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Woody vegetation dynamics in a floodplain *campo de murundus* in central Brazil

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ABSTRACT

Campos de murundus (grasslands dotted with knolls that are covered with savanna-like woody vegetation) are a common landscape in central Brazil. In this study, we assessed for the first time the dynamics of the vegetation in a floodplain *campo de murundus*, describing changes in composition and structure of the woody vegetation. In 2005, we established 16 permanent 25 × 25 m plots, where we identified and mapped individuals with a trunk diameter at the base ≥ 2.86 cm, as well as measuring the height of those individuals. In 2008 (after two fire events), we resampled the plots. In 2005, we had registered 4.54 m² ha⁻¹ of basal area, 430 individuals, 42 species, 36 genera and 24 families. In 2008, we found an increase in basal area (to 4.65 m² ha⁻¹) and a decrease in numbers of individuals (to 399), species (to 41), genera (to 35) and families (to 23). Species diversity did not differ between the two surveys. Mortality exceeded recruitment (2.68% year⁻¹ vs. 1.29% year⁻¹). Nevertheless, the community showed a gain in basal area owing to the growth of surviving individuals and, particularly, to the rise in the number of basal sprouts. We argue that the small floristic turnover may be related to the great resilience of the woody vegetation, whereas the structural changes might reflect the effects of the burnings in the area.

Key words: earth mounds, fire, mortality, recruitment, savanna

Introduction

An adequate description of the current situation of native vegetation remnants and temporal changes due to natural and anthropic factors is part of research priorities to subsidize future efforts for conserving biodiversity. In this context, dynamics studies can produce detailed assessments of mortality, recruitment, growth and regeneration, which may further the understanding of ecological processes driving community and ecosystem functioning (Korning & Balslev 1994; Oliveira-Filho *et al.* 1997; Sheil *et al.* 2000; Felfili *et al.* 2000; Henriques & Hay 2002; Pinto & Hay 2005; Aquino *et al.* 2007; Mews *et al.* 2011; Ribeiro *et al.* 2012). In addition, vegetation dynamics studies contribute to conservation initiatives by subsidizing strategies for management and restoration ecology, because they allow species behavior to be evaluated in natural environments (Aquino *et al.* 2007).

Despite the fact that savanna accounts for most of the landscape in the Cerrado Biome of Brazil (MMA 2007;

Sano *et al.* 2008), there have been few temporal dynamics studies of these formations. Important studies in areas of *cerrado sensu stricto* (Brazilian savanna) include those conducted by Felfili *et al.* (2000), Henriques & Hay (2002), Fiedler *et al.* (2004), Libano & Felfili (2006), Aquino *et al.* (2007), Roitman *et al.* (2008), Lima *et al.* (2009), Mews *et al.* (2011) and Ribeiro *et al.* (2012). Those studies comprised the *cerrado sensu stricto* on deep soil. However, none investigated temporal changes in the woody vegetation of other savanna systems of the Cerrado Biome, such as the floodplain *campo de murundus* (CM), which is subject to hyperseasonal climate marked by distinct flooding and dry periods (Cianciaruso & Batalha 2009), as well as by a intense fire regime (Marimon *et al.* 2008; 2012).

Also known as *parque de cerrado* (*sensu* Ribeiro & Walter 2008), CM is a vegetation formation that is still poorly studied (Marimon *et al.* 2012). It is characterized by woody vegetation on *murundus* (earth mounds) dispersed in a grassland matrix in floodplains (Oliveira-Filho 1992a; 1992b). The spatial distribution, physical characteristics and biological characteristics of CMs reflect the seasonal flood

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pulse (Silva *et al.* 2010; Marimon *et al.* 2012), acting as the main environmental filter in the dichotomy between herbaceous and woody vegetation (Oliveira-Filho 1992b; Marimon *et al.* 2012). In general, the plains and smaller earth mounds are populated by herbaceous-subshrub vegetation, whereas woody savanna vegetation populates larger mounds (Araújo Neto *et al.* 1986; Furley 1986; Oliveira-Filho 1992a, 1992b; Ponce & Cunha 1993; Resende *et al.* 2004; Ribeiro & Walter 2008; Silva *et al.* 2010; Marimon *et al.* 2012).

According to Marimon *et al.* (2008; 2012), the most extensive areas of CM occur in the Araguaia River floodplain, also known as the Bananal Sedimentary Plain or *Pantanal do Araguaia* (Marimon & Lima 2001), the largest continuous area of preserved CM being within Araguaia State Park (ASP), located in the northeastern part of the state of Mato Grosso, Brazil. The authors demonstrated that the areas of CM in ASP are subjected to water stress related to climate seasonality, as well as to cattle trampling, cattle farming, and anthropogenic burning for pastureland management.

