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the Brazilian Pantanal

Flood regime and water table determines tree distribution in a forest-savanna gradient in the Brazilian Pantanal

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ABSTRACT

This study aimed to recognized the preferential location of species of the tree sinusiae in response to a moisture gradient in Pantanal Matogrossense, Brazil. We established sampling plots of arboreal sinusiae along a soil moisture and flood gradient. Piezometers were installed, allowing monthly measurements of water table depth and flood height during one year. Detrended Correspondence Analysis, Gradient Direct Analysis, Multi-response Permutation Procedures and Indicator Species Analysis were performed to evaluate the effect of moisture gradient on tree distribution. The annual variation of water table is shallower and similar in Seasonally Flooded Forest and Termite Savanna, with increasing depths in Open Savanna, Savanna Forest and Dry Forest. Circa 64% of the species were characterized as having a preferential location in "terrestrial habitats normally not subjected to inundation", while 8% preferentially occur in "wet habitats". Lowest tree richness in flood-affected vegetation types is related to both present-day high climatic seasonality and Late Pleistocene dry paleoclimates in the Pantanal wetland. The tree distribution across different formations in the Pantanal shows a direct relationship with soil moisture gradient.

Key words: floristic composition, flood pulse concept, wetlands, RPPN SESC Pantanal.

INTRODUCTION

The Pantanal Matogrossense is one of largest wetland systems in the world, and the largest seasonally flooded area in South America (Nunes da Cunha and Junk 2015). The great diversity of

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permanent habitats and seasonally waterlogged and permanent dry areas is the ecological basis for the diversity of species in Pantanal (Junk et al. 2006).

Flood is one of the controlling factors of maintenance of fauna, flora and landscape diversity in Pantanal (Junk et al. 1989, Nunes da Cunha and Junk 1999, 2001). Flood cycle determines the availability of dry and wet areas, which in turn

influences the spatial distribution of many species. Flood provides a permanent exchange of water, sediments, chemical components and organisms between the main river channel and adjacent floodplains, resulting in a great environmental heterogeneity (Lourival et al. 2000).

Based on the concept of flood pulse in floodplain systems (Junk et al. 1989), Nunes da Cunha and Junk (2001) stated that tree vegetation in Pantanal is distributed over a flooding gradient, in accordance to tolerance to either flood or drought. This differential tolerance, with morphological and physiological adaptations of species, leads to formation of peculiar forest communities.

Phillips and Gentry (1994) reported that different disturbances, at different scales, are responsible for the environmental heterogeneity observed in tropical forests, exerting strong influence on structure, dynamics and composition of species of tree communities. Among these disturbances, flood acts in a regional scale, similarly fragmentation, burning and wind-exposure, all affecting the composition and structure of plant communities (Ferreira and Laurance 1997, Cochrane and Schulze 1999).

In tropical forests, rivers are important sources of disturbances due to the annual flooding regime, and also because of river dynamics at landscape scale (Klinge et al. 1990). Some plant communities on floodplains represent the initial phases of primary succession and are, usually, formed by a small group of fast growing species, well adapted to periodic flood (Junk 1989). Permanent water movement and deposition of sediments affect the establishment, growth and reproduction of different species, resulting in instability and a constant reorganization of plant communities (Siebel and Blom 1998).

Flood imposes varying changes on physical, chemical and biological soil processes, affecting soil structure, O_2 diffusion, CO_2 emissions, anaerobic decomposition of organic matter, depletions or toxicity of iron and manganese, all limiting the soil capacity for supporting plant growth (Kozlowski 2002, Bailey-Serres and Voesenek 2008).

Plant tolerance to flood varies according to species, genotype and age of the plant; intensity and duration of the flood, and chemical composition of water (Kozlowski 2002). Flood promotes strong effects on germination and initial development of seedlings because physiological processes needed for germination requires hight O_2 availability (Kozlowski and Pallardy 1997). Adverse effects from flooding are responsible for changes on distribution, species composition and successional processes, as demonstrated by Arieira and Nunes da Cunha (2006) and Amorim and Batalha (2007).

The aim of this work was to evaluate the preferential location of species of the tree sinusiae in response to a moisture gradient in the Pantanal. We determined the pattern of water table annual oscillation and flood found in the main tree formations along a "savanna (cerrado)-forest" gradient. Accordingly, we expected to answer the following questions: i) Is species composition variable with different annual water table and flood oscillation patterns? ii) Is the water table oscillation pattern similar in areas free from annual flood (Dry Forests and Savannas)? iii) Which species show preferential distribution in the wet or dry extremes of the moisture gradient? iv) Which tree species present wide spatial distribution across the gradient?

MATERIALS AND METHODS

Study Site

This study was carried out within the Reserva Particular de Patrimônio Natural SESC Pantanal (RPPN SESC Pantanal) (16°34'50"S and 56º15'58"W), in Barão de Melgaço, Mato Grosso State, western Brazil. It is located on the Cuiabá and São Lourenço rivers interfluve (Fig. 1). Average precipitation is from 1,100 to 1,200 mm (Hasenack et al. 2003). We observed the predominance of herbaceous fields, savannas (cerrados) and forests mixed to water bodies and aquatic vegetation.
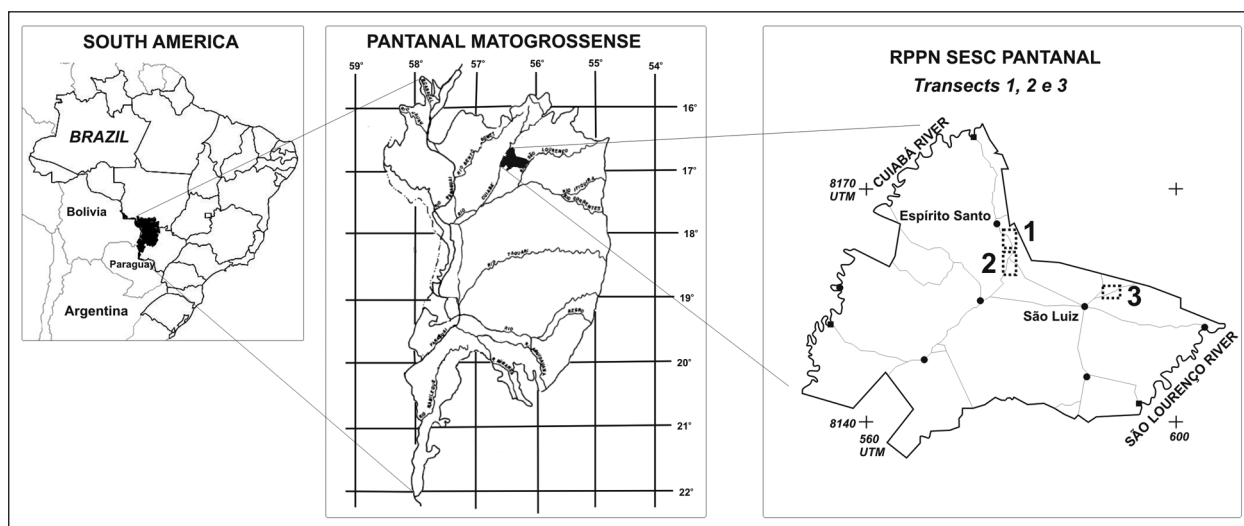
Figure 1 - Localization of Pantanal Matogrossense, RPPN SESC Pantanal and transects (1, 2 and 3), Barão de Melgaço, Mato Grosso, Brazil.

