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STRUCTURE OF TWO COMMUNITIES DOMINATED BY *COPERNICIA ALBA* AND ASSOCIATIONS WITH SOIL AND INUNDATION IN PANTANAL WETLAND, BRAZIL

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ABSTRACT

Known for its high degree of biodiversity, the tropics have a number of sites in which one or few species dominate large areas, as occurs in the Pantanal wetland, Brazil, with the 'carandá' palm, *Copernicia alba*, in monodominant formations known regionally as 'carandazal'. The aim of the present study was to analyze variations in species richness and diversity of herbs, shrubs and trees in two communities dominated by *Copernicia alba* with different flood patterns and determine whether soil fertility and time of inundation are associated with tree/shrub species composition and abundance. Vegetation was analyzed in 50 plots measuring 100m^2 in each area, with the determination of the tree/shrub component (CBH ≥ 5cm). Three subplots measuring 1m^2 were demarcated within each plot for the sampling of herbs, sub-shrubs, shrubs (CBH < 5cm) and juvenile arboreal species. Soil samples were taken from three depths in each 100m^2 plot. Associations between soil data, time of inundation and absolute density of tree/shrub vegetation were tested using canonical correspondence analysis (CCA). For the tree/shrub component, a total of 22 species belonging to 12 families were sampled in the two communities. Richness was greater in the area submitted to a lesser time of inundation. *Copernicia alba* had the greatest importance values in both study areas, followed by *Tabebuia aurea* in one community and *Mimosa glutinosa* in the other. In the subplots, 178 species belonging to 39 families were sampled, for which Fabaceae, Poaceae, Asteraceae and Cyperaceae figured prominently. The herbaceous component predominated over the others in species richness in both areas, but similarity was low. CCA detected associations between soil fertility, time of inundation and composition of tree/shrub species. The richness of the tree/shrub component was greater in the area with a shorter inundation time, which makes this event an important factor in the determination of *C. alba* monodominance in the Pantanal wetland. The herbaceous component demonstrated a high degree of richness and diversity in both communities, although there are differences in the inundation pattern between the two areas.

Keywords: monodominance; carandazal, CCA, herbaceous component, tree/shrub component.

RESUMO

ESTRUTURA DE DUAS COMUNIDADES DOMINADAS POR *COPERCIA ALBA* E ASSOCIAÇÕES COM SOLO E INUNDAÇÃO NO PANTANAL, BRASIL. A região tropical conhecida por elevada diversidade detém, em alguns locais, uma ou poucas espécies dominantes em extensas áreas, como ocorre no Pantanal com a palmeira 'carandá' *Copernicia alba* que constitui formações monodominantes denominadas regionalmente como 'carandazal'. O Objetivo do presente estudo foi analisar a variação na riqueza e diversidade de espécies herbáceas, arbustivas e arbóreas em duas comunidades dominadas por

Copernicia alba sob diferentes regimes de inundação e determinar se a fertilidade do solo e o tempo de inundação estão associados à composição e densidade absoluta das espécies arbóreo/arbustivas. Avaliamos a vegetação a partir de 50 parcelas de 100m^2 implantadas em cada área, onde incluímos o componente arbóreo/arbustivo (CAP ≥ 5cm). Dentro de cada parcela demarcamos três subparcelas de 1m^2 para amostragem das ervas, subarbustos, arbustos (CAP < 5cm) e juvenis de espécies arbóreas. As amostras de solo foram retiradas de três profundidades em cada parcela de 100m^2. Associações entre os dados de solo, tempo de inundação e densidade da vegetação arbóreo/arbustiva foram testadas utilizando a análise de correspondência canônica (CCA). Nas duas comunidades, amostramos para o componente arbóreo/arbustivo um total de 22 espécies pertencentes a 12 famílias. A riqueza foi maior na área sujeita a um menor tempo de inundação. *Copernicia alba* apresentou o maior VI nas duas áreas de estudo, seguido por *Tabebuia aurea* em uma comunidade e por *Mimosa glutinosa* na outra. Para as subparcelas o total amostrado foi de 39 famílias com 178 espécies, com destaque para Fabaceae, Poaceae, Asteraceae e Cyperaceae. O componente herbáceo predominou sobre os demais em riqueza de espécies em ambas as áreas, mas a similaridade foi baixa. A CCA detectou associações entre a fertilidade do solo, tempo de inundação e a composição das espécies arbóreo/arbustivas. A riqueza do componente arbóreo/arbustivo foi maior na área com menor tempo de inundação, o que torna esse evento um fator importante na monodominância de *C. alba* no Pantanal. O componente herbáceo demonstrou um elevado grau de riqueza e diversidade em ambas as comunidades, embora haja diferenças no padrão de inundação entre as duas áreas.
Palavras-chave: monodominância; carandazal; CCA; componente herbáceo; componente arbóreo/arbustivo.