Here, we investigated changes in the woody vegetation of an area of CM, aiming at describing, for the first time, variations in the floristic composition and structure of the woody vegetation over time, after fires occurring in two consecutive years. To that end, we attempted to determine how CM woody vegetation responds to consecutive burning events, in terms of temporal changes in floristic composition and structure, and how the woody species populations of the CM respond to this disturbance.

Material and methods

Study area

The study was conducted in an area of CM (12°02'29.3"S; 50°43'49.7"W; elevation, 194.6 m) in ASP (Fig. 1), municipality of Novo Santo Antônio, northeastern Mato Grosso (Marimon *et al.* 2012). The park comprises an area of 223,619.5 hectares, bordered by the das Mortes River on the west, the Araguaia River on the east, the mouth of the Mortes River on the north (Fig. 1) and the Água Bela Farm on the south (Marimon *et al.* 2008). The climate of the region is type Aw in the Köppen classification system, characterized by well-defined dry and rainy periods, with an average annual temperature of 25.7-27.3°C and average annual rainfall ranging of 1,800-1,200 mm (Marimon & Lima 2001; Marimon *et al.* 2008).

Soils in the plains portion of the CM are seasonally floodable, following the main flooding regime in the region (Marimon *et al.* 2008). The dominant soils in the plains portion are Dystrophic Argiluvic Plinthosols with ferruginous concretions, whereas the soils of the mounds are Dystrophic Cambic and Dystroferic Plinthic Brown Oxisols (RadamBrasil 1981). The CM in ASP presents deep and poorly drained soils, such as hydromorphic Plinthosols, a dystrophic and strongly to moderately acidic soil (Marimon *et al.* 2012).

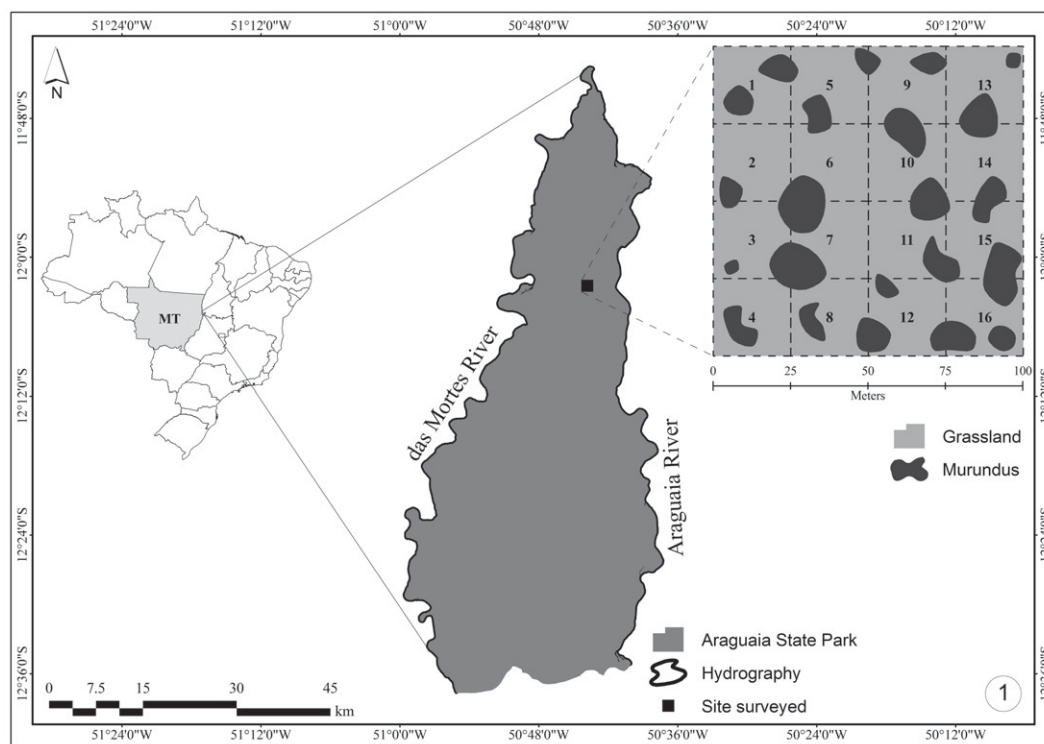


Figure 1. Location of the study area and distribution of the 16 plots of 25 × 25 m in the *campo de murundus* sampled in Araguaia State Park, in the state of Mato Grosso, Brazil.

