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**Análise da vegetação em cerrado hiperestacional e
estacional no Brasil Central (Parque Nacional das
Emas, GO)**

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**Análise da vegetação em cerrado hiperestacional e
estacional no Brasil Central (Parque Nacional das
Emas, GO)**

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“As certezas que creio ter

Mantêm-me em pé

As incertezas que tenho e as que hão de vir

Mantêm-me a caminhar”

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Resumo

O Domínio do Cerrado é a segunda região fitogeográfica brasileira, originalmente cobrindo cerca de dois milhões de quilômetros quadrados, ou aproximadamente 23% do território brasileiro. O Parque Nacional das Emas (PNE) é uma das maiores e mais importantes reservas de Cerrado no Brasil e foi incluído na Lista dos Patrimônios Naturais da Humanidade por ser um dos sítios que contêm a flora, a fauna e os habitats-chave que caracterizam o Cerrado. No Domínio do Cerrado, como o nome implica, predomina a vegetação de cerrado, cuja maior parte das fisionomias se enquadra na definição de ‘savana’.

Savanas são formações vegetais em que o componente herbáceo-subarbusivo é quase contínuo, interrompido apenas por arbustos e árvores em densidades variáveis, e em que os principais padrões de crescimento estão fortemente associados às estações úmida e seca alternantes. As savanas, de acordo com sua estacionalidade, podem ser divididas em: savanas semi-estacionais, savanas estacionais, savanas hiperestacionais e esteros. Em fevereiro, maio, agosto e novembro de 2003, estudamos duas comunidades vegetais no Parque Nacional das Emas, em cerrado hiperestacional e em cerrado estacional, no que diz respeito à composição florística, riqueza, diversidade, densidade, área basal e volume cilíndrico.

Utilizando os dados florísticos de todas as coletas, encontramos 63 espécies, pertencentes a 18 famílias no cerrado hiperestacional e 107 espécies, pertencentes a 31 famílias no cerrado estacional. Em todas as estações a espécie dominante no cerrado hiperestacional foi a gramínea *Andropogon leucostachyus* e no cerrado estacional, a gramínea *Tristachya leiostachya*. Verificamos uma baixa similaridade florística entre os dois cerrados em todas as coletas, havendo maior variação na composição de espécies no cerrado hiperestacional ao longo do ano, em relação ao cerrado estacional.

A densidade de espécies foi sempre maior no cerrado estacional e apenas no cerrado hiperestacional encontramos estacionalidade para esse descritor. A densidade de plantas somente apresentou estacionalidade no cerrado hiperestacional, diferindo significativamente entre os tipos

vegetacionais apenas em fevereiro, quando o hiperestacional estava alagado. No cerrado hiperestacional, encontramos os maiores valores de volume cilíndrico durante toda estação chuvosa e, no cerrado estacional, apenas em novembro e fevereiro. Os menores valores foram encontrados na estação seca para ambos os cerrados. A diversidade foi sempre maior no cerrado estacional. Portanto, concluímos que a comunidade do cerrado hiperestacional é mais dinâmica – florística e estruturalmente – do que a comunidade do cerrado estacional.

Nossos resultados corroboraram a idéia de que mudanças em curto prazo nos determinantes das savanas, como, por exemplo, a umidade disponível para as plantas, afetam tanto a composição florística quanto a estrutura dessas comunidades.

Palavras-chave: cerrado, cerrado hiperestacional, diversidade, estacionalidade, florística, Parque Nacional das Emas, savana.

Abstract

The Cerrado Domain is the second most widespread phylogeographic region in Brazil, occupying formerly 23% of the Brazilian territory. The Emas National Park (ENP) is one of the largest and most important reserves in the cerrado region, and was included in the World Natural Heritage List as one of the sites containing fauna, flora, and key habitats that characterize the Cerrado. In the Cerrado Domain, as the name implies, the cerrado vegetation prevails, whose most physiognomies fit the definition of tropical savanna.

Savannas are tropical and subtropical formations in which the almost continuous grass layer is occasionally interrupted by trees and shrubs and the main growth patterns are closely associated with alternating wet and dry seasons. The savannas may be divided according to their seasonality into semi-seasonal, seasonal, hyperseasonal, and marshy savannas. In February, May, August and November 2003, we studied two plant communities in ENP, in hyperseasonal and seasonal cerrados, concerning their floristic compositions, richness, diversity, density, basal area, and cylindrical volume.