RESUMEN

ESTRUCTURA DE DOS COMUNIDADES DOMINADAS POR *Copernicia Alba* Y ASOCIACIONES CON SUELO E INUNDACION EN EL PANTANAL, BRASIL. La región tropical es conocida por su alta diversidad, aunque en algunos lugares una o pocas especies son dominantes en grandes áreas, tal como ocurre en el Pantanal, en Brasil, en donde la palmera "carandá" *Copernicia alba* establece formaciones monodominantes conocidas regionalmente como "carandazal". El objetivo de este estudio fue analizar la variación de la riqueza y diversidad de especies herbáceas, arbustivas y arbóreas en dos comunidades dominadas por *Copernicia alba* con diferentes regímenes de inundación y determinar si la fertilidad del suelo y el tiempo de inundación están asociados a la composición y densidad absoluta de las especies arbóreas/arbustivas. Se evaluó la vegetación en 50 parcelas de 100 m^2 en cada área, determinándose el componente arbóreo/arbustivo (CAP ≥ 5cm). Dentro de cada parcela se demarco tres sub-parcelas de 1 m^2 para muestreo de hierbas, sub-arbustos, arbustos (CBH < 5cm) y especies arbóreas juveniles. Se tomaron muestras de suelo de tres profundidades en cada parcela de 100 m^2. Asociaciones entre los datos suelo, tiempo de inundación, y densidad absoluta de la vegetación arbóreo/arbustiva fueron probadas usando análisis de correspondencia canónica (CCA). En las dos comunidades muestreamos para el componente arbóreo arbustivo un total de 22 especies pertenecientes a 12 familias. La riqueza fue mayor en el área sujeta a un menor tiempo de inundación. *Copernicia alba* tuvo los mayores valores de importancia en ambas áreas de estudio, seguida por *Tabebuia aurea* en una comunidad y *Mimosa glutinosa* en otra. En las sub-parcelas, se muestrearon 178 especies pertenecientes a 39 familias, destacando las Fabaceae, Poaceae, Asteraceae y Cyperaceae. El componente herbáceo predominó sobre los demás en riqueza de especies en ambas áreas, pero la similaridad fue baja. El CCA detectó asociaciones entre la fertilidad del suelo, tiempo de inundación y la composición de especies arbóreo/arbustivas. La riqueza del componente arbóreo/arbustivo fue mayor en el área con menor tiempo de inundación, haciendo de este evento un factor importante en la determinación de la monodominancia de *C. alba* en el Pantanal. El componente herbáceo demostró un elevado grado de riqueza y diversidad en ambas comunidades, aunque hubo diferencias en el patrón de inundación entre ambas áreas.
Palabras clave: monodominancia; carandazal; CCA; componente herbáceo; componente arbóreo/arbustivo.

INTRODUCTION

Monodominance in the tropics has emerged as the subject of a number of studies and its causes have been discussed (Connell & Lowman 1989, Hart *et al*. 1989, Hart 1990). Monodominance may be caused by different factors working in conjunction that lead to a low degree of diversity in particular regions. Several factors favor the dominance of a few species, such as soil conditions, flood patterns, fire events, associations with fungi and succession (Hart 1990). These factors have been tested as possible causes of monodominance in a number of studies (Veblen *et al.* 1979, Hart 1995, Van Groenendael *et al.* 1996, Martijena 1998, Torti *et al.* 2001, Henkel 2003, Read *et al.* 2006, Peh *et al.* 2011). However, many questions have yet to be answered with regard to this issue.

Although not restricted to a particular type of environment, monodominance and low diversity among arboreal species in the tropics are often associated with the conditions of seasonally floodable environments (Campbell 1986, Hart 1990). The low number of arboreal species in such environments has been attributed to their inability to tolerate flood conditions (Marques & Joly 2000). Moreover, post-flood effects, such as periods of severe drought, strongly determine the composition of species in tropical monodominant formations (Lopez & Kursar 1999, 2007).

In Brazil, studies on monodominant formations generally characterize the community with regard to structure and floristic composition, relating these aspects to different variables. Such formations include the *Peltogyne gracilipes* forest, studied with regard to herbivory, soil, population dynamics and chemical composition of the litter (Nascimento & Proctor 1994, Nascimento & Proctor 1997a, 1997b, Nascimento *et al.* 1997, Villela & Proctor 1999); the *Brosimum rubescens* forest analyzed with regard to soil, foliar nutrients of the species and seed rain (Marimon *et al.* 2001a, 2001b, Marimon & Felfili 2006); the formation dominated by *Vochysia divergens* associated with the flood gradient (Nascimento & Nunes da Cunha 1989, Arieira & Nunes da Cunha 2006); and *Tabebuia aurea* analyzed with regard to herbivory, soil and flood patterns (Ribeiro & Brown 2002, 2006, Soares & Oliveira 2009).