Although the ASP is a fully protected conservation area, its areas of CM are commonly used as natural pasture, being burned annually for pastureland management (Marimon *et al.* 2008). After the first survey (in 2005), the area was burned in July 2006 and August 2007, both during the peak of the dry season.

Woody vegetation surveys

In 2005, we established 16 permanent, contiguous 25 × 25 m (1 ha) plots within an area of CM, in order to survey the woody vegetation (Fig. 1; Marimon *et al.* 2012). We identified and mapped individuals with a trunk diameter at the base ($Db_{30\text{ cm}} \geq 2.86\text{ cm}$), as well as measuring the height of those individuals. In the second survey, conducted in 2008, we remeasured surviving individuals, registered dead individuals and included recruits (individuals not included in the first survey). In 2008, we also measured the $Db_{30\text{ cm}}$ of all basal or underground sprouts of woody individuals that suffered top-kill. Forked stems less than 30 cm apart at ground level were considered to belong to the same individual and, in such cases, we considered that the sum of the basal area of each ramification described the individual (Moro & Martins 2011).

The botanical material collected was processed and identified in accordance with the specialized literature, comparisons in herbaria (NX and UB Herbaria) and consulting specialists. The voucher were deposited at Mato Grosso State University Herbarium, in Nova Xavantina, Brazil (code, NX). The complete list of species found in the ASP areas of CM areas, as well as the herbarium accession numbers for their voucher specimens, can be found in Marimon *et al.* (2012). We used the Angiosperm Phylogeny Group III classification system (APG III 2009), and the taxa names were updated from the List of Species in the Flora of Brazil (Lista de Espécies da Flora do Brasil 2012).

Data analyses

To compare woody species diversity between the two surveys, we created diversity profiles based on Rényi's exponential series (Tóthmérész 1995). According to Tóthmérész (1995) and Melo (2008), diversity profiles generalize the weight that different indices give to rare species (in this case, low abundant), in order to avoid choosing one index over another. Thus, we can generate a graph with values from different diversity metrics, such as species richness (S), Shannon's diversity index (H') and Simpson's diversity index (D). In this graph, the closer factor α gets to zero, the higher is the weight given to rare species, so that when $\alpha = 0$, $H_0 = S$. Rényi's exponential series is given by the formula $H_\alpha = (\ln(p_1^\alpha + p_2^\alpha + p_3^\alpha \dots + P_s^\alpha)) / (1 - \alpha)$, where H_α is the diversity index value for parameter α ($\alpha \geq 0$, $\alpha \neq 1$) and p_1, p_2, p_3, \dots and p_n are the proportions of individuals in species 1, 2, 3... and S. We also obtained 95% confidence intervals for

the diversity profiles using the bootstrapping option based on 2000 replicates. Diversity profiles and 95% confidence intervals were calculated using PAST 2.15 (Hammer *et al.* 2001). We also used Czekanowski's quantitative coefficient (Sc) (Kent & Coker 1992) to compare the floristic similarity among surveys.

Density and basal area of individuals were used in order to describe the community structure in 2005 and 2008. In addition, we distributed the individuals into diameter and height classes using class intervals equivalent to those normally used to describe savanna formations of the Cerrado Biome (5-cm diameter class interval and 1-m height class interval). Both distributions (2005 and 2008) were compared by the Kolmogorov-Smirnov (K-S) test (Zar 1999) using BioEstat 5.0 (Ayres *et al.* 2007), for diameter and height classes. Only live individuals with a $Db_{30\text{ cm}} \geq 2.86\text{ cm}$ or individuals with sum of ramifications included in the minimum inclusion criterion were considered in the diameter and height distribution classes.

We estimated vegetation and woody populations dynamics calculating the average annual rates of mortality ($M = \{1 - [(N_0 - m)/N_0]^{1/t}\} \times 100$), recruitment ($R = [1 - (1 - r/N_t)^{1/t}] \times 100$) (Sheil *et al.* 2000) and net change ($ML = [(N_t/N_0)^{1/t} - 1] \times 100$) (Korning & Balslev 1994), where t is the time elapsed between both surveys; N_0 and N_t are initial and final counts of individuals; and m and r are the number of dead individuals and recruits, respectively (Sheil *et al.* 2000). We applied the correction factor proposed by Lewis *et al.* (2004) to the average annual mortality and recruitment rates with the aim of adjusting for the effect that the interval between surveys had on the final values. Finally, to evaluate the impact of burnings on the vegetation structure, we compared the numbers of sprouts/individual/species between the surveys carried out before and after the burnings (in 2005 and 2008, respectively), by the Wilcoxon test at a 5% significance level (Zar 1999) using the BioEstat 5.0 (Ayres *et al.* 2007).

