Campo Cerrado. La biomasse souterraine des cerrados doit être prise en compte dans les études sur les effets du feu, le changement d'utilisation de la terre et le cycle global de carbone.

biomasse souterraine / Brésil / cerrado / feu / racine / savane tropicale

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1. INTRODUCTION

The distribution, structure and function of cerrado ecosystems are conditioned by the tropical climate, with a rainy summer and a dry winter, associated with acid, sandy soils of high aluminium concentration and low fertility. Besides climate and nutrient availability, fire has also been identified as an important factor in structuring these ecosystems, and fire recurrence has been considered a limiting factor in biomass development and accumulation [8, 15].

In spite of being one of the main South American ecosystems, covering an area of more than 1.8 million km^2, information on cerrado biomass is scarce. Some data are available on the herbaceous layer aboveground biomass [7, 9, 24] and on wood layer biomass [2, 6, 11]. However, less attention has been paid to the belowground portion, probably because of the technical difficulties involved [16, 38]. Early observations have pointed to the abundance of belowground organs and to their importance for plant adaptation and community structure. The reported occurrence of different types of belowground organs may indicate the diversification of strategies to explore the soil-limited resources [27]. It was shown, particularly, that deep well-developed belowground systems were common among plants and that, in some cases, they reached the very deep water table [8, 13, 27]. The great amounts of belowground biomass and its concentration in the upper soil layers have only recently been quantified in Brazilian ecosystems [2, 6, 25].

The objective of this study was to analyse the seasonal changes in belowground biomass at different soil depths in two different Brazilian savannahs with different fire histories and to test if these seasonal changes are related to seasonal climatic fluctuations.

2. MATERIALS AND METHODS

2.1. Study Area

This work was carried out at the Cerrado of Emas, in the municipality of Pirassununga, São Paulo State, in the Southeast region of Brazil, (47°23' W and 21°58' S).

The climate belongs to the tropical type, with a rainy summer and a dry winter (Type II of Walter & Lieth, [39]). Mean annual values of temperature and rainfall are about 21.2 °C and 1379 mm, respectively, and show a clear seasonal pattern (*figure 1* [10]). The monthly rainfall from April to September is lower than 80 mm, and from June to August it is below 40 mm. During the drier months there is a water deficit of 80 to 100 mm [5, 32], and the vegetation shows many symptoms of water

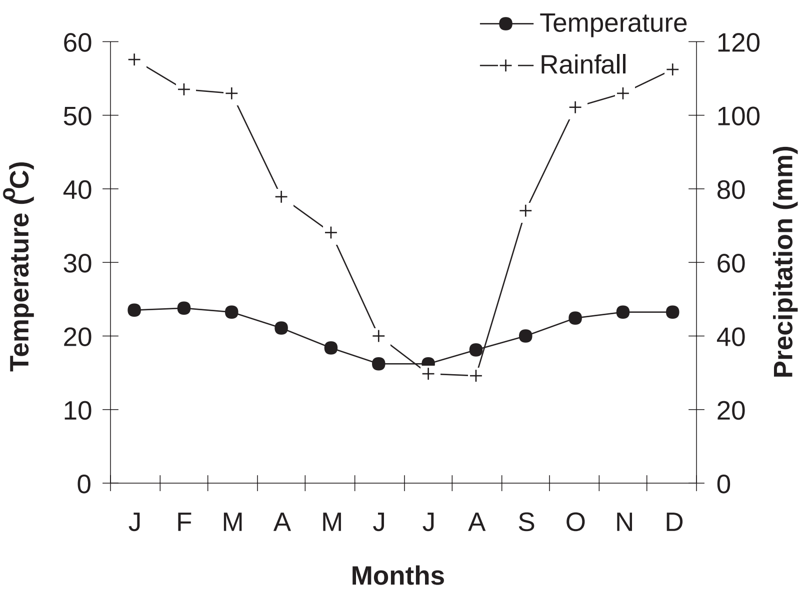

Figure 1. Climate diagram for Cerrados region. Mean monthly temperature and rainfall are presented (n = 21). Data from DAEE, 1974–1994.

stress, such as increased litterfall, and slow-down or absence of growth. During these months fires often occur [8].