Using floristic data from all field trips, we found 63 species and 18 families in the hyperseasonal cerrado and 107 species and 31 families in the seasonal cerrado. In the hyperseasonal cerrado, at all seasons, the dominant species was the grass *Andropogon leucostachyus*, and, in seasonal cerrado, the grass *Tristachya leiostachya*. We found low floristic similarity between the hyperseasonal and seasonal cerrados in all seasons, with more pronounced floristic seasonal changes in the hyperseasonal cerrado.

Species density was always higher in the seasonal cerrado, and we found seasonal changes only in the hyperseasonal cerrado. Plant density changed seasonally only in the hyperseasonal cerrado and was significantly different between the vegetation forms only at mid rainy season. In the hyperseasonal cerrado, we found the highest values of cylindrical volume throughout the rainy season and, in the seasonal cerrado, only at mid and late rainy seasons. The lowest values were found at dry season in both cerrados. Diversity was higher in the seasonal cerrado than in the

hyperseasonal one at all seasons. In general, the hyperseasonal cerrado was more dynamic – in terms of floristic and structural changes – than the seasonal cerrado.

Our results corroborated the idea that changes in the short-term determinants of savannas, as, for example, plant available moisture, will affect their floristic composition and community structure.

Key-words: cerrado, diversity, Emas National Park, floristics, hyperseasonal cerrado, savanna, seasonality.

I – Introdução geral

Introdução geral

Savanas são formações tropicais e subtropicais em que o componente herbáceo-subarbusitivo é quase contínuo, interrompido apenas por arbustos e árvores em densidades variáveis, em que o fogo é um evento freqüente e em que os principais padrões de crescimento estão fortemente associados às estações úmida e seca alternantes (Bourlière & Hadley 1983). A estacionalidade representa uma das características fundamentais para se definir uma savana, quer quando se considere as mudanças ambientais cíclicas ao longo do ano, quer quando se considere os ritmos biológicos das espécies vegetais que acompanham essas flutuações externas (Sarmiento 1983).

Sarmiento (1983) propôs uma classificação ecológica das savanas, em que elas são divididas em quatro grupos de acordo com sua estacionalidade: *a)* savanas semi-estacionais, sob clima na maior parte do tempo úmido, com uma ou duas pequenas estações secas. Essas savanas aparecem geralmente como manchas em regiões de floresta pluvial, tais como as manchas de savana no Domínio Amazônico; *b)* savanas estacionais, em que uma estação sem chuvas maior faz com que o fogo e a seca definam a ritmicidade do seu funcionamento. Esse é o tipo mais comum de savana na América tropical, incluindo a maior parte das duas maiores regiões savânicas sul-americanas, os lhanos e o cerrado; *c)* savanas hiperestacionais, em que há alternância de dois estresses contrastantes durante o ciclo anual, um induzido pela seca e fogo e outro induzido pela saturação hídrica do solo; tais savanas aparecem normalmente em locais cuja drenagem é muito baixa ou lenta, como no Pantanal e em parte dos lhanos bolivianos e venezuelanos; e *d)* esteros, em que o período de excedente hídrico persiste pela maior parte do ano.

O cerrado é a maior região de savana nas Américas, ocupando originalmente cerca de dois milhões de quilômetros quadrados, ou aproximadamente 23% do território brasileiro (Ratter *et al.* 1997) e mais de 90% do Planalto Central Brasileiro (Rizzini 1997). O clima normalmente é estacional, com verão chuvoso e inverno seco, podendo ser classificado como Am, Aw ou Cwa, de acordo com o sistema de Köppen (1948), ou ZBII, segundo o sistema de Walter (1986).

Como mencionado anteriormente, o cerrado normalmente se enquadra como uma savana estacional, de acordo com a divisão ecológica de Sarmiento (1983), devido à estacionalidade climática. As savanas hiperestacionais e os esteros são bastante restritos dentro da região do cerrado (Sarmiento 1983). Ademais, aquilo que Sarmiento (1983) citou como exemplo de savana hiperestacional dentro da região de cerrado, “uma faixa estreita separando o cerrado de terras mais altas da floresta ripícola”, é, na verdade, o campo úmido, cuja flora é diferente daquela do cerrado.