Monodominant areas of the 'carandá' palm, *Copernicia alba* Morong ex Morong and Britton (Arecaceae), occur in extensive seasonally floodable areas in the Pantanal wetland in Brazil, but distribution of these formations also extends to the Chaco plain in Argentina, Paraguay and eastern Bolivia (Hueck 1972, Ramella & Spichiger 1989). Veloso (1992) classified these formations as "steppe-savannah" (Savana Estépica Parque), but regionally this formation is denominated 'carandazal' in Brazil or 'palmares de carandá' in Argentina, Bolivia and Paraguay (Hueck 1972, Silva *et al.* 1998).

The aim of the present study was to analyze variations in species richness and diversity of herbs, shrubs and trees in two communities dominated by *C. alba* with different flood patterns and determine whether soil fertility and time of inundation are associated with the structure of tree/shrub vegetation. As monodominant formations, the expectation is that the low degree of diversity in tree/shrub vegetation is similar between these study areas and that soil characteristics and inundation are somehow related to tree/shrub species abundance.

MATERIAL AND METHODS

CHARACTERIZATION OF STUDY AREA

In Brazil, the 'carandazal' occurs in the Pantanal, a large South American wetland in the states of Mato Grosso and Mato Grosso do Sul (140,000 km^2) in the central-western region of the country, but it also occurs in Bolivia (15,000 km^2) and Paraguay (5000 km^2) (Junk *et al*. 2011). Based on physio-morphological and geopolitical aspects, Silva & Abdon (1998) divide the Pantanal into 11 regions: Cáceres, Poconé, Barão de Melgaço, Paraguai, Paiaguás, Nhecolândia, Abobral, Aquidauana, Miranda, Nabileque and Porto Murtinho.

The climate of the Pantanal is seasonal Aw in the Köppen classification, with the rainy season concentrated between October and March, annual rainfall ranges from 1000 to 1400mm (Cadavid-Garcia 1984). The predominant soils in the regions studied are Planosols, with the occurrence of patches of Vertisols and Gleysols (Soares *et al.* 2006).

Flooding in these regions is distinctly seasonal and the flood period tends to be delayed after the rains due to slow passage of floodwaters through the Pantanal. Flooding in Miranda and Porto Murtinho is differentiated with regard to intensity and duration and these areas are flooded by riverine overflows or pluvial water (Hamilton *et al.* 1996, Silva & Abdon 1998). In Porto Murtinho, the nearby Paraguay River exerts a strong influence, with floods that inundate a large portion of the region and can last as many as five months. In Miranda, the areas are drier, with shorter flood periods lasting around two months (Hamilton *et al.* 1996, Damasceno-Júnior *et al.* 2005).

In Miranda, sampling was carried out between August and October 2004 on plots approximately 21km from the Miranda River (municipality of Corumbá, Mato Grosso do Sul; 19º48'03.2"S and 57º09'25.6"W; 93m height). In Porto Murtinho, sampling was carried out in January and February 2005 on plots approximately 2km from the Paraguay River (municipality of Porto Murtinho, Mato Grosso do Sul; 21º29'44.4"S/57º54'59.3"W; 90m height). The sampling sites are displayed in Figure 1.