The landscape is gently rolling, with a predominance of plateaux. The main soil type is red-yellow latosol, characterised by its low clay content, low cationic-exchange capacity, low base saturation, acidity, low concentration in organic matter, deficiency in several nutrients and high aluminium concentration [23]. Soils are old and deep, and plant water availability varies seasonally along the soil profile. The water table may reach depths of up to 18–20 meters, and the upper soil layers dry out during the winter [31].

Emas region is covered by a campo cerrado (open savannah) with a physiognomy and flora similar to those found in other Brazilian regions [13]. It is characterised by a continuous herbaceous/grassy layer; the woody elements are sparsely distributed, with average density of 2047 woody individuals/hectare. The herbaceous layer is formed by 95 species of which the most representative are *Echinolaena inflexa*, *Psidium suffruticosum*, *Trachypogon spicatus*, *Diandrostachya chrysotryx* and *Veronia cognata*. Among the 47 woody species, some of the most representative are *Byrsonima coccolobifolia*, *Erythroxilum suberosum*, *Kielmeyera coriacea*, *Ouratea spectabilis*, *Stryphnodendron adstringens*, and *Tabebuia caraiba* [36].

The study area is located in a region that has been very intensely modified by human activities, and the occurrence of annual or biannual burns has been observed during the last fifty years. Since 1946, a section of the area was protected from fire, by researchers from the Dept. of Botany of the University of São Paulo. In the years that followed, a great change in this protected ecosystem structure was observed, and after 20 years the area had changed from the open savannah (Campo Cerrado) to the most closed and dense cerrado type (Cerradão), which now has forest physiognomy. The surrounding vegetation that continued to be burnt at 1- to 2-year intervals maintained the original open structure (Campo Cerrado). Cerradão presented higher tree density, taller and bigger trees and scarcer herb layer than the open savannah. Tree species are similar to those found in the open savannah, but their relative proportions in the community structure were different. Frequent species in the Cerradão area are *Bowdichia virgilioides, Copaifera langsdorfii, Guapira noxia, Machaerium acutifolium, Qualea grandiflora, Stryphnodendron adstringens, Tapirira guianensis*, and *Xylopia aromatica*. The litter layer was thicker in the Cerradão and the closed canopy conditioned a different microclimate from the open savannah.

2.2. Methods

The samples were collected at random in the two types of cerrado ecosystems, corresponding to the extremes in fire regime mentioned above, that is, Campo cerrado (frequently burned open savannah) and Cerradão (closed savannah unburned since 1946). The samples were taken from October 1987 to October 1988 in the Campo cerrado, and from October 1990 to October 1991 in the Cerradão, by the sequential soil coring method [38]. Every other month, three consecutive soil layers (0–12, 12–24, 24–36 cm) were sampled at 15 randomly selected points. Each sample was at least 20 meters from the other and they were avoided in the following sampling. From each layer, one litre of structured soil was collected using a metal corer; litter and all aboveground organic material were avoided. All samples were then taken to the laboratory, in order to separate the soil particles from the biological components. This step involved sieving the samples through a 250 m mesh to remove clay and silt particles as well as soil organic matter. Then, sand and biological components were separated by flotation in water, followed by a second sieving with the mesh [20]. The upper diameter limit accepted was 20 mm, and dead organs were also separated based in previous tests using the 2, 3, 5-Triphenyltetrazolium chloride (TTC) reduction techniques [28], and non functional organs were not considered in the analysis. Larger organs were also discarded because the sampling method was not considered adequate to these structures [41]. The samples were then oven dried at 80 °C to constant weight.

Differences between factors (fire history, month and depth) were analysed using the analysis of variance; pairwise comparisons were performed by post-hoc Scheffé test.