SAMPLING AND CHARACTERIZATION OF FORMATIONS

Three vegetation transects were selected, where tree physiognomies were sampled in plots with 20 m × 100 m, divided in subplots with 20 × 20 m. **Transect 1** began with a Termite Savanna (*Campo de Murundus*) adjacent to the paleo-levée (*cordilheira*) towards to its highest central section, crossing four forested phytophysiognomies. The *Cordilheiras* are geomorphological units formed by river sandy bars of former high energy sedimentation, now stabilized and forming the highest parts of the landscape, usually with sandy sedimentary material (Nunes da Cunha and Junk 2011). **Transect 2** began in a Semi Evergreen Forest, across a Termite Savanna, followed by a *cordilheira* with a Savanna Forest (*Cerradão*), ending with a Forest in the sequence. **Transect 3** began with a Termite Savanna, followed by Open Savanna (*Cerrado stricto sensu*) physiognomy. Only individuals with DBH (diameter at 1.30 m above ground level) ≥ 4.77 cm for areas with forest physiognomy were sampled and identified. For Open Savanna physiognomy a inclusion criteria of DSL (diameter at soil level) ≥ 4.77 cm was used (Felfili et al. 2005).

Dry Forest and Savanna facies were identified, each facies named considering the populations of tree species more abundant, based on the structure. The moisture gradient was monitored measuring the seasonal water table depth oscillation, using piezometers at each site, including Termite Savannas, and measuring flood height.

DATA ANALYSIS

Classification and ordination analyses were applied to a matrix of binary data. Species with single occurrences (singleton species) were excluded in order to better understand the possible grouping of the samples, according to their most frequent elements. A Detrended Correspondence Analysis - DCA (Hill and Gaugh 1980) was performed to detect floristic patterns, or gradients.

Multi-response Permutation Procedures - MRPP (Mielke Jr et al. 1981) with the Jaccard index and pairwise comparisons was used to check the differences in species composition between the phytophysionomies along the moisture gradient. The MRPP reports a test statistic (T) describing the separation between groups, with smaller, or negative values indicating greater separation. The

agreement statistic (A) describes within-group homogeneity compared to random, where values close to zero indicating the degree of heterogeneity expected by chance, and values close to one indicating highly homogeneous groups. Values below zero correspond to highly heterogeneous groups (Faith et al. 1987)

The way in which the moisture gradient affects the preferential localization of plant species was evaluated by Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997) and Direct Analyses of Gradients (Gauch-Jr 1991) with the distribution of the species with greater indicator value (IV) derived from the Indicator Species Analysis (ISA). The statistical significance of species IV was assessed via Monte Carlo randomizations. DCA, MRPP and ISA analyses were performed with the PC-ORD program, version 6.0.

Finally, species were classified according to their preferential habitat (Nunes da Cunha and Junk 1999). These authors classified the Pantanal species based on their preferential localization in: S = terrestrial habitats normally not subjected to inundation, T = habitats inundated during short periods (< two months); A = habitats inundated during long periods (> two months).

RESULTS

VEGETATION FACIES

Fig. 2 shows the phytophysiognomies and their respective facies sampled in the studied transects. Dry Forest, Seasonally Flooded Semi Evergreen Forest (*Cambarazal*), Savanna Forest (*Cerradão de Carvoeiro*) and Open Low-tree Savanna (*Cerrado de Lixeira*) are the arboreal formations, whereas Termite Savanna represents the grassland formation (Fig. 2).

The Dry Forest, located in well-drained habitats (paleo-levée), were divided in five facies: 1. Transitional Dry Forest with *Scheelea phalerata*; 2. Dry Forest with *S. phalerata* and *Callisthene*

fasciculata; 3. Dry Forest with *S. phalerata* and *Myracrodruon urundeuva*; 4. Dry Forest with *S. phalerata*, *M. urundeuva* and *C. fasciculata*; 5. Dry Forest with *S. phalerata*, *M. urundeuva* and *Combretum leprosum* (Fig. 2).

A Seasonally Flooded Semi Evergreen Forests dominated by *Vochysia divergens* Pohl (regionally know as *Cambarazal*) (Arieira and Nunes da Cunha 2006) are located in the hydromorphic lowlands, representing wet areas along the moisture gradient. The Savanna Forest (*Cerradão*) and the Open Low-tree Savanna (*Cerrado sensu stricto*) were the two savanna phytophysiognomies studied, locally called *Cerradão de Carvoeiro* and *Cerrado de Lixeira*, respectively. The *Cerradão de Carvoeiro* were divided in two facies: 1. *Cerradão de Carvoeiro* with *Magonia pubescens* and 2. *Cerradão de Carvoeiro* with *Lafoensia pacari*. The *Cerrado de Lixeira* was represented by a single facie: 1. *Cerrado de Lixeira* with *Terminalia argentea* (Fig. 2).

VEGETATION VERSUS MOISTURE GRADIENT

The relation between phytophysiognomy and water table depth is illustrated in Table I and Fig. 3.