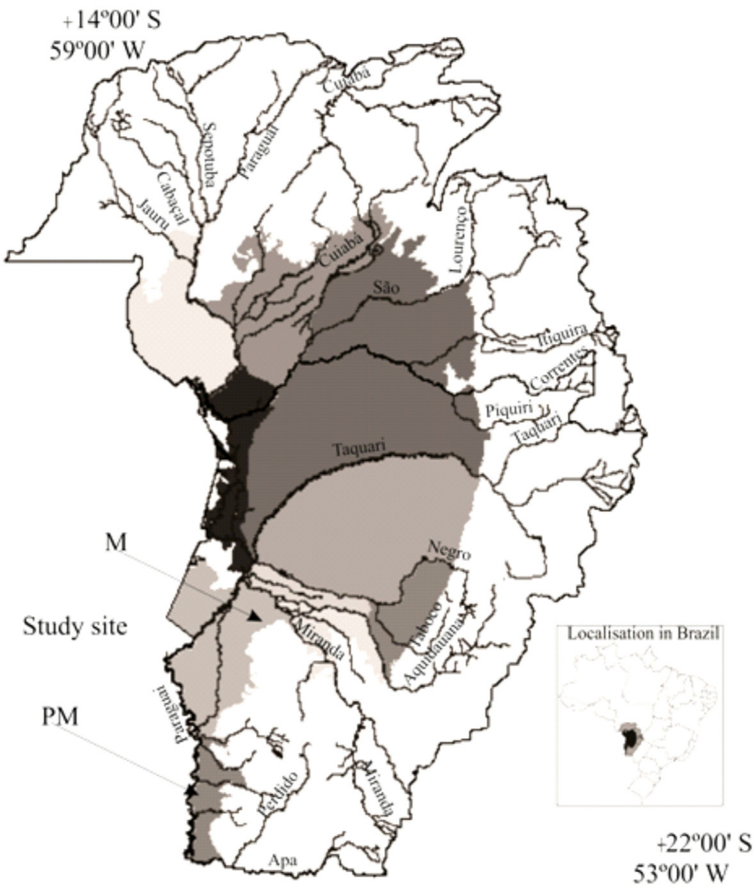

Figure 1. Location of sampling areas in Pantanal wetland, Brazil; arrows indicate sampling sites in Miranda (M) and Porto Murtinho (PM) regions. Different gray tones indicate regions of Patanal wetland. Names distributed on map indicate main rivers in the region. Adapted from Silva & Abdon (1998).

***Figura 1**. Localização das áreas de coleta no Pantanal, Brasil. Setas indicam os locais das coletas na região do Miranda (M) e Porto Murtinho (PM). Diferentes tons de cinza indicam regiões do Pantanal. Os nomes distribuídos no mapa indicam os principais rios da região. Adaptado de Silva & Abdon (1998).*

DATA COLLECTION AND ANALYSIS

The multiple plot method (Mueller-Dumbois & Ellenberg 1974) was employed in each area with 50 non-continuous plots, each measuring 100m^2, totaling 0.5 hectares (ha) of 'carandazal' sampled, in which the tree/shrub component was determined using the circumference at breast height (CBH) measure ≥ 5cm. Three subplots measuring 1m^2 were demarcated within each plot (total: 150m^2) for the sampling of herbs, sub-shrubs, shrubs (CBH < 5cm) and juvenile arboreal species. Life forms were classified based on field observations and descriptions by Pott & Pott (1994). To broaden the floristic list of the study areas, fertile specimens were collected from areas adjacent to the 100m^2 plots. Voucher of specimens were deposited in the CGMS Herbarium of the *Universidade Federal de Mato Grosso do Sul* – Campo Grande. Classification was based on APG III (2009).

The usual formulae were used for the calculation of the phytosociological parameters for trees and shrubs (Mueller-Dombois & Ellenberg 1974) using the FITOPAC software (Shepherd 1994). Besides species richness, the Shannon diversity index (H', Log-normal) and Pielou evenness index (J') were determined. Analysis of similarity between areas was determined with data from the subplots using the Jaccard index (Magurran 1988). Simple soil samples were taken from three depths in each 100m^2 plot: 0-20cm, 21-40cm and 41-60cm. The analyses were performed at the Soil Laboratory of the *Universidade Estadual de São Paulo* – Ilha Solteira Campus (Brazil). The following attributes were analyzed: aluminum (Al), exchangeable cations with the extraction of calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na) through ion-exchange resin (Raij *et al.* 1987). Organic matter (OM) was determined using the colorimetric method. Active acidity was measured through the determination of pH in $CaCl_2$. Based on the results of the chemical analyses, the percentage of saturation of the soil (V%) was determined.

The Kolmogorov-Smirnov test (Zar 1996) was performed to test the differences between the frequency distribution of the individuals of *C. alba* in different height classes for the two communities. Canonical correspondence analysis (CCA) among samples was used to determine possible associations between soil fertility, time of inundation and tree/shrub species composition and abundance patterns using the PC-ORD software (McCune & Mefford 1997). Two matrices were used – one containing data on absolute density of tree/shrub species per plot in each area and an environmental matrix with data on soil per plot and time of inundation for each area. CCA was performed in an exploratory manner, using the actual data of the soil attributed at each depth as well as mean values per depth. In the environmental matrix, time of inundation was two months for Miranda and five months for Porto Murtinho, calculated based on Hammilton *et al.* (1996). The Monte Carlo test was performed with 999 permutations to determine the level of significance of the main axis of the canonical order (Ter Braak & Prentice 1988).

RESULTS

SPECIES RICHNESS AND FLORISTIC

In the Miranda community, 428 tree/shrub individuals (CBH ≥ 5cm) belonging to 11 families, 19 genera and 19 species were sampled (Table 1). Fabaceae exhibited the greatest richness (8 species), followed by Bignoniaceae (3 species). *Copernicia alba* had the greatest importance value, followed by *Tabebuia aurea* (Bignoniaceae). The H' index was 1.15 and the J' index was 0.38.