We analysed the relation of biomass values and climatic data [10] using correlation analysis and then analyses of covariance. We tested the significance of precipitation (P) and actual evapotranspiration (AET) of the sampled month (P_i, AET_i), of the previous month (P_{i-1}, AET_{i-1}), and the sum of both the sampled and the previous month ($P_i + P_{i-1}$, $AET_i + AET_{i-1}$). Actual evapotranspiration was computed by the standard method of Thorntwaite and Mather [35]. Statistical analysis were performed using the SPSS (Statistical Programs for Social Sciences), version 8 for Windows.

3. RESULTS

The estimates of belowground biomass showed spatial variation in both its horizontal and vertical distribution (*table I*). At both sites about 58% of the total belowground biomass was concentrated in the upper layer, vs. 25% from 13 to 24 cm and 17% from 25 to 36 cm, on average.

Clear seasonal variations in the belowground biomass of these ecosystems were observed on both sites (*table I*). The maximum biomass values were found during the rainy season (Cerradão) and at the end of this season

Table I. Belowground biomass according to soil layers in Campo Cerrado and Cerradão (Brazilian savannahs). Values (Mg ha^{-1}) are mean and standard deviations (in brackets). Different lower-case letters indicate significant ($p < 0.05$) differences between months; different upper-case letters indicate significant ($p < 0.05$) differences between layers. Differences between sites (Campo cerrado and Cerradão) are significant ($p < 0.05$) for all months and all layers.

Months	1–12 cm	13–24 cm	25–36 cm	Total
	Campo Cerrado (burned open savanna)			
October 1987	4.93 (1.74)	2.07 (0.79)	1.54 (0.66)	8.54 (1.63)
	A a	B ab	C a	a
December	6.73 (2.58)	3.12 (1.42)	2.01 (0.97)	11.86 (2.55)
	A ab	B bc	C a	ab
February 1988	7.29 (2.78)	3.13 (1.46)	1.36 (0.46)	11.78 (3.29)
	A ab	B c	C a	ab
April	8.64 (3.68)	3.78 (1.21)	3.78 (1.21)	14.48 (4.22)
	A b	B c	C a	b
June	4.87 (1.95)	2.00 (0.70)	1.85 (0.82)	8.71 (2.51)
	A a	B a	C a	a
August	5.92 (2.40)	2.21 (0.72)	1.73 (0.82)	9.86 (2.69)
	A ab	B a	C a	a
October	4.97 (2.18)	2.15 (0.83)	1.54 (0.77)	8.66 (2.32)
	A a	B a	C a	a
	Cerradão (unburned closed savanna)			
Months	1–12 cm	13–24 cm	25–36 cm	Total
October 1990	7.59 (1.64)	3.30 (1.00)	2.38 (0.50)	13.27 (1.84)
	A ab	B a	C a	a
December	9.94 (2.05)	4.71 (1.05)	2.90 (0.82)	17.54 (2.93)
	A b	B ab	C ab	b
February 1991	10.76 (2.31)	5.61 (1.50)	2.94 (0.46)	19.30 (3.32)
	A bc	B ab	C b	b
April	11.16 (2.14)	5.57 (1.28)	3.23 (0.50)	19.97 (3.03)
	A bc	B b	C b	b
June	6.59 (1.26)	3.85 (0.88)	2.88 (0.45)	13.31 (1.95)
	A a	B a	C a	a
August	5.62 (1.14)	3.29 (0.85)	2.67 (0.42)	11.59 (1.88)
	A a	B a	C a	a
October	6.93 (1.41)	3.33 (0.78)	2.72 (0.42)	12.98 (1.66)
	A a	B a	C a	a

(April, Campo Cerrado), and the minimum ones, during the dry period. The belowground biomasses collected during the rainy season were significantly higher than that collected during the dry period in both open and closed savannah (*table I*). Unburned closed savannah showed significantly higher belowground biomass in all months and all layers than the frequently burned open savannah.