Results

Floristic composition, richness and species diversity

We found small changes in the floristic composition within the studied period. In the 2005 survey, we registered 42 species distributed in 36 genera and 24 families, whereas 41 species, 35 genera and 23 families were catalogued in the 2008 survey (Tab. 1). The most species-rich genera and families were the same in both surveys, mainly the genera *Myrcia* (4 species), *Annona* (2 species) and *Byrsonima* (2 species), as well as the families Fabaceae (6 species), Myrtaceae (6 species), Anacardiaceae (3 species) and Annonaceae (3 species). The monospecific genera and families were also the same in both surveys, except for the genus *Protium* (Burseraceae), which was not registered in

Table 1. Structural parameters of the woody species sampled in an area of *campo de murundus* in 2005 and 2008, in Araguaia State Park, in the state of Mato Grosso, Brazil. N – number of individuals; BA – basal area ($\text{m}^2 \text{ha}^{-1}$); Spr. – number of individuals with sprouts (sprouts/individual/species); M and R – average annual mortality and recruitment rates (% year⁻¹), respectively; and NCi and NCba – average annual net change rates in number of individuals and basal area (% year⁻¹), respectively. Species are presented in decreasing order by their N in 2008.

Species	Family	2005			2008			2005-2008			
		N	BA	Spr.	N	BA	Spr.	M	R	NCi	NCba
<i>Curatella americana</i> L.	Dilleniaceae	68	1.482	0.0	71	1.661	0.1	0	1.56	1.45	3.87
<i>Byrsonima cydoniifolia</i> A.Juss.	Malpighiaceae	38	0.145	0.0	39	0.178	0.4	0	1.90	0.87	6.98
<i>Erythroxylum suberosum</i> A.St.-Hil.	Erythroxylaceae	35	0.240	0.4	31	0.185	0.9	4.33	1.19	-3.96	-8.30
<i>Heteropterys byrsonimifolia</i> A.Juss.	Malpighiaceae	35	0.178	0.5	31	0.107	2.1	4.33	0	-3.96	-15.60
<i>Andira cujabensis</i> Benth.	Fabaceae	27	0.573	0.1	28	0.695	0.3	0	2.66	1.22	6.65
<i>Tabebuia aurea</i> (Silva Manso) Benth. & Hook.f. ex S.Moore	Bignoniaceae	31	0.296	0.0	24	0.249	0.1	8.93	0	-8.18	-5.59
<i>Myrcia guianensis</i> (Aubl.) DC.	Myrtaceae	19	0.156	0.2	21	0.170	0.2	0	3.58	3.39	2.94
<i>Myrcia multiflora</i> (Lam.) DC.	Myrtaceae	15	0.127	0.2	13	0.089	0.4	5.09	0	-4.66	-11.26
<i>Euplassa inaequalis</i> (Pohl) Engl.	Proteaceae	12	0.116	0.3	10	0.166	0.3	6.44	0	-5.90	12.62
<i>Ouratea castaneifolia</i> (DC.) Engl.	Ochnaceae	12	0.060	0.2	10	0.069	0.1	6.44	0	-5.90	5.15
<i>Syagrus comosa</i> (Mart.) Mart.	Arecaceae	6	0.034	0.0	10	0.069	0.0	0	17.10	18.56	27.17
<i>Tapirira guianensis</i> Aubl.	Anacardiaceae	10	0.065	4.0	10	0.018	10.2	0	0	0	-35.09