Dry Forests have the lowest water table during the year, with low seasonal variability. The water table oscillation regime in *Cerrados* was similar for *Cerradão de Carvoeiro* and *Cerrado de Lixeira*, however, with slight higher depths during the dry season in the latter (Table I; Fig. 3). The *Cerrado* assumes a denser forested physiognomy (*Cerradão de Carvoeiro*) with accompanying increment in richness (23 species in *Cerrado da Lixeira* to 33 species in *Cerradão de Carvoeiro*), as water table remains deeper during the wet season (1.90 m and 3.21 m, respectively). This suggest that the different *Cerrado* phytophysiognomies in Pantanal are strongly conditioned by the water table depth in the wet season. *Cerrados* occupy the intermediate position across the moisture gradient, and are not subjected to inundation. They only remain with waterlogged during short spells in the rainy season.
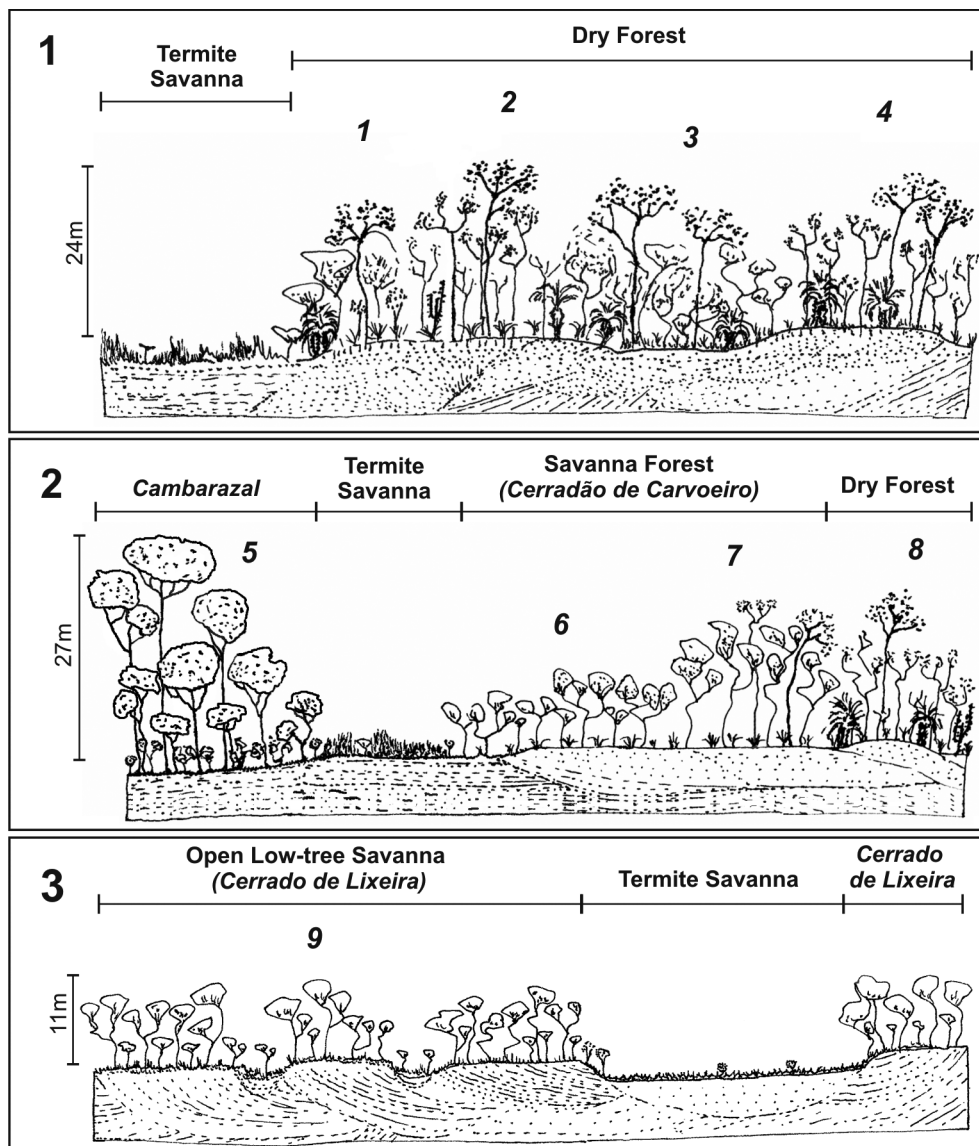
Figure 2 - Phytophysiognomies and the respective vegetation facies sampled in transects 1, 2 and 3 in RPPN SESC Pantanal, Brazilian Pantanal, where: **1.** Transitional Dry Forest (DF) with *Scheelea phalerata*; **2.** DF with *S. phalerata* and *Callisthene fasciculata*; **3.** DF with *S. phalerata* and *Myracrodruon urundeuva*; **4.** DF with *S. phalerata, M. urundeuva* and *C. fasciculata*; **5.** *Cambarazal*; **6.** *Cerradão de Carvoeiro* with *Lafoensia pacari*; **7.** *Cerradão de Carvoeiro* with *Magonia pubescens*; **8.** DF with *S. phalerata, M. urundeuva* and *Combretum leprosum*; **9.** *Cerrado de Lixeira* with *Terminalia argentea.*

At the other extreme of the moisture regime are Termite Savannas and *Cambarazal*, where water table oscillation is close to the surface year round, with waterlogged soils during the rainy season. However, *Cambarazal* differs from the other phytophysiognomies for being subject to annual seasonal flood (Table I; Fig. 3).

Concerning the water table and flood oscillations over the year (Table I, Fig. 3), we ranked the Pantanal phytophysiognomies by increasing water saturation and flooding, as follows: Dry Forests < *Cerradões de Carvoeiro* (Savanna Forest) < *Cerrado de Lixeira* (Open Low-tree Savanna) < Termites Savannas < *Cambarazal* (Semi Evergreen Forest).

TABLE I
Water table average depth and average height of flood in all phytophysiognomies studied in RPPN SESC Pantanal, Brazilian Pantanal. Wet season = from December to May; Dry season = from June to November. Average values ± standard deviation.

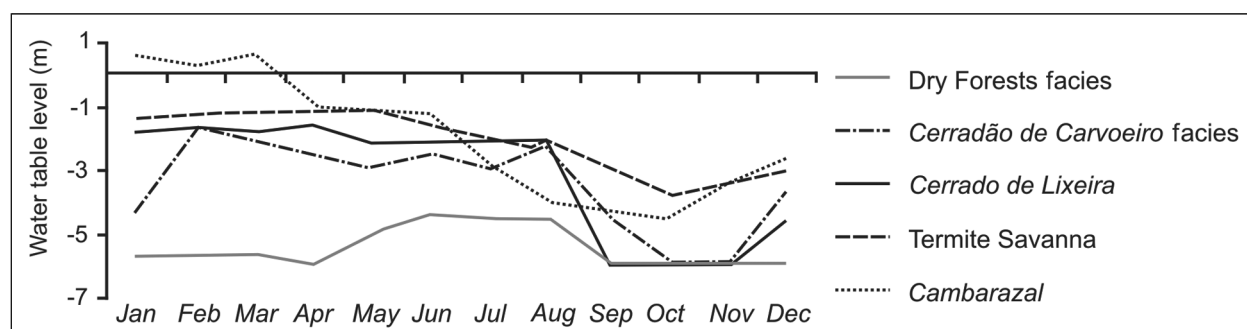| Phytophysiognomies	Water table average depth (m)		Flood (m)
	Wet season	Dry season	(Jan/Feb/Mar)
Dry Forest facies	5.60 ± 0.33	5.30 ± 0.82	-
Cerradão de Carvoeiro **facies**	3.21 ± 1.36	4.00 ± 1.75	-
Cerrado de Lixeira	1.90 ± 0.26	4.10 ± 2.10	-
Termite Savanna	1.32 ± 0.27	2.75 ± 0.86	-
Cambarazal	1.30 ± 0.46	3.30 ± 1.19	0.50 ± 0.17

Figure 3 - Mean values (m) of annual range of water table depth and flood height in the studied formations in RPPN SESC Pantanal, Brazilian Pantanal.