Belowground biomass in Campo Cerrado was only significantly ($p < 0.05$) correlated to the actual evapotranspiration of the previous month (AET_{i-1}), while for Cerradão, both actual evapotranspiration (AET_{i-1}, $AET_i + AET_{i-1}$) and precipitation (P_i, P_{i-1}, $P_i + P_{i-1}$) were significant (*table II*). ANCOVA analysis shows that the relations are significantly different for each savannah type (*table II, figure 2*).

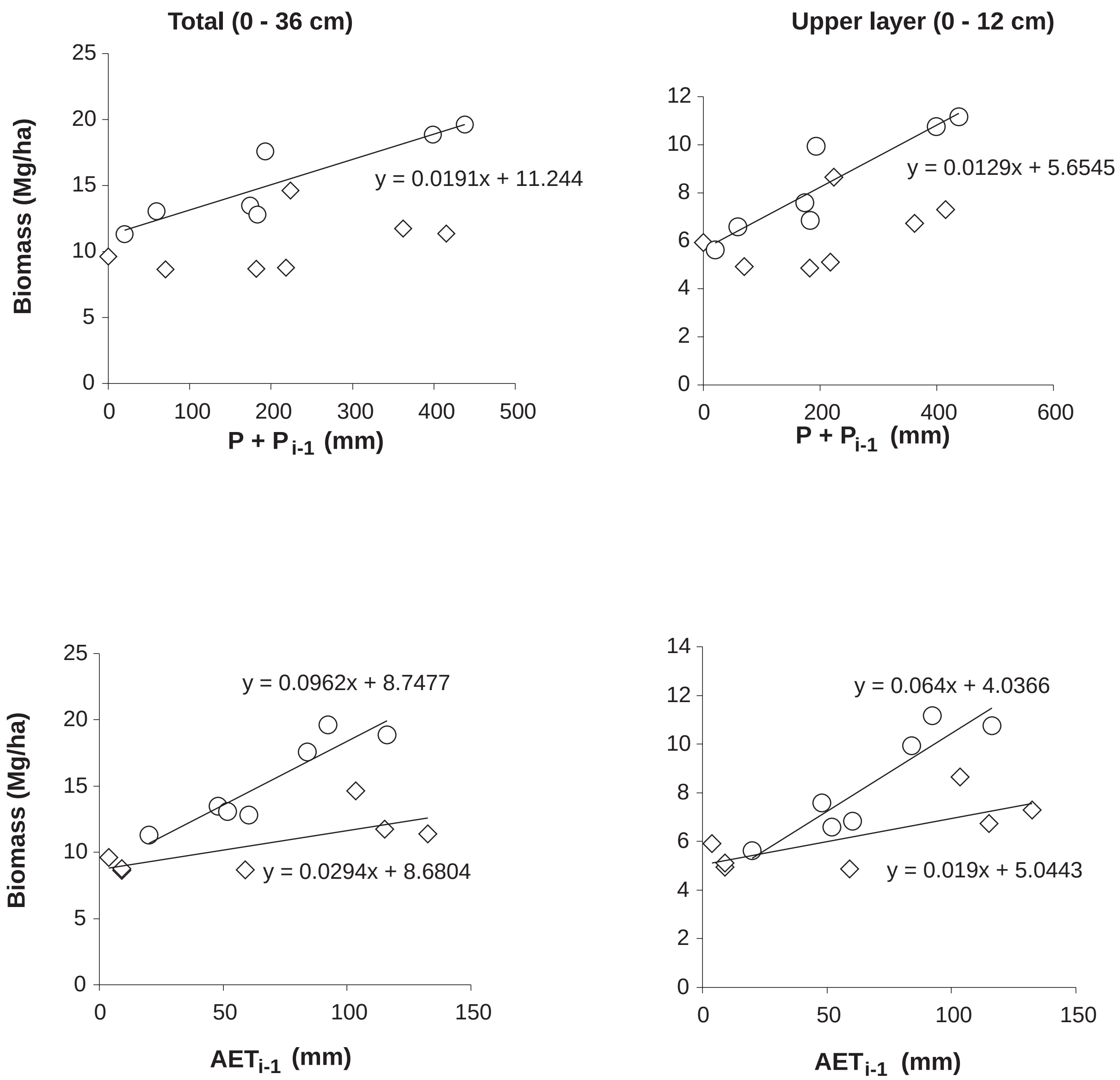

Figure 2. Relation between belowground biomass (upper soil layer and total soil layers)and climatic variables for cerrado ecosystems (circle: Cerradão; square: Campo Cerrado). Lines are significant fits ($p < 0.05$).

Table II. Correlation between selected climate variables (P: precipitation; AET: actual evapotranspiration) and belowground biomass for the upper soil layer (0–12 cm) and for the total soil sampled (0–36 cm) in the two ecosystems studied (Campo cerrado and Cerradão), and significance of the analysis of covariance (ANCOVA) where the covariate is the climatic variables and the main effect the two ecosystems. Bolded correlation coefficients are significant at the level of $p < 0.05$.

Variables*	Correlation (r)				ANCOVA (p)	
	Campo Cerrado (burned open savanna)		Cerradão (unburned closed savanna)			
	upper	total	upper	total	covariate	main
P_i	0.516	0.518	**0.866**	**0.826**	0.049	0.005
P_{i-1}	0.527	0.494	**0.851**	**0.861**	0.011	0.001
$P_{i-1} + P_i$	0.482	0.459	**0.915**	**0.903**	0.007	0.003
AET_i	0.483	0.493	0.635	0.571	0.060	0.006
AET_{i-1}	**0.742**	**0.733**	**0.925**	**0.926**	0.008	0.002
$AET_i + AET_{i-1}$	0.573	0.571	**0.819**	**0.733**	0.016	0.002

* *i*: sampled month; *i*–1: month before the sampling.

4. DISCUSSION

The belowground biomass distribution in the soil profiles decrease quickly with depth and varies on a seasonal basis, with the greatest concentration (50–60%) in the upper layer. This pattern of biomass distribution in the soil and of seasonal variation is common in tropical savannahs from South America and Africa [6, 17, 25, 26, 28, 30, 34]. The upper layer shows more clearly the seasonal variation due to the fact that it is more exposed to weather changes. This layer also presents the greatest amounts and flows of nutrient due to litterfall and ash accumulation after fires.