O Parque Nacional das Emas (PNE) localiza-se na área nuclear do cerrado e é uma das maiores e mais importantes reservas dentre aquelas que representam o cerrado, com cerca de 133.000 ha. O PNE foi incluído pela Unesco (2001) na lista dos Patrimônios Naturais da Humanidade, como um dos sítios que contêm a flora, a fauna e os hábitats-chave que caracterizam o cerrado. Recentemente, relatamos a primeira ocorrência de um cerrado hiperestacional (Batalha et al. no prelo), localizado na porção sudoeste do PNE, com aproximadamente 300 ha, evidenciando ainda mais a importância do PNE para a conservação da biodiversidade do cerrado.

Uma área de cerrado hiperestacional, como aquela que estudamos neste trabalho, forneceu uma situação propícia para o estudo dos fatores que determinam a ecologia do cerrado. Como, na área de estudo (Fig. 1), encontramos além do cerrado hiperestacional (Fig. 2), o cerrado estacional (Fig. 3), foi possível analisar e comparar florística e funcionalmente duas áreas de cerrado, uma com um único período de estresse e outra com dois períodos de estresse. Em todos os momentos deste trabalho, procuramos levar em conta três idéias principais: *i*) a comunidade vegetal nas savanas é dinâmica (Hopkins 1983); *ii*) os ritmos biológicos das espécies vegetais de savana acompanham a estacionalidade climática (Sarmiento 1983); e *iii*) no cerrado hiperestacional, as plantas do componente herbáceo estão sujeitas a dois tipos de estresse contrastantes – a seca e o alagamento – enquanto que, no cerrado estacional, o único momento de estresse é a seca (Sarmiento 1992).

O primeiro capítulo traz os dados vegetacionais do cerrado hiperestacional para quatro

estações do ano, analisando a variação temporal de alguns descritores da comunidade. Neste capítulo, procuramos responder à seguinte pergunta: *i*) a densidade de espécies, densidade de plantas, área basal, volume cilíndrico e a diversidade variaram ao longo do ano no cerrado hiperestacional?

No segundo capítulo, nosso interesse também foi a variação temporal da comunidade ao longo do ano, mas analisando o cerrado hiperestacional e o cerrado estacional ao mesmo tempo. Neste capítulo, estávamos interessados também na composição e variação florística ao longo do ano em ambos os cerrados. Testamos o postulado, proposto por Silva (1996), de que, frente a uma perturbação, a estabilidade relativa de uma comunidade depende da sua composição florística. Como o cerrado hiperestacional passa por dois estresses – seca e alagamento – esperamos que nele houvesse uma maior variação florística ao longo do ano em relação ao cerrado estacional. Assim, procuramos responder às seguintes perguntas: *i*) a composição florística variou ao longo do ano nos cerrados hiperestacional e estacional?; *ii*) a similaridade florística entre os cerrados hiperestacional e estacional foi menor quando aquele está alagado?; *iii*) a densidade de espécies, densidade de plantas, volume cilíndrico e diversidade variaram ao longo do ano no cerrado hiperestacional?; e *iv*) estes padrões foram similares aos encontrados em uma área de cerrado estacional próxima?

Escolhemos apresentar a dissertação em capítulos, que formatamos de acordo com as normas das revistas científicas a que foram submetidos. Como as revistas que escolhemos para publicá-los exigem a sua redação em inglês, nossos capítulos foram escritos nesse idioma. O primeiro capítulo foi enviado ao periódico “Flora” e será publicado no quarto número do volume 200, enquanto que o segundo foi enviado ao periódico “Plant Ecology”. A divisão em capítulos se justifica, pois torna a publicação dos artigos científicos menos trabalhosa, embora, devido à independência de um capítulo em relação aos demais, repetições tornem-se inevitáveis.