<i>Pouteria ramiflora</i> (Mart.) Radlk.	Sapotaceae	9	0.218	0.6	9	0.295	0.8	0	0	0	10.67
<i>Eugenia aurata</i> O.Berg	Myrtaceae	10	0.036	0.0	9	0.036	0.7	3.77	0	-3.45	0.37
<i>Myrcia splendens</i> (Sw.) DC.	Myrtaceae	9	0.027	0.7	8	0.010	3.0	4.20	0	-3.85	-28.89
<i>Byrsonima laxiflora</i> Griseb.	Malpighiaceae	8	0.040	0.4	7	0.061	1.6	4.75	0	-4.35	15.23
<i>Matayba guianensis</i> Aubl.	Sapindaceae	7	0.025	2.3	7	0.005	6.0	0	0	0	-40.21
<i>Qualea parviflora</i> Mart.	Vochysiaceae	6	0.288	0.0	6	0.310	0.0	0	0	0	2.46
<i>Casearia sylvestris</i> Sw.	Salicaceae	6	0.027	1.3	6	0.014	2.0	0	0	0	-18.90
<i>Xylopia aromatica</i> (Lam.) Mart.	Annonaceae	10	0.029	1.2	5	0.013	1.7	22.53	0	-20.63	-22.79
<i>Diospyros hispida</i> A. DC.	Ebenaceae	6	0.012	0.2	5	0.003	3.0	6.44	0	-5.90	-38.31
<i>Simarouba versicolor</i> A.St.-Hil.	Simaroubaceae	5	0.061	0.0	4	0.029	0.8	7.83	0	-7.17	-21.73
<i>Eugenia gemmiflora</i> O.Berg	Myrtaceae	4	0.028	0.0	4	0.027	0.0	0	0	0	-0.12
<i>Couepia grandiflora</i> (Mart. & Zucc.) Benth.	Chrysobalanaceae	3	0.036	0.0	3	0.043	0.0	0	0	0	6.25
<i>Rourea induta</i> Planch.	Connaraceae	3	0.013	0.0	3	0.008	1.7	0	0	0	-15.94
<i>Anacardium occidentale</i> L.	Anacardiaceae	3	0.021	0.0	3	0.025	0.0	0	0	0	6.46
<i>Copaifera martii</i> Hayne	Fabaceae	3	0.008	2.3	3	0.002	5.0	0	0	0	-42.46
<i>Dypterix alata</i> Vogel	Fabaceae	2	0.039	0.0	2	0.050	0.5	0	0	0	8.78
<i>Annona coriacea</i> Mart.	Annonaceae	3	0.015	0.0	2	0.009	0.0	13.80	0	-12.64	-15.90
<i>Tocoyena formosa</i> (Cham. & Schltdl.) K.Schum.	Rubiaceae	2	0.003	0.0	2	0.001	5.5	0	0	0	-32.83
<i>Annona aurantiaca</i> Barb.Rodr.	Annonaceae	2	0.002	1.0	2	0.001	4.5	0	0	0	-24.09
<i>Lacistema aggregatum</i> (P.J.Bergius) Rusby	Lacistemataceae	2	0.006	1.0	2	0.001	1.0	0	0	0	-57.03
<i>Tachigali aurea</i> Tul.	Fabaceae	3	0.088	0.0	1	0.018	0.0	33.48	0	-30.66	-41.43
<i>Vatairea macrocarpa</i> (Benth.) Ducke	Fabaceae	1	0.012	0.0	1	0.017	0.0	0	0	0	11.69
<i>Leptolobium dasy carpum</i> Vogel	Fabaceae	7	0.019	0.1	1	0.012	0.0	52.11	0	-47.72	-13.96
<i>Myrcia</i> sp.	Myrtaceae	1	0.004	2.0	1	0.005	2.0	0	0	0	5.16
<i>Astronium fraxinifolium</i> Schott	Anacardiaceae	1	0.004	0.0	1	0.004	0.0	0	0	0	3.23
<i>Alibertia edulis</i> (Rich.) A.Rich.	Rubiaceae	1	0.002	2.0	1	0.001	6.0	0	0	0	-33.50
<i>Alchornea discolor</i> Poepp.	Euphorbiaceae	1	0.004	2.0	1	0.001	4.0	0	0	0	-53.19
<i>Ocotea cernua</i> (Nees) Mez	Lauraceae	1	0.001	1.0	1	<0.001	4.0	0	0	0	-33.06
<i>Maprounea guianensis</i> Aubl.	Euphorbiaceae	2	0.009	0.0	1	0.002	1.0	22.53	0	-20.63	-77.26
<i>Protium unifoliolatum</i> Engl.	Burseraceae	1	0.001	1.0	0	0.000	0.0	100	0	-100	-100.00
Total		430	4.546	-	399	4.656	-	2.68	1.29	-2.46	0.80