RICHNESS AND FLORISTIC COMPOSITION

We sampled one hundred and eleven tree and shrub species distributed in 77 genus and 35 families. Among the studied formations, we recorded 68 species in Dry Forests, 33 species in the *Cerradão de Carvoeiro*, 23 species in *Cerrado de Lixeira* and 15 species in *Cambarazal*.

Quantitative analyses confirm a floristic differentiation among the studied phytophysiognomies. The Dry Forests facies sampled are separated from *Cerradão de Carvoeiro* on the left of the first axis of DCA (Fig. 4), not forming a isolated floristic group, but rather a gradient. The other two studied phytophysiognomies, *Cerrado de Lixeira* and *Cambarazal*, formed distinct floristic group.

A moisture gradient was confirmed in the axis 1 of the DCA (Fig. 4). The Seasonally Flooded Semi Evergreen Forest (*Cambarazal*), situated in hydromorphic lowlands, are on the right position
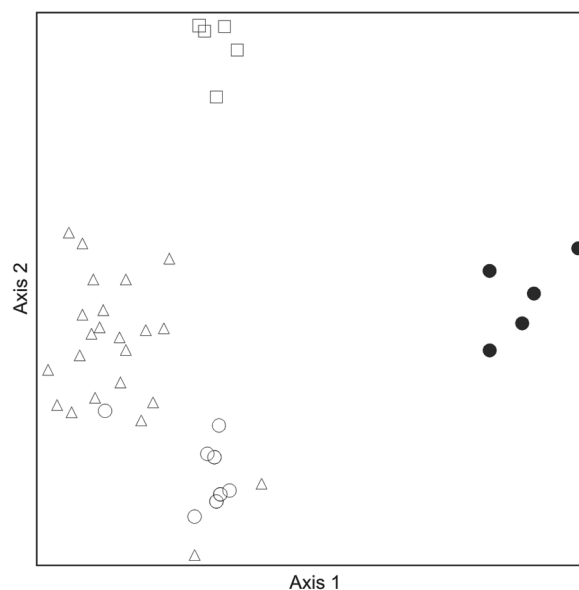

Figure 4 - Two-dimensional plots ordination diagram derived from DCA for arboreal sinusiae along a soil moisture and flood gradient in RPPN SESC Pantanal, Brazilian Pantanal. ∆ - Dry Forests facies; ○ - *Cerradão de Carvoeiro* facies (Savanna Forest); □ - *Cerrado de Lixeira* (Open Low-tree Savanna); ● - *Cambarazal* (Seasonally Flooded Semi Evergreen Forest).

in axis 1; the *Cerradão de Carvoeiro* and *Cerrado de Lixeira*, in the middle of the axis 1, are in an intermediate position in the moisture gradient; finally, the Dry Forests on the left of the axis 1, are in the driest habitats.

There were significant differences in species composition between the four phytophysiognomies (T value = -20.52; observed δ = 0.200; expected δ = 0.500; A = 0.59; p< 0.0000) based on MRPP analysis. The pairwise comparisons (Table II) indicated differences between all phytophysiognomies, in term of the arboreal sinusiae. In this regard, Dry Forest and *Cambarazal* and Dry Forest and *Cerrado de Lixeira* show greater distinction, while *Cambarazal* and *Cerrado de Lixeira* are less differentiated.

TABLE II

Summary statistics for pairwise comparison (MRPP) among the studied phytophysiognomies along a soil moisture and flood gradient in RPPN SESC Pantanal, Brazilian Pantanal. T = degree of separation between the groups, higher negative values indicating greater separation A = level of within-group agreement, comparing the distance within and between the groups, higher values indicating greater separation.

Pairwise comparison of phytophysiognomies (MRPP)	T	A	*p*
Dry Forest facies vs. *Cambarazal*	-14.91	0.36	0.0000
Dry Forest facies vs. *Cerradão de Carvoeiro* facies	-12.74	0.29	0.0000
Dry Forest facies vs. *Cerrado de Lixeira*	-14.24	0.34	0.0000
***Cambarazal* vs. *Cerradão de Carvoeiro* facies**	-7.63	0.46	0.0002
Cambarazal* vs. *Cerrado de Lixeira	-5.59	0.45	0.0017
Cerradão de Carvoeiro* facies vs. *Cerrado de Lixeira	-6.98	0.40	0.0001

The Indicator Species Analysis and Gradient Direct Analysis can detect ecological preferences of certain tree species in a moisture gradient. The indicator value (IV) of six major indicative species in each phytophysiognomy is illustrated in Fig. 5. ISA results (p<0.05) presented six species indicators of Dry Forest (in descending order of IV), as follows: *Scheelea phalerata* (Mart.) Bur., *Myracrodruon urundeuva* (Engl.) Fr. All., *Tabebuia roseo-alba* (Rid.) Sandw., *Casearia gossypiosperma* Briquet., *Combretum leprosum* Mart. and *Platypodium elegans* Vog.

For *Cerradão de Carvoeiro*, the species with significant IV were *Lafoensia pacari* A. St. Hil., *Qualea parviflora* Mart., *Plathymenia reticulata* Benth., *Callisthene fasciculata* Mart., *Pseudobombax tomentosum* (Mart. & Zucc.) Robyns, *Magonia pubescens* A. St. -Hil. (Fig. 5) and *Cordia glabrata* (Mart.) A. DC. (IV=37.1). For

Cerrado de Lixeira, the species were *Zanthoxylum hasslerianum* (Chodat) Pirani, *Diospyros hispida* DC., *Byrsonima coccolobifolia* (L.) H. B. K., *Erythroxylum suberosum* A. St.-Hil., *Pouteria ramiflora* (Mart.) Radlk., *Davilla elliptica* A. St.-Hil. (Fig. 5), *Mouriri eliptica* Mart. (IV=60), *Terminalia argentea* Mart. & Zucc. (IV=58), *Bowdichia virgilioides* Kunth (IV=56.3), *Luehea paniculata* Mart. (IV=54.2), *Tabebuia aurea* (Manso) B. & H. ex Moore (IV=52.3), *Curatella americana* L. (IV=41.6), *Hancornia speciosa* Gom., *Kielmeyera coriacea* Mart. and *Andira cuyabensis* Benth., *Qualea grandiflora* Mart. and *Himatanthus obovatus* (Mull. Arg.) Woods (IV=40) and *Simarouba versicolor* A. St.-Hil. (IV=36.1).