The different sampling periods in burned and protected areas limits our comparisons between the belowground biomass in the two sites, but as the years presented very similar climate patterns, some observations can be made. Recurrent fires may limit the production of aboveground [11], and belowground biomass (*tables I* and *II*). The protected cerrado showed mean belowground biomass values 30% greater than those measured in the Campo Cerrado. In Mediterranean ecosystems, fire effects were also observed in belowground biomass [19] and disturbance significantly effected root biomass in deciduous forests studied in India [34].

There is a clear relation between seasonal fluctuation in belowground biomass and available water in the unburned Cerradão, whereas this relation is weaker for the frequently burned Campo Cerrado (*table II*). The actual evapotranspiration of the previous month seems to be the best predictor variable for estimating belowground biomass; this parameter was found to be significant for both the burned Campo Cerrado and the unburned Cerradão but the relationship was significantly different between these two ecosystems (*figure 2*). All of this suggests the possibility that recurrent fire produce a disturbance effect on ecosystem structure, both by directly damaging plants, causing nutrient losses [24] and by changing soil properties [40]. The recurrent fires maintain a more heterogeneous habitat with a sparse woody plant layer, which is less fire resistant than herbs [8]. The heterogeneity is also due to the irregular fire spread and intensity in the area from year to year. In the Campo Cerrado recurrente fire and low nutrient availability may be controlling productivity more than rainfall and this may be the reason for the weaker relation observed between belowground biomass and climate. In the unburned closed savannah (Cerradão), on the other hand, the absence of fires allowed the ecosystem to store more nutrients and develop a more complex and homogeneous vegetation cover, where the belowground biomass variations are more strikingly related to climatic seasonal changes. Our data confirm the seasonality of ecosystem functions in cerrados; that is, the weather determines a strong lowering in plant metabolism during the dry winter. The decrease in leaf biomass [12], the decrease in net primary production [21], as well as the mortality of the aboveground parts of the majority of the herb layer are accompanied by a decrease in the belowground biomass present in the upper soil layers which are submitted to a severe drought [31].