Table 1. Phytosociological parameters for species of the Miranda and Porto Murtinho 'carandazal', Pantanal wetland, Brazil; Site: Miranda (M) and Porto Murtinho (PM); AF: absolute frequency (%); RF: relative frequency (%); AD: absolute density (ind.ha^{-1}); RD: relative density (%); ADo: absolute dominance (m^2/ha); RDo: relative dominance (%); CV: coverage value; IV: importance value; species listed in decreasing IV.

Tabela 1*. Parâmetros fitossociológicos para as espécies do 'carandazal' do Miranda e Porto Murtinho, Pantanal, Brasil. Site: Miranda (M) e Porto Murtinho (PM); AF: freqüência absoluta (%); RF: freqüência relativa (%); AD: densidade absoluta (ind.ha^{-1}); RD: densidade relativa (%); ADo: dominância absoluta (m^2/ha); RDo: dominância relativa (%); CV: valor de cobertura; IV: valor de importância. Espécies em valores decrescentes de IV.*

Species	Site	AF	RF	AD	RD	ADo	RDo	CV	IV
Copernicia alba	M	97	48.9	670	73.6	169.11	79.04	152.64	201.58
Tabebuia aurea	M	21	10.6	85	9.3	28.21	13.19	22.53	33.17
Astronium fraxinifolium	M	12	6.3	46	5.1	0.73	3.44	8.58	14.96
Mimosa polycarpa	M	12	6.3	23	2.5	0.01	0.07	2.64	9.02
Banara arguta	M	6	3.1	8	0.9	0.12	0.56	1.5	4.69
Ipomoea fistulosa	M	6	3.1	12	1.4	0.01	0.03	1.44	4.63
Machaerium hirtum	M	4	2.1	6	0.7	0.31	1.46	2.16	4.29

Continuation Table 1

Species	Site	AF	RF	AD	RD	ADo	RDo	CV	IV
Albizia niopoides	M	6	3.1	8	0.9	0.00	0.02	0.95	4.14
Inga vera	M	6	3.1	6	0.7	0.01	0.04	0.74	3.93
Acacia farnesiana	M	4	2.1	12	1.4	0.01	0.08	1.48	3.61
Sapium haematospermum	M	4	2	4	0.4	0.02	0.10	0.57	2.7
Andira inermis	M	2	1	2	0.2	0.29	1.38	1.61	2.68
Anadenanthera colubrina var. *cebil*	M	2	1	8	0.9	0.07	0.35	1.28	2.35
Handroanthus heptaphyllus	M	2	1	4	0.4	0.00	0.01	0.47	1.54
Jacaranda cuspidifolia	M	2	1	2	0.2	0.04	0.21	0.44	1.5
Adenaria floribunda	M	2	1	2	0.2	0.00	0.01	0.24	1.31
Baillonia amabilis	M	2	1	2	0.2	0.00	0.00	0.24	1.3
Albizia inundata	M	2	1	2	0.2	0.00	0.00	0.24	1.3
Sideroxylon obtusifolium	M	2	1	2	0.2	0.00	0.00	0.24	1.3
Total		**194**	**100**	**904**	**100**	**198.94**	**100**	**200**	**300**
Copernicia alba	PM	100	67.6	846	91.4	15.89	92.3	183.7	251.3
Mimosa glutinosa	PM	40	27	72	7.7	1.21	7.08	14.85	41.88
Sphinctanthus hasslerianus	PM	4	2.7	4	0.4	0.03	0.23	0.66	3.36
Acacia sp.	PM	2	1.35	2	0.2	0.05	0.33	0.55	1.9
Machaerium hirtum	PM	2	1.35	2	0.2	0.00	0.02	0.24	1.59
Total		**148**	**100**	**926**	**100**	**17.18**	**100**	**200**	**300**

In the Porto Murtinho community, 463 tree/shrub individuals (CBH ≥ 5cm) belonging to three families, five genera and five species were sampled (Table 1). Fabaceae accounted for three species and Arecaceae and Rubiaceae each accounted for one. *C. alba* had the greatest importance value, followed by *Mimosa glutinosa* (Fabaceae). The H’ index was 0.33 and the J’ index was 0.21.

In the subplots of the Miranda community, 84 species were identified (H’ = 3.92) and the collection in the areas adjacent to the plots resulted in 16 species, totaling 100 species distributed among 33 families (Appendix 1). The families with the greatest richness were Fabaceae (14 species), Asteraceae (13 species), Malvaceae (9 species) and Poaceae (7 species). The most frequent species in the subplots were *Paullinia pinnata* (Sapindaceae), *Steinchisma laxa* (Poaceae) and *Ipomoea chiliantha* (Convolvulaceae).

In the subplots of the Porto Murtinho community, 94 species were identified (H’ = 4.12) and the collection in the areas adjacent to the plots resulted in 17 species, totaling 111 species distributed among 29 families (Appendix 1). The most representative families were Poaceae (15 species), Fabaceae (15 species), Cyperaceae (12 species) and Asteraceae (10 species). The most frequent species in the subplots were *Galactia striata* (Fabaceae), *Croton andinus* (Euphorbiaceae) and *Paspalum plicatulum* (Poaceae).