For *Cambarazal*, in turn, typical species were *Vochysia divergens*, *Rheedia brasiliensis* (Mart.) Pl. & Tr., *Licania parvifolia* Huber, *Alchornea discolor* Poepp., *Andira inermis* H. B. K., *Eugenia*

florida DC. (Fig. 5), *Mouriri guianensis* Aubl. (IV=40) and *Brosimum lactescens* (Moore) Berg (IV=40).

Although not a single species has been sampled in all the studied phytophysiognomy, *Astronium fraxinifolium* Schott showed the widest distribution in the moisture gradient, occurring in eight of the nine facies (89% of occurrence), being absent only in *Cambarazal*. Other four species, *Callisthene fasciculata*, *Curatella americana*, *Magonia pubescens* and *Dipteryx alata* Vog. were sampled in seven facies (78%).

In line with Fig. 6, we can observe that the number of species associated with seasonally flood areas (AT) is reduced, compared with species typical of well-drained habitats, normally not subject to inundation (S). *Casearia gossypiosperma*, *Combretum leprosum*, *Tabebuia roseo-alba*, *Myracrodruon urundeuva*, *Astronium*

fraxinifolium, *Anadenanthera colubrina*, *Pouteria ramiflora*, *Scheelea phalerata* and *Qualea parvifolia* are some of the 71 species (64%) with a preferential location in terrestrial habitats normally not subject to inundation (S) (Fig. 6).

The other 20 species (18%) are from terrestrial habitats, but can stand flooding during short periods (ST), as for example, *Curatella Americana*,, *Cecropia pachystachya* Trécul and *Simarouba versicolor* (Fig. 6).

Only nine species (8%) are typical from "inundated habitats" (AT), for example, *Vochysia divergens*, *Licania parvifolia*, *Rheedia brasiliensis*, *Mouriri guianensis* and *Brosimum lactescens*. The remaining species, 11 (10%), have unespecific, wide distribution along the moisture gradient (STA, TAS, TSA, ATS) (Fig. 6). For example, *Bromelia balansae* Mez. was observed in the understorey of all facies in Dry Forest and in facies in *Cerradão*
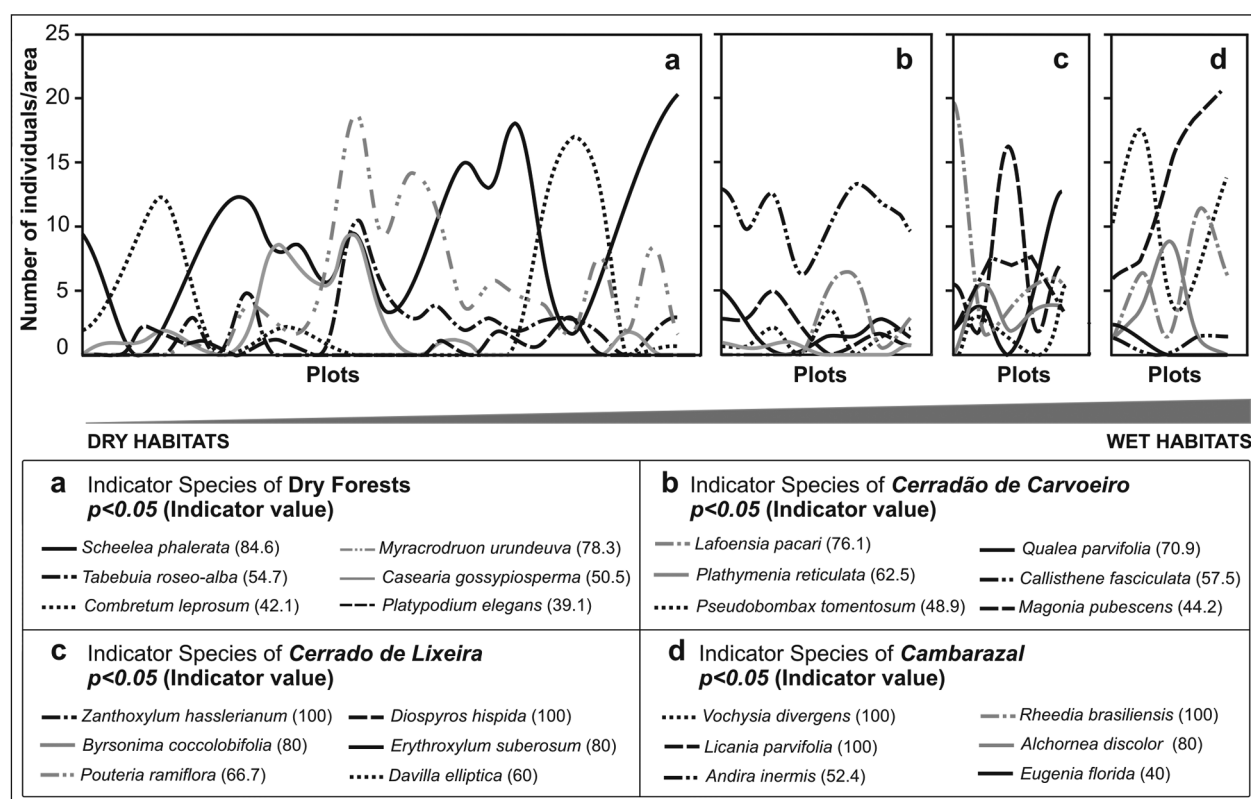

Figure 5 - Gradient direct analysis with distribution of the species identified as significant indicators based on Indicator Species Analysis (ISA) in each phytophysiognomy of Brazilian Pantanal.
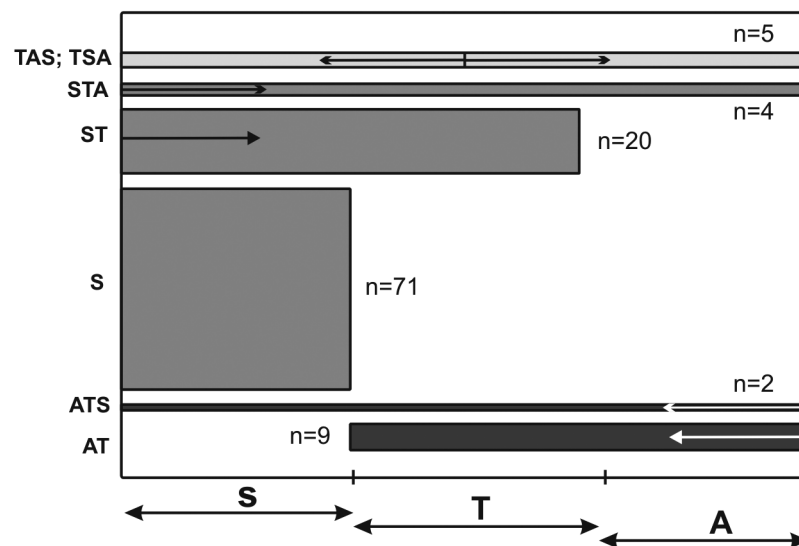
Figure 6 - Distribution of 111 tree species in the Brazilian Pantanal according to their preference along the moisture gradient. S = terrestrial habitats normally not subjected to inundation; T = habitats inundated during short periods (<two months), A = habitats inundated during long periods (> two months). Arrows indicate the supposed direction of expansion of the species from the center of maximum density (according to Nunes da Cunha and Junk 1999).

de Carvoeiro, but was absent in *Cerrado de Lixeira* and in *Cambarazal*.