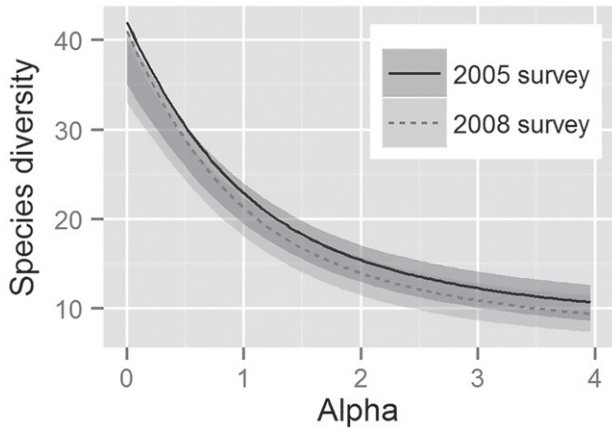


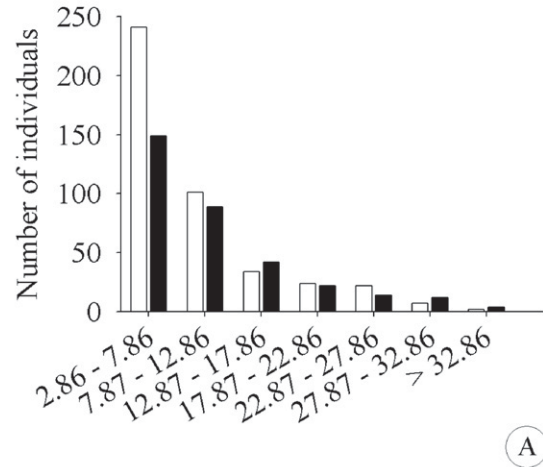
Figure 2. Diversity profiles based on the Rényi's exponential series for the woody vegetation sampled in an area of *campo de murundus* in Araguaia State Park, in the state of Mato Grosso, Brazil. Gray bands represent 95% confidence intervals.

2008. As a result of the small variations, we observed high floristic similarity between both survey years ($S_c = 0.93$). The diversity profiles indicated that species diversity did not differ among surveys (Fig. 2), regardless of the weight given to low-abundant species locally. The lack of difference was demonstrated by the overlap of 95% confidence intervals in both diversity profiles (Fig. 2).

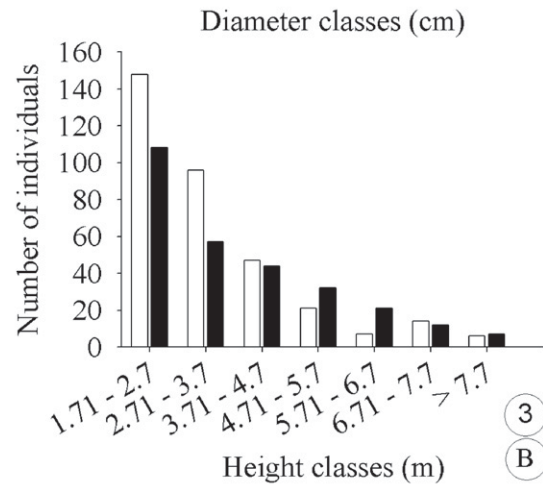
Vegetation and population structure

As shown in Tab. 1, the total number of individuals decreased during the study period, from 430 (in 2005) to 399 (in 2008), which corresponds to a net reduction of 31 (7.2%), resulting from the death of 45 individuals and the recruitment of 14. However, in 2008, the sum of the basal area of surviving individuals, recruits and sprouts of individuals that suffered top-kill resulted in $4.65 \text{ m}^2 \text{ ha}^{-1}$, which sum $0.11 \text{ m}^2 \text{ ha}^{-1}$ (2.4%) rise compared to that recorded in 2005 ($4.54 \text{ m}^2 \text{ ha}^{-1}$). Between 2005 and 2008, the number of individuals increased for five species (11.9% of the total), decreased for 17 (40.5%) and remained the same for 20 (47.6%), whereas basal area increased for 15 species (35.7%), decreased for 25 (59.5%) and remained the same for two (4.8%). The 12 main species represented the community well in terms of floristic composition (accounting for 28.6% and 29.3% of the richness in 2005 and 2008, respectively). This group of species was the same in both surveys (Tab. 1).

In our analysis of the distribution of individuals by diameter class (Fig. 3A), we found that the number of individuals in certain classes fell after the burning events, especially in the first class (2.86-7.86 cm). There was a significant difference between the 2005 and 2008 distributions (K-S, $\chi^2 = 9.138, p = 0.010$). Similarly, the distribution of individuals by height class presented a reduction in the numbers of individuals of the first classes and a rise in



(A)



(3)

(B)

Figure 3. Distribution of the individuals by diameter class (A) and height class (B) for the woody vegetation sampled in an area of *campo de murundus* in 2005 (□) and 2008 (■) in Araguaia State Park, in the state of Mato Grosso, Brazil.

those of the later classes (Fig. 3B), resulting in a significant difference between the 2005 and 2008 distributions (K-S, $\chi^2 = 12.479; p = 0.002$).