Estimates of the belowground biomass in Campo Cerrado showed that this component equals, and even outweighs aboveground herb biomass. Six determinations of aboveground biomass in the same Campo Cerrado indicated values ranging from 4.9 to 7.7 Mg ha^{-1} [24]. As our determination involves only the upper soil layer, it must be considered an underestimation of the total value. However, the belowground biomass may equal or exceed aboveground biomass in the frequently burned ecosystem. In Mogi Guaçu the Campo Cerrado showed a belowground biomass of 12.4 Mg ha^{-1} (0–80 cm) while the aboveground biomass was 4.2 Mg ha^{-1}. In Central Brazil the belowground biomass has been studied to deeper soil layers and the values varied from 16.3 Mg ha^{-1} in the grassy savannah to 52.9 in the more dense one [6]. Another area studied in Brasília presented a belowground biomass of 41.1 Mg ha^{-1} [2]. Root biomass ranged from 4 to 16 Mg ha^{-1} in savannah ecosystems studied by Santantonio et al. [29] and presented maximum values of more than 300 Mg ha^{-1} in tropical rain forests [4].

Well-developed belowground systems allow the tropical savannah vegetation to survive during the winter when both drought and fire occur. Seasonal variations in belowground biomass are due to translocations of carbohydrates and nutrients between shoots and roots. These transferences allow plant communities to adapt to the changing conditions in savannah environments [22, 38]. Our data indicate the high investments needed to survive under low nutritional resources and seasonal weather pattern.

In the open savannah, the belowground biomass significantly varied around 6 Mg ha^{-1} between the dry and the rainy seasons. In the ecosystem free from fire the significant variation in the belowground biomass was about 10 Mg ha^{-1}, indicating that at least these amounts were transferred from the aerial plant parts to the belowground ones (*table I*). Total transference may be greater since it is known that the measurement of belowground production by sampling between biomass maximum and minimum may imply errors since it does not take decomposition rates into account [28, 33, 37]. The present study was not designed to estimate belowground production and we measured only the total living biomass [37], but it does suggest reconsidering productivity estimates for this kind of ecosystem, where only aboveground biomass is usually taken into account. Other studies in cerrado ecosystems [2, 6], in Venezuelan savannahs [28], in the Lower Subtropical Evergreen Broad-leaf Forest of China [41] and in many other ecosystems [38] lead to similar conclusions.

Aboveground estimates of herb layer productivity range from 2.5 Mg ha^{-1} yr^{-1}, for a campo cerrado in Brasilia [3] to up to 8 Mg ha^{-1} yr^{-1} in the Emas open savannah [9]; the latter being the same one studied in this work. This indicates that nearly half of the net production is transferred to the belowground system.

Belowground biomass in cerrado soils must be considered in global change studies, especially when analysing the Carbon cycle, since the cerrados are the ecosystem most affected by Brazilian agricultural expansion, losing estimated 34,000 km² area every year [18]. The cerrados are cut-down, burned and substituted by annual monocultures (e.g. soybean), that allocates less carbon to belowground systems than the native vegetation. We believe that if this type and rate of land-use change is continued, the capacity of CO_2 storage may be significantly affected at a global scale as the cerrados cover a very significant portion of the terrestrial ecosystems. Alternatively, better management of tropical savannah ecosystems could lead to increased productivity, as well as, increased carbon storage in soil [14].

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