Among the total of 178 species sampled in the subplots alone, 114 (64%) were part of the herbaceous component, which was the most abundant in both communities. Floristic similarity between areas (estimated by only the species collected in the subplots) was low (Sj = 0.12).

The frequency distribution of the individuals of *C. alba* in different height classes for the two communities (Figure 2), shows that the classes with the greatest representativity were between 7.0 and 12.5m in Miranda and between 4.3 and 9.7m in Porto Murtinho. The initial and final classes had the lowest density of individuals. However, the Kolmogorov-Smirnov test (Zar 1996) revealed non-significant differences in the frequency distribution of *C. alba* height between the communities (p = 0.69).

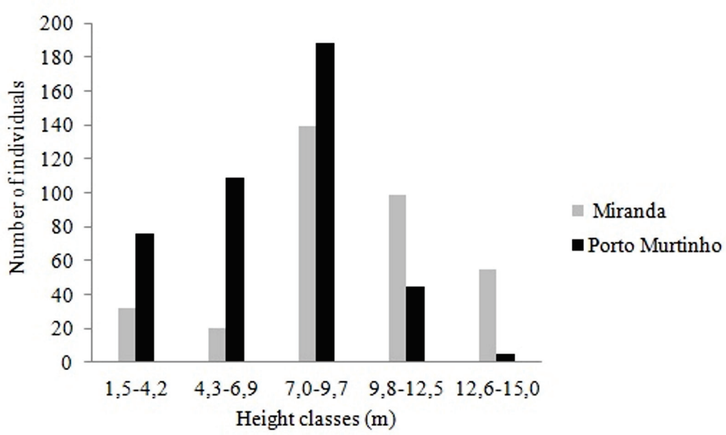

Figure 2. Frequency distribution of individuals of *Copernicia alba* in different height classes in Miranda and Porto Murtinho 'carandazal' communities, Pantanal wetland, Brazil

Figura 2. *Distribuição da frequência de indivíduos de Copernicia alba em diferentes classes de alturas no 'carandazal' do Miranda e Porto Murtinho, Pantanal, Brasil.*

SOIL FERTILITY

The chemical analyses reveal soils with base saturation (V%) greater than 75%, indicating a high degree of fertility, with mean values of 93% in Miranda and 80% in Porto Murtinho. The mean soil attributes at the different depths are displayed in Table 2.

Table 2. Chemical attributes of soil at three depths in Miranda (M) and Porto Murtinho (PM) 'carandazal' communities, Pantanal wetland, Brazil; Means and standard deviations of 50 samples in each area: P, OM, pH, K, Ca, Mg, Na, Al, V; nd: not detected

Tabela 2. *Atributos químicos do solo analisados em três profundidades no 'carandazal' do Miranda (M) e de Porto Murtinho (PM), Pantanal, Brasil. Médias e desvio padrão das 50 amostras em cada área. P, OM, pH, K, Ca, Mg, Na, Al, V; nd: não detectado.*

Attributes	Miranda			Porto Murtinho		
	0-20 (cm)	21-40 (cm)	41-60 (cm)	0-20 (cm)	21-40 (cm)	41-60 (cm)
P (mg/dm^3)	13.08±14.6	3.8±4.02	3.27±5.53	5±1.46	2.9±1.61	2±1.26
OM (g/dm^3)	30.76±11.89	11.39±6.43	6.94±6.6	40.8±10.89	23.76±6.05	16.55±4.76
pH ($CaCl_2$)	6.46±0.74	6.97±0.93	7.31±0.91	4.73±0.26	5.43±0.72	6.08±0.80
K ($molc/dm^3$)	2.1±1.2	1.22±0.59	1.1±0.46	2.21±1.2	0.88±0.52	0.65±0.31
Ca ($molc/dm^3$)	205.6±179.27	270.4±247.62	333.7±303.51	77.72±36	160.4±92.12	186.9±73.36
Mg ($molc/dm^3$)	90.1±53.17	109.9±65.71	124.2±78.77	34.88±14.10	56.92±19.84	65.88±17.57
Na ($molc/dm^3$)	0.99±2.62	1.91±4.27	2.32±5.1	nd	nd	nd
Al ($molc/dm^3$)	nd	nd	nd	2.68±3.54	2.88±5.92	0.8±2.48
V (%)	92.02±5.88	93.83±6.36	95±5.69	67.42±11.49	83.62±14.17	91.49±9.32

ASSOCIATION BETWEEN SPECIES AND ENVIRONMENT

CCA detected associations between species composition and the environmental features measured. In the analysis of the means of the attributes per plot, the eigenvalues for the first two axes were 0.292 (Axis 1) and 0.195 (Axis 2), explaining 17.1% of the total accumulated variance regarding the environmental variables (Figure 3). The Monte Carlo test revealed a significant result for Axis 1 ($p = 0.02$). The parameters with the strongest correlation with Axis 1 were inundation (negative correlation) and the soil attributes Mg, Ca and pH (positive correlations).