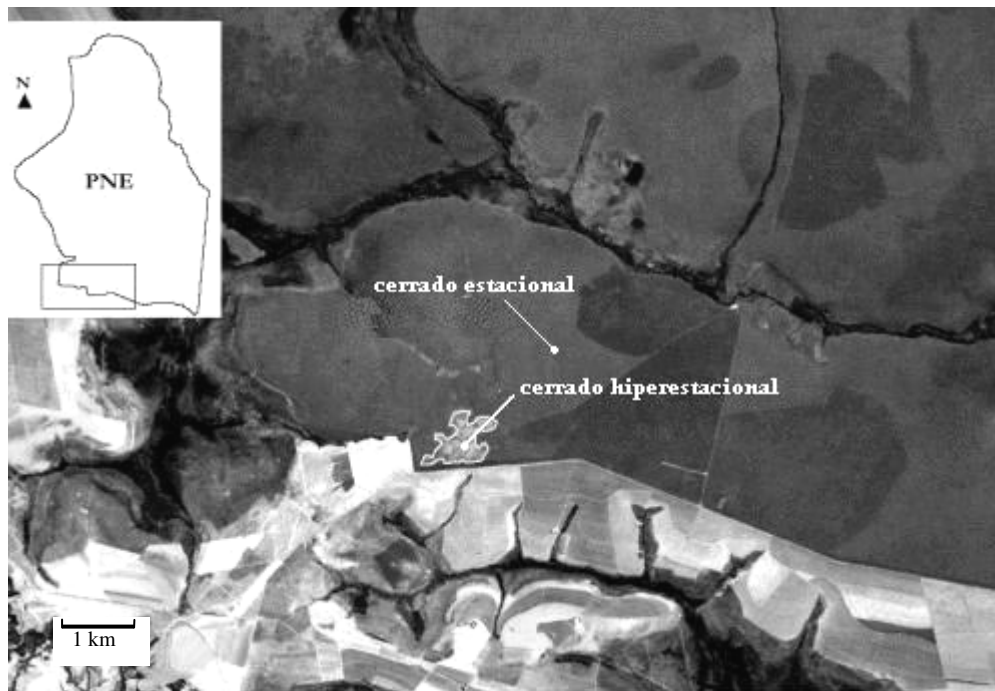


Figura 1 – Localização da área de estudo, mostrando o sudoeste do Parque Nacional das Emas (GO) e ressaltando a área coberta pelo cerrado hiperestacional.



Figura 2 – Cerrado hiperestacional no Parque Nacional das Emas (GO) em fevereiro de 2003, ressaltando o alagamento e o predomínio de *Andropogon leucostachyus*. (Foto: M.A. Batalha)



Figura 3 – Cerrado estacional no Parque Nacional das Emas (GO) em fevereiro de 2003, ressaltando o predomínio de *Tristachya leiostachya*. (Foto: M.A. Batalha)

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II - Capítulo 1

"Crê nos que buscamos a verdade. Duvida dos que a encontraram "

(André Gide)

Variação estacional de um cerrado hiperestacional no Parque Nacional das Emas, Goiás¹

¹ Trabalho aceito pelo periódico *Flora* com o título “Seasonal variation of a hyperseasonal cerrado in Emas National Park, central Brazil”.

Seasonal variation of a hyperseasonal cerrado in Emas National Park, central Brazil

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Summary

Hyperseasonal savannas are characterized by the alternation of two contrasting stresses during each annual cycle, one induced by drought and fire and the other, by waterlogging. In South America, the largest savanna region is the Brazilian cerrado, in which there are few hyperseasonal areas. Our aim was to study temporal changes in some community descriptors, such as species density, plant density, basal area, cylindrical volume, diversity, and evenness, in a hyperseasonal cerrado at four different seasons in the year. We placed randomly ten 1 m² quadrats in a 1-ha area, in which we sampled all vascular plants. We used one-way analyses of variance to test for differences among the seasons. We found in all seasons high cover values of the caespitose grass *Andropogon leucostachyus* Kunth, which is the dominant species in the hyperseasonal cerrado. Waterlogging caused a decrease in species density, diversity, and plant density, but not in evenness, basal area, and cylindrical volume. The low values of species and plant densities in the waterlogging period may indicate the non-adaptation of most cerrado species to waterlogged conditions. The many savanna plant responses to environmental perturbations may explain the persistence of savanna communities within a broad range of environmental variation. Waterlogging may act as an environmental filter, restricting the number of cerrado species able to stand that condition.

Key words: cerrado, diversity, Emas National Park, hyperseasonal cerrado, savanna, species density

Introduction

Savannas are tropical and subtropical formations in which the almost continuous grass layer is occasionally interrupted by trees and shrubs, fire is frequent, and the main growth patterns are closely associated with alternating wet and dry seasons (BOURLIÈRE & HADLEY 1983). They are dynamic communities, which vary in space and time, and where long- and short-term changes are constantly modifying its physiognomy, composition, and ecological processes (HOPKINS 1983).