Dynamics parameters

We registered an average annual mortality rate that was higher than the average annual recruitment rate (2.68% year⁻¹ vs. 1.29% year⁻¹). Consequently, the average annual net change rates in number of individuals was negative (-2.46% year⁻¹). However, as a response to the rise in basal area, the average annual net change rates in basal area was positive (0.80% year⁻¹).

Among the 42 species recorded in the 2005 survey, we observed mortality in 17 species (40.5%) and recruitment in six (14.3%), as detailed in Tab. 1. In addition, mortality exceeded recruitment in 17 (40.5%) species, whereas the inverse was observed in only five (11.9%). Regarding

net change rates in the number of individuals, 17 species (40.5%) presented negative values, five (11.9%) presented positive values, and 20 (47.6%) presented no alterations (Tab. 1). In terms of basal area, the net change rates was negative for 25 species (59.5%) and positive for 17 (40.5%).

During the study period, 33 species (78.6%) sprouted. The proportion of sprouting species increasing from 57.1% in 2005 to 73.2% in 2008, a significant difference ($U = 2.1739$; $p = 0.0149$). Of the 42 species evaluated, 26 (61.9%) presented a higher number of sprouts in 2008, whereas two (4.9%: *Ouratea castaneifolia* (DC.) Engl. and *Leptolobium dasycarpum* Vogel) presented a higher number in 2005, and 13 (31.7%) presented an equal number of sprouts in both surveys (Tab. 1). The species presenting the greatest number of sprouts were *Tapirira guianensis* Aubl., *Matayba guianensis* Aubl., *Alibertia edulis* (Rich.) A.Rich., *Copaifera martii* Hayne and *Tocoyena formosa* (Cham. & Schltdl.) K.Schum.

Discussion

The absence of distinctive changes in floristic composition, richness and diversity of woody species in the CM during the study period may be related to the short period of time between survey years, given the three-year interval recommended by Felfili *et al.* (2005) for *cerrado sensu stricto*. As a general rule, the few alterations in richness occur to the detriment of exclusion of species with low density in the sample, such as *Protium unifoliolatum* Engl., as has also been demonstrated by Felfili *et al.* (2000), Fiedler *et al.* (2004), Lima *et al.* (2009), Mews *et al.* (2011) and Ribeiro *et al.* (2012). Those authors observed that the savannic vegetation of the Cerrado Biome, particularly that of the *cerrado sensu stricto*, is very resilient in terms of floristic variations due to disturbances such as fire. Nevertheless, the occurrence of frequent burnings may cause a reduction in species richness (Ribeiro *et al.* 2012; Moreira 2000; Fiedler *et al.* 2004), whereas protection against fire may promote an increase in number of woody species in areas of *cerrado sensu stricto* (Henriques & Hay 2002; Libano & Felfili 2006; Roitman *et al.* 2008). It is noteworthy that, because of the scarcity of dynamics studies in CM, we have compared our results with those reported for *cerrado sensu stricto* in view of the floristic and structure similarities (Marimon *et al.* 2012), despite distinct environmental characteristics.

In terms of structure, the reduction in density (7.2%) and increase in basal area (2.37%) registered in the CM suggest that the vegetation sampled is in the initial post-disturbance recovery phase (Machado & Oliveira-Filho 2010). The processes of vegetation dynamics are influenced by alterations in environmental conditions (Oliveira-Filho *et al.* 1997; Aquino *et al.* 2007) and mortality rates exceeding recruitment rates often indicate that the vegetation is under the effects of disturbances (Hoffmann & Moreira 2002; Medeiros & Miranda 2005; Fiedler *et al.* 2004; Aquino *et al.* 2007; Lima *et al.* 2009; Machado & Oliveira-Filho 2010), as

seems to be the case here. However, the results of dynamics studies involving only a small number of remeasurements must be interpreted with caution (Pinto & Hay 2005), given the cyclical variations in temporal scales (Felfili *et al.* 2000; Libano & Felfili 2006).

Burnings are considered one of the main environmental filters for the woody vegetation in areas of *cerrado sensu stricto* (Coutinho 1990; Higgins *et al.* 2000; Miranda *et al.* 2002; Libano & Felfili 2006; Roitman *et al.* 2008). Fire extinction in these areas promotes an increase in density and basal area of the woody vegetation up to the carrying capacity of the area (Henriques & Hay 2002; Roitman *et al.* 2008). In contrast, increases in fire frequency increase damage to the woody vegetation and, in most instances, reduce density (Medeiros & Miranda 2005; Ribeiro *et al.* 2012), as observed in the CM under study here.