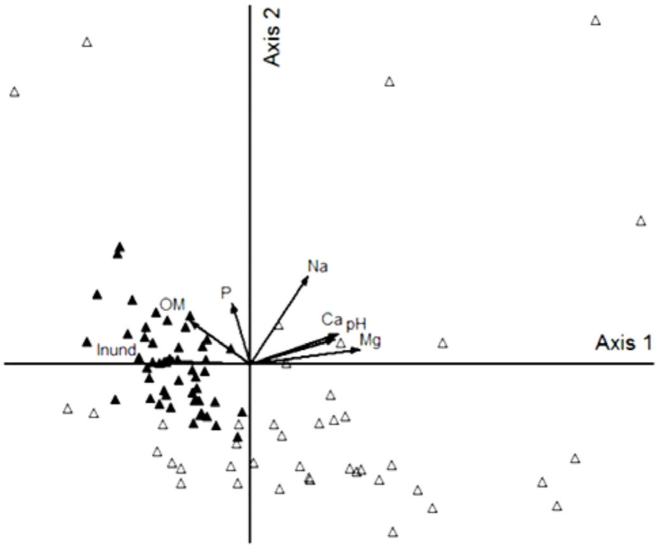

Figure 3. Canonical correspondence analysis between chemical characteristics of soil, time of inundation and tree/shrub species absolute density per plot in two areas of 'carandazal' in Pantanal wetland, Brazil. Inund: inundation; OM: organic matter; P: phosphorus; Na: sodium; Ca: calcium; pH; Mg: magnesium. Miranda (△); Porto Murtinho (▲).

Figura 3. *Análise de correspondência canônica entre as características químicas do solo, tempo de inundação e densidade absoluta das espécies arbustivo/arbóreas por parcela em duas áreas de 'carandazal' no Pantanal, Brasil. Inund: Inundação; OM: matéria orgânica; P: fósforo; Na: sódio; Ca: cálcio; pH; Mg: magnésio. Miranda (△); Porto Murtinho(▲).*

For the CCA with data from the soil at 0-20 cm and 21-40 cm, the results of the Monte Carlo test were non-significant ($p = 0.06$ and $p = 0.12$, respectively). The CCA with data from 41-60 cm explained 15.7% of the overall variation on the first two ordination axes and was significant ($p = 0.03$). Thus, the mean values proved more effective at determining relationships between the vegetation and fertility of the soil.

DISCUSSION

The low number of tree/shrub species found in the areas studied is characteristic of monodominant formations. In the Pantanal wetland, the low richness of tree/shrub species in floodable monodominant areas is also reported in other studies on vegetation structure (Nascimento & Nunes da Cunha 1989, Arieira & Nunes da Cunha 2006, Soares & Oliveira 2009). The low number of species per ha is a characteristic found in monodominant formations in different geographic regions (Hart *et al.* 1989, Marimon *et al.* 2001a), any small sample in monodominant formations will contain fewer species than a sample of the same size in a mixed area (Hart 1990).

Diversity and evenness indices tend toward low values in monodominant formations due to the concentration of a large number of individuals of the same species (Hart *et al.* 1989, Nascimento & Nunes da Cunha 1989, Arieira & Nunes da Cunha 2006), as in the 'carandazal', where *C. alba* had the greatest importance index in both areas, with a higher density of individuals in comparison to other tree/shrub species, resulting in low H' and J' indices.

The arboreal species found in the Miranda 'carandazal' are characteristic of adjacent dry forests, such as *Anadenanthera colubrina* var. *cebil*, *Astronium fraxinifolium*, *Inga vera*, *Jacaranda cuspidifolia*, *Sideroxylon obtusifolium* and *Tabebuia aurea* (Damasceno-Júnior *et al*. 1999). When associated with *C. alba,* these species form a mixed forest, which may explain the presence of a larger number of species of this component in Miranda in comparison to the Porto Murtinho community. In drier years, these species likely become denser, initiating a new process of succession that may culminate in the formation of new areas of dry forest (Damasceno-Júnior *et al.* 1999).