DISCUSSION

EXAMPLES OF ADAPTATION TO DROUGHT AND FLOODING

Overall, these results indicated that water table depth and flood height influence the species composition and distribution at each plant community in the vegetation gradient. In line with that, we observed that a given group of species is well adapted to flooding, such as those from *Cambarazal*. Similarly, another group is typical of high water table level, but not subjected to inundation, in the *Cerrado da Lixeira* and the *Cerradões de Carvoeiro*, and finally, the Dry Forest is composed of species with very low tolerance to waterlogging and seasonal flood conditions.

Tree vegetation in Pantanal is distributed along a moisture gradient according to its degree of tolerance to inundation or drought. In some cases, survival during flood periods is due to the existence

of physiological and phenological peculiarities of the species. *V. divergens*, a dominant species in *Cambarazal*, for example, have seedlings and young individuals that can stand inundation and survive until the end of flooding period. On the other hand, adult individuals show decidity at the end of flooding period, followed by a rapid leaf replacement (Nunes da Cunha and Junk 2001).

Survival to water stress in the dry season is due to phenological, anatomical and physiological adaptations, as observed with *A. colubrina* and *Anadenanthera macrocarpa* (Benth.) Brenan. Both loose virtually all leaves in the dry season, and have tuberous root system, in addition to reduced growth rate during periods of low water availability (Silva and Barbosa 2000, Monteiro et al. 2006). Other species, such as *Curatella americana*, *Bowdichia virgilioides* and *Casearia sylvestris* Sw., have leaf mesophile structure with typical xeromophic traits which reduce water losses. The main features are reduced intercell space, large vascular bundles, colorless parenchyma, very thick

cuticles and trichomes (Sarmiento et al. 1985), and fire resistence.

WHY ARE THERE MORE SPECIES IN DRIER HABITATS OF PANTANAL?

Recent estimates of the number of plant species for Pantanal show a total richness of 2,000 species distributed in 144 families, in which 104 families are exclusively of terrestrial habitats, 21 families are exclusively aquatic and 19 both terrestrial and aquatic species. Most species (1,656) are terrestrial: 900 are herbs, grasses, vines, epiphytes and parasites, whereas the remaining 756 are woody plants like shrubs, sub shrubs, trees, lianas and palms. Only 247 species are considered as hydrophytes or aquatic macrophytes (Pott et al. 2011, Junk et al. 2006).

In Pantanal there is less flood-resistant trees than species adapted to well-drained lands. Concerning this, Nunes da Cunha and Junk (1999) reported for the Pantanal of Mato Grosso (Brazil), north of Poconé that only four were exclusive from flooded environments, out of 86 tree species sampled. Two possible and complementary explanations for the low richness of flood-resistant tree species in Pantanal are: (1) the highly seasonal moisture regime in the present, and (2) inheritance from prevailing semi-arid paleoclimates in the Late Quaternary of the Pantanal lowland (Ab'Sáber 2006).

Before the onset of Late Quaternary wet climates, the Pantanal remained a vast semi-arid lowland, unfavourable to species typical to wetlands (Pott et al. 2011). In fact, the rainfall of the part of Pantanal, towards the borders with Bolivia and Paraguay, is greatly reduced to less than 800 mm/year (Ab'Sáber 2006), while most areas have rainfall ranges from 1,000 mm to 1,400 mm/year (Hasenack et al. 2003), with very high seasonality and long dry season.

The paleoclimatic history of Pantanal is marked by alternating dry spells during the Late Pleistocene and early Holocene, which accounted for the "invasion" of a xeric and mesic flora from the adjacent drylands, like Chaco and Cerrado (Ab'Sáber 2006, Junk et al. 2006). The occurrence of dry paleoclimate spells in the Late Pleistocene (between 23,000 – 13,000 y.b.p.) enabled the expansion of the semi-arid arboreal and shruby flora on the Pantanal plains (Prado 2000, Ab'Sáber 2006).

The biodiversity of Pantanal has experienced strong climate disturbances in the past. Nonetheless, the expected raise in climate fluctuations will occur with unprecedented levels by human impacts (Úbeda et al. 2013). Typical examples are (1) eutrophication of rivers resulting in cyanobacteria blooms (Cózar et al. 2012), (2) conversion of natural vegetation into pastures for cattle grazing, (3) conversion of Cerrado vegetation into crop fields in the high plateau headwaters, (4) environmental contamination (eg. agricultural chemicals and mercury contamination by gold mining), (5) unregulated tourism, (6) introduction of exotic species and (7) infrastructure and unplanned human occupation (Alho 2011, Nunes da Cunha and Junk 2015). According to Prado and Gibbs (1993), Pennington et al. (2004), Caetano et al. (2008) and Linares-Palomino et al. (2009) Dry Forests occur in South America along an extensive arch named "Pleistocene Arc of Dry Formations", where Dry Forests expanded during the Late Pleistocene, followed by fragmentation in the Holocene. Its maximum extension occurred in the dry, cool period between 18,000 to 12,000 years ago.

The species *Anadenanthera colubrina*, *Myracrodruon urundeuva*, *Pterogyne nitens* Tul., *Combretum leprosum*, *Cereus peruvianus* (L.) Mill., *Combretum leprosum*, *Cordia glabrata* and *Maclura tinctoria* (L.) Engl. have been described as typical of the Pleistocene Arc of Dry Formations of South America (Prado and Gibbs 1993, Prado 2000). Accordingly, the presence of these species

can be interpreted as relics of a former wider xeric flora which remained in places where current local environmental conditions (microclimate, soils) were favourable to the their maintenance.