The mortality rate found here (2.68% year⁻¹) was lower than the 6-15% year⁻¹ reported for woody vegetation in areas of *cerrado sensu stricto* under a fire regime (Hoffmann & Moreira 2002). Increasing fire frequency can have a negative effect on recruitment and a positive effect on mortality, particularly in smaller individuals (Ribeiro *et al.* 2012). This was confirmed in the CM, where we found that the mortality rate correlated inversely with the diameter class, as was also observed by Hoffmann & Solbrig (2003), Fiedler *et al.* (2004), Medeiros & Miranda (2005), Lima *et al.* (2009) and Ribeiro *et al.* (2012). In this case, the higher proportion of dead individuals among younger and smaller individuals in the CM likely indicates that their bark thickness and maximum height were not sufficient to protect them from the direct effects of fire (Higgins *et al.* 2000; Medeiros & Miranda 2005).

Another line of evidence supporting the idea that the woody vegetation of the CM studied is under the negative effects of fire is related to the fact that most of the populations showed negative net changes in terms of density and basal area, whereas only five species (11.9%) and 15 species (35.7%) presented a rise in density and a gain in basal area, respectively. According to Hoffmann & Moreira (2002), fires may differently influence the species dynamics within the community, favoring the demographic parameters of some populations and impairing those of others. Few of the species evaluated in the present study presented mortality and recruitment, which occurred in only 40.4% and 14.3%, respectively. Recruitment rates exceeded mortality rates in only a few species, which explains the low number of species whose population density increased, whereas in areas protected from fire most woody species tend to show recruitment rates higher than their mortality rates, thereby increasing density (Henriques & Hay 2002; Ribeiro *et al.* 2012). To a certain extent, these results suggest that areas under frequent-fire regimes tend to present reductions in density and basal area for most species, whereas fire suppression favors population increases in accordance with the carrying capacity of the area (Henriques & Hay 2002; Pinheiro & Durigan 2009).

Among the individuals recorded as dead in 2008, most presented only one trunk, 70% were 4.2-7.3 cm in diameter, and 53% were 2-3 m in height. This explains the fact that most woody species in CM (63.4%) presented higher number of sprouts in the second survey, because of the top-kill suffered after the fire events of 2006 and 2007. Another interesting point is that 95% of the sprouts found in the second survey did not exceed 2.22 cm in diameter and none presented diameters greater than 4.45 cm. This supports the idea that basal sprouts are more common in the lower diameter classes (Medeiros & Miranda 2005). Therefore, species capable of sprouting are favored because they can persist in a community frequently affected by fire events (Hoffmann 1998). However, aboveground death and appearance of basal sprouts promote a decrease in basal area and, consequently, a shift toward the lower diameter classes (Coutinho 1990), making them sensitive to repeated burnings (Miranda *et al.* 2002).

It is likely that the resilience of larger individuals, due to fire-resistant characteristics, together with the sprouting capacity of smaller individuals, also control the dynamics of the woody vegetation in the CM of ASP, as has been reported for the woody vegetation of the *cerrado sensu stricto* (Ribeiro *et al.* 2012). Consequently, the dynamics of the woody vegetation sampled over the study period, considering the record of two fire events, enables us to infer two possible future scenarios. First, if fire frequency remains high, the community will remain in a state of nonequilibrium marked by an imbalance between mortality and recruitment (decrease in density), together with a reduction in vegetation height and diameter, with negative consequences for the composition, richness and diversity of woody species in the CM. However, if the burning regime comes to be controlled, the community may trend toward equilibrium and present recruitment rates higher than its mortality rates, typical of the initial stage of post-disturbance reconstruction, as stated by Henriques & Hay (2002) and Machado & Oliveira-Filho (2010).

Overall, despite two consecutive fire events within only three years, the woody vegetation of the CM studied did not show significant floristic changes. Structurally, however, the vegetation presented a reduction in density because of the negative net balance between mortality and recruitment, despite the gain in basal area as a consequence, particularly, of the increase in the number of sprouts. The main structural alteration was caused by the number of damaged stems (due to death or top-kill), which modified the horizontal and vertical structure by creating a new diameter class (≤ 2.8 cm). The appearance of this new class is related to the resistance of the CM woody vegetation to fire, with the consequent rise in the number of basal sprouts. It is noteworthy that most populations presented behavior similar to that registered for the community, mainly in terms of an imbalance between mortality and recruitment. If this behavior continues in the medium- and long-term, the woody vegetation will undergo

greater structural changes, with size reductions, increasing its susceptibility to fire damage. If that becomes the case, we predict the simplification of the floristic composition and structure of the community, as is typical of degraded environments.

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