Tabebuia aurea obtained the second highest importance index in Miranda, is dominant in the proximities of the study area and constitutes another monodominant formation, known regionally as 'paratudal' (Ribeiro & Brown 2002, Soares & Oliveira 2009). Besides *C. alba*, only *Machaerium hirtum* was recorded in both areas. This species is characteristic of saline and calcareous soils of the Pantanal wetland (Pott & Pott 1994). Among the tree/shrub species found in Porto Murtinho, *Mimosa glutinosa* had the second greatest importance index. This tree is found along the Paraguay River and its tributaries and its occurrence is related to monodominant formations of *C. alba* in Brazil, Paraguay and the Chaco plain in Argentina (Hueck 1972).

The low number of tree species in the Porto Murtinho community is related to the inundation pattern, as this event is more severe in areas near the Paraguay River, where inundation can last up to five months (Hamilton *et al.* 1996). This likely inhibits the colonization of tree species from adjacent mixed areas (Damasceno-Júnior *et al.* 2004), thereby favoring the monodominance of *C. alba*. In the Pantanal wetland, only 5% of tree species exclusively inhabit zones of prolonged flooding (Nunes da Cunha & Junk 1999). In many cases, inundation acts as a filter, restricting the number of tree species occurring in a given area (van der Valk 1981).

Connell & Lowmann (1989) classify monodominant formations into different types. The 'carandazal' can be included in type I, in which the dominant species remains abundant and persists for more than one generation. Although it has a high degree of density in the two communities, the greater frequency of *C. alba* specimens in the intermediate height class in comparison to the initial class may indicate a past condition more favorable to the establishment of this species, after which the population remained at lower levels. However, the limited data of the present study do not allow exploring the population aspect of *C. alba*. Despite the differences found regarding the frequency of height classes of specimens of *C. alba* between the two communities, the populations exhibited statistically equal height distributions.

While conditions that are unfavorable to the establishment and development of plants, such as a high degree of acidity and low fertility of the soil, are commonly found in monodominant formations in other tropical areas (Hart *et al.* 1989, Read *et al*. 1995, 2006, Nascimento *et al.* 1997a, Marimon *et al.* 2001a, 2001b), no undesirable conditions to the establishment and mineral nutrition of the plants in the 'carandazal' were detected. Ribeiro & Brown (2002) also report a high degree of fertility in the soil of the monodominant formation 'paratudal' in the Pantanal wetland.

Flooding has the effect of diminishing species richness proportionately to the magnitude and duration of the inundation (Junk 1989, Damasceno-Júnior *et al.* 2005, Parolin & Wittmann 2010). One may therefore infer that flooding is likely the main condition determining monodominance in the formations studied, as demonstrated in the canonical correspondence analysis, since soil fertility was similar in both areas.

Nutrients such as Ca and Mg occurred in greater concentrations in the Miranda community. This is related to the chemical composition of the waters of the Miranda, which travels through regions rich in carbonate rocks (Scremin-Dias *et al.* 1999). However, it is difficult to state that greater concentrations of Ca and Mg offer better conditions for the colonization of tree species from dry areas, as the levels of these nutrients were not considered low in the Porto Murtinho community. Thus, factors such as inundation are likely more decisive to restrictions to the establishment of species from adjacent areas than the concentration of nutrients in the soil. In any case, these issues should be investigated in further studies.

Lewis (1991) considers monodominant areas of *C. alba* to be floristically poor. However, this profile does not apply to the other components, as high degrees of richness and diversity were found in the present study, especially in the herbaceous component, which accounted for more than 60% of the total richness of the areas. The 'carandazal' supports the idea put forth by Read *et al.* (2006)

that low diversity in one component of some tropical monodominant formations may not be repeated in other components.

The low degree of similarity between the areas due to the species in the subplots (where herbaceous species occurred in greater number) may be the result of the differences in the time the sampling was performed (dry season in the Miranda community and rainy season in the Porto Murtinho community, where greater richness and diversity were found). Rebellato & Nunes da Cunha (2005) also found greater richness and diversity in the rainy season in comparison to the dry period in a floodable field in the Poconé wetland. The alternating inundation and dry events in the Pantanal wetland are fundamental to the maintenance of the structure and floristic composition of the communities, leading to diversity in the herbaceous component (Rebellato & Nunes Da Cunha 2005, Nunes Da Cunha *et al.* 2010).

The 'carandazal' is an important physiognomic element due to its uniqueness in relation to other physiognomies of the Pantanal wetland and the Chaco plain. However, changes in the landscape are considerably accentuated. The occurrence of environmental perturbation is revealed in the evidence of slash-and-burn techniques and pasture management.

In conclusion, the richness of the tree/shrub component was greater in the area with a shorter inundation time, which makes this event an important factor in the determination of *C. alba* monodominance in the Pantanal wetland. The composition and abundance of tree/shrub species in the 'carandazal' was associated to a greater degree to inundation and levels of Ca and Mg in the soil. Notwithstanding the monodominant profile of these formations, the herbaceous component demonstrated a high degree of richness and diversity in both communities, although there are differences in the inundation pattern between the two areas.

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