After the Late Pleistocene dry spells, the newly established trend of wetter conditions in the Holocene allowed elements coming from Cerrado and Pre-Amazon source to invade the former dry space. The Cerrado flora, present in the adjacent high tableland *(chapadas*, entered the Pantanal through the northeastern and eastern sectors of the depression, mainly along the the alluvial fan of Taquari river (Ab'Sáber 2006, Junk et al. 2006).

EFFECT OF FLOOD ON TREE PHYTOCENOSES IN PANTANAL AND FLOODPLAIN FORESTS IN THE AMAZON REGION

The number of tree species in Pantanal adapted to long periods of flood is much lower compared with the that observed for the Amazon floodplain. It is estimated that on Amazonian floodplains, there are more than 1,000 tree flood-resistant species. For the Pantanal, the estimates account for 355 species tolerating different degrees and intensities of flood (Junk et al. 2006).

Species richness and composition, structure (Ferreira 2000), total area, number and composition of species of canopy gap regenerations (Ferreira and Almeida 2005) and phenological events of tree species of lowland forests in Central Amazon (Ferreira and Parolin 2007) vary with flood suscetibility, where typical plant communities develop in response to their adaptation to flood.

Areas subjected to longer flood periods showed lower richness and diversity in function of selective pressure of adaptation to low oxygen in the rizosphere (Junk 1989). Reduction on species richness and diversity in function of increasing flood duration and intensity was also registered by Ferreira (2000) in flooded Forests in the Jaú and Tarumã-Mirim floodplains, although this author claimed that other factors, such as the distance of the study area from upland forest and class

diversity, might also contribute to the differences observed. Concerning the Pantanal, Arieira and Nunes da Cunha (2006) observed a negative correlation between flood height and species diversity in a Seasonally Flooded Semi Evergreen Forest (*Cambarazal*) on the floodplain of river Cuiabá, in Pantanal of Poconé.

The differences in distribution of dominant species in flooded forests is probably related to their ability to tolerate seasonal floods. However, the role the soil and topographical attributes on the distribution of plant species become significant, especially for less dominant species, locally rare or generalists (Ferreira 2000).

The coexistence of species with very contrasting environmental requirements in Pantanal is only possible because of the proximity of large adjacent phytogeographical spaces (*Chaco*, *Cerrado* and Amazonia). Due to a great geomorphological and soil diversity over short distances, the Pantanal landscape offers diverse habitats that, under varying flooding intensity/height, allows the establishment and survival of a peculiar flora.

We concluded that the moisture gradient is determining factor to explain floristic variations of plant communities. Hence, flood and soil water table oscillations are key environmental (abiotic) variables which define plant community patterns in Pantanal.

RESUMO

O objetivo deste estudo foi conhecer a localização preferencial de espécies da sinúsia arbórea em resposta ao gradiente de umidade no Pantanal Matogrossense, Brasil. Foram estabelecidas parcelas para amostragem da sinúsia arbórea ao longo dos gradiente de umidade do solo e de inundação. Piezômetros foram instalados permitindo medições mensais da profundidade do lençol freático e da altura da lâmina de inundação durante um ano. Análise de Correspondência Destendenciada, Análise Direta de Gradientes, Procedimento de Permutação Multi-resposta e Análise de Espécies Indicadoras foram realizadas para avaliar o efeito do gradiente de umidade sobre a distribuição das plantas. A oscilação do lençol freático é mais superficial e similar na Floresta Sazonalmente Inundada e nos Campos de Murundus, com acréscimo da profundidade no Cerrado no Cerradão e nas Florestas Secas. Cerca de 64% das espécies foram caracterizadas como de localização preferencial em "habitats terrestres normalmente não sujeitos a inundação", enquanto 8% ocorrem preferencialmente em "habitats inundáveis". A baixa riqueza de espécies arbóreas em tipos vegetacionais sujeitos a inundação está relacionada à alta sazonalidade climática atual e aos paleoclimas secos do Pleistoceno Superior no Pantanal. A composição de espécies arbóreas ao longo das diferentes formações no Pantanal apresenta uma relação direta com o gradiente de umidade no solo estudado.

Palavras-chave: composição florística, conceito de pulso de inundação, áreas úmidas, RPPN SESC Pantanal.

REFERENCES

AB'SÁBER AN. 2006. Brasil: paisagens de exceção. O litoral e o Pantanal Mato-Grossense, patrimônios básicos. São Paulo, Cotia: Ateliê Editorial, 182 p.

ALHO CJR. 2011. Biodiversity of the Pantanal: its magnitude, human occupation, environmental threats and challenges for conservation. Braz J Biol 71(1): 229-232.

AMORIM PK AND BATALHA MA. 2007. Soil-vegetation relationships in hyperseasonal cerrado, seasonal cerrado, and wet grassland in Emas National Park (Central Brazil). Acta Oecol 32: 319-327.

ARIEIRA JC AND NUNES DA CUNHA C. 2006. Fitossociologia de uma floresta inundável monodominante de *Vockysia divergens* Pohl (Vochysiaceae), no Pantanal Norte, MT, Brasil. Acta Bot Bras 20(3): 569-580.

BAILEY-SERRES J AND VOESENEK LACJ. 2008. Flooding Stress: Acclimations and Genetic Diversity. Annu Rev Plant Biol 59: 313-324.

CAETANO S, PRADO D, PENNINGTON RT, BECK S, OLIVEIRA-FILHO AT, SPICHIGER R AND NACIRI Y. 2008. The history of seasonally dry tropical forests in eastern South America: inferences from the genetic structure of the tree *Astronium urundeuva* (Anacardiaceae). Mole Ecol 17: 3147-3159

COCHRANE MA AND SCHULZE MD. 1999. Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass, and species composition. Biotropica 31: 2-16.

CÓZAR A, BRUNO M, BERGAMINO N, UBEDA B, BRACCHINI L, DATTILO AM AND LOISELLE SA. 2012. Basin-scale control on the phytoplankton biomass in Lake Victoria, Africa. PLoS ONE 7(1): e29962.

DUFRÊNE M AND LEGENDRE P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67: 345-366.

FAITH DP, MINCHIN PR AND BELBIN L. 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69: 57-68.

FELFILI JM, CARVALHO FA AND HAIDAR RF. 2005. Manual para o monitoramento de parcelas permanentes nos biomas Cerrado e Pantanal. Brasília: UNB, 54 p.

FERREIRA LV. 2000. Effects of flooding duration on species richness, floristic composition and forest structure in river margin habitat in Amazonian blackwater floodplain forests: implications for future design of protected areas. Biodivers Conserv 9: 1-14.

FERREIRA LV AND ALMEIDA SS. 2005. Relação entre a altura de inundação, riqueza específica de plantas e o tamanho de clareiras naturais em uma Floresta Inundável de Igapó, na Amazônia Central. Rev Árvore 29(3): 445-453.

FERREIRA LV AND LAURANCE WF. 1997. Effects of forest fragmentation on mortality and damage of selected trees in central Amazonia. Conserv Biol 11: 797-801.

FERREIRA LV AND PAROLIN P. 2007. Tree phenology in Central Amazonian Floodplain Forests: effects of water level fluctuation and precipitation at community and population level. Pesqui Bot 58: 139-156.

GAUCH-JR HG. 1991. Multivariate analysis in community ecology. Cambridge: Cambridge University Press, 298 p.

HASENACK H, CORDEIRO JLP AND HOFMANN GS. 2003. O clima da RPPN SESC Pantanal. Porto Alegre: Universidade Federal do Rio Grande do Sul, Instituto de Biociências e Centro de Ecologia, 31 p.

HILL MO AND GAUCH HG. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42: 47-58.

JUNK WJ. 1989. Flood tolerance and tree distribution in Central Amazonian floodplains. In: Nielsen LB and Balslev H (Eds), Tropical forests: botanical dynamics, speciation and diversity. London: Academic Press, p. 47-64.

JUNK WJ, BAYLEY PB AND SPARKS RE. 1989. The flood pulse concept in river-floodplain-systems. Can Spec Public Fish Aquat Sci 106: 110-127.

JUNK WJ, NUNES DA CUNHA C, WANTZEN KM, PETERMANN P, STRÜSSMANN C, MARQUES MI AND ADIS J. 2006. Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil. Aquat Sci 68: 278-309.

KLINGE H, JUNK WJ AND REVILLA CJ. 1990. Status and distribution of forested wetlands in tropical South America. Forest Ecol Manag 33/34: 81-101.

KOZLOWSKI TT. 2002. Physiological-ecological impacts of flooding on riparian forest ecosystems. Wetlands 22(3): 550-561.

KOZLOWSKI TT AND PALLARDY SG. 1997. Growth control in woody plants. San Diego: Academic Press, 632 p.

LINARES-PALOMINO R, OLIVEIRA-FILHO AT AND PENNINGTON RT. 2010. Neotropical seasonally dry forests: diversity, endemism and biogeography of woody plants. In: Dirzo R, Mooney H, Ceballos G and Young H (Eds), Seasonally Dry Tropical Forests: Biology and Conservation, Washington: Island Press, Washington, USA, p. 127-141.

LOURIVAL R, HARRIS M AND MONTAMBAULT JM. 2000. Introdução ao Pantanal, Mato Grosso do Sul, Brasil. In: Willink PW, Chernoff B, Leeanne EA, Jensen RM and Reinaldo L (Eds), A Biological Assement of the Aquatic Ecosystems of the Pantanal, Mato Grosso do Sul, Brasil. Rapid Assessment Program Bulletin of Biological Assement 18, Washigton, DC: Conservation International, Washington, USA, p. 147-151.

MIELKE JR PW, BERRY KJ AND BRIER GW. 1981. Application of Multi-Response Permutation Procedures for Examining Seasonal Changes in Monthly Mean Sea-Level Pressure Patterns. Mon Weather Rev 109: 120-126.

MONTEIRO JM, ALBUQUERQUE UP, LINS-NETO EMF, ARAÚJO EL, ALBUQUERQUE MM AND AMORIM ELC. 2006. The effects of seasonal climate changes in the Caatinga on tannin levels in *Myracrodruon urundeuva* (Engl.) Fr. All. and *Anadenanthera colubrina* (Vell.) Brenan. Rev Bras Farmacog 16: 338-344.

NUNES DA CUNHA C AND JUNK WJ. 1999. Composição florística de capões e cordilheiras: localização das espécies lenhosas quanto ao gradiente de inundação no Pantanal de Poconé, MT, Brasil. In: Anais do II Simpósio sobre recursos naturais e sócio-econômicos do Pantanal de Poconé, Mato Grosso, Brasil. Embrapa - CPAP, Corumbá, p. 387-406.

NUNES DA CUNHA C AND JUNK WJ. 2001. Distribution of woody plant communities along the flood gradient the Panatanal of Poconé, Mato Grosso, Brazil. Inter J Ecol Env Sci 27: 63-70.

NUNES DA CUNHA C AND JUNK WJ. 2011. Landscape units of the Pantanal: their structures, functions and human use. In: Junk WJ, da Silva CJ, Nunes da Cunha C and Wantzen KM (Eds), The Pantanal: Ecology, biodiversity and sustainable management of a large neotropical seasonal wetland. Sofia-Moscou: PENSOFT Publishers, Sofia-Moscou, Russia, p. 301-326.

NUNES DA CUNHA C AND JUNK WJ. 2015. A Classificação dos Macrohabitats do Pantanal Mato-grossense. In: Nunes da Cunha C, Fernandez MTP and Junk WJ (Eds), Classificação e Delineamento das Áreas Úmidas Brasileiras e de seus Macrohabitats. 1ª ed., Cuiabá: EdUFMT, p. 77-122.

PENNINGTON RT, LAVIN M, PRADO DE, PENDRY CA, PELL SK AND BUTTERWORTH CA. 2004. Historical climate change and speciation: neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. Philos T Roy Soc Biol Sci 359: 515-537.

PHILLIPS OL AND GENTRY AH. 1994. Increasing turnover through time in tropical forests. Science 263: 954-958.

POTT A, OLIVEIRA AKM, DAMASCENO-JUNIOR GA AND SILVA JSV. 2011. Plant diversity of the Pantanal wetland. Braz J Biol 71(1): 265-273.

PRADO DE. 2000. Seasonally dry forest of tropical South America; from forgotten ecosystems to a new phytogeographic unit. Edinburgh J Bot 57(3): 437-461.

PRADO DE AND GIBBS P. 1993. Patterns of species distributions in the dry seasonal forests of South America. Ann Missouri Bot Gard 80(4): 902-927.

SARMIENTO G, GOLDENSTEIN G AND MEINZER F. 1985. Adaptative strategies of woody species in neotropical savannas. Biol Rev 60: 315-355.

SIEBEL HN AND BLOM CWPM. 1998. Effects of irregular flooding on the establishment of tree species. Acta Bot Neerl 47: 231-240.

SILVA LMB AND BARBOSA DCA. 2000. Crescimento e sobrevivência de *Anadenanthera macrocarpa* (Benth.) Brenan (Leguminosae), em uma área de Caatinga, Alagoinha, PE. Acta Bot Bras 14(3): 251-261.

ÚBEDA B, DI GIACOMO AS, NEIFF JJ, LOISELLE SA, POI ASG, GÁLVEZ JA, CASCO S AND CÓZAR A. 2013. Potential effects of climate change on the water level, flora and macro-fauna of a large Neotropical Wetland. PLoS ONE 8(7): e67787.