Usually, savannas have been classified following only a structural and physiognomic approach, based on height, canopy cover, and arrangement of woody elements (e.g., EITEN 1979, COUTINHO 1990, RIBEIRO & WALTER 1998). Nevertheless, seasonality represents one of the most essential features to define a savanna, whether the cyclic changes in the environment during the year are considered or the biological rhythms of plant species that accompany those external fluctuations (SARMIENTO 1983a).

SARMIENTO (1984) proposed an ecological classification of savannas, in which he divided them into four major classes according to the seasonality: a) semi-seasonal savannas, which occur under a mostly wet climate, with one or two short dry seasons; b) seasonal savannas, with a season with sufficient moisture in the upper soil layers – but without waterlogging – alternating with another season with marked soil water deficit; c) hyperseasonal savannas, with two contrasting stresses, one induced by drought and fire and other, by waterlogging; and d) marshy savannas, in which the water excess period lasts for the whole year.

The cerrado is by far the largest savanna region in South America, occupying an area of approximately 2 millions km² of the Brazilian territory (RATTER et al. 1997), especially in the Central Plateau. The climate is seasonal, with wet summer and dry winter, classified as Aw or Cwa following KÖPPEN's (1931) system. Hyperseasonal savannas normally occur on poorly drained bottomlands or depressed regions with slow and ill-defined drainage, especially in the Bolivian and Venezuelan llanos, being very restricted in the cerrado region, which is basically

seasonal (SARMIENTO 1983a). BATALHA et al. (in press) related the first occurrence of a hyperseasonal cerrado in Emas National Park (ENP), central Brazil.

Hyperseasonal savannas shows a reinforced seasonality in which four contrasting seasons follow each other throughout the year: one extended dry season, then a short period when soil water ranges between the permanent wilting point and field capacity, then a long season when the soil remains saturated that include a period of waterlogging or flooding, and finally another short period when the soil is neither dry nor water-saturated, that will be followed by the dry season in a new, iterative annual cycle (SARMIENTO 1984). Hence, in a hyperseasonal cerrado, herbaceous plants are subjected to two contrasting types of stress: drought and waterlogging (SARMIENTO 1992).

Drought results from restricted water supply and high evaporation rate, typical of tropical savannas during dry season (BARUCH 1994). Water retention capacity of savanna soils decreases on the superficial soil layers during this season (SARMIENTO & ACEVEDO 1991, SARMIENTO 1996a), reaching, for example, values lower than permanent wilting point of crop plants (FRANCO et al. 1996). Thus, drought represents one marked stressing moment to cerrado plants for it drastically affects the herbaceous vegetation with superficial roots (SARMIENTO 1996a).

In a hyperseasonal cerrado, the plants experience a second stressing moment, caused by waterlogging at the rainy season. The waterlogging is due to the soil saturation by rainfall, generally associated with impermeable and poorly structured clay horizons (SARMIENTO & MONASTERIO 1975). Waterlogging drastically reduces oxygen diffusion into the soil causing hypoxia, which is the main limitation that reduces root aerobic respiration and the absorption of nutrients and water. In intolerant plants, ethanol and acetaldehyde, products of anaerobic respiration, may damage the general metabolism (JACKSON & DREW 1984).

BATALHA et al. (in press) sampled the hyperseasonal and seasonal cerrados in ENP, at mid rainy season, when the former was waterlogged, and found values of species density and

diversity of 18 species and 1.92 nats ind⁻¹ in the hyperseasonal cerrado and 54 species and 3.16 nats ind⁻¹ in the seasonal cerrado. So, as a consequence of these two contrasting stresses, the hyperseasonal cerrado in ENP is an impoverished form of cerrado, with fewer species and lower diversity than seasonal cerrado communities. But how does the plant community vary throughout the year in the hyperseasonal cerrado?

Our aim here was to study temporal changes in some community descriptors, such as species density, plant density, basal area, cylindrical volume, and diversity in a hyperseasonal cerrado throughout the year, taking into account three main ideas: a) savanna plant communities are dynamic (HOPKINS 1983); b) the biological rhythms of savanna plant species accompany the climatic seasonality (SARMIENTO 1984); and c) in hyperseasonal savannas, herbaceous plants are subjected to two contrasting forms of stress, drought and waterlogging (SARMIENTO 1992). We tried to answer the following question: do species density, plant density, basal area, cylindrical volume, and diversity vary throughout the year in the hyperseasonal cerrado?

Material and Methods

The Emas National Park (ENP) is located in the Brazilian Central Plateau, southwestern Goiás State (17°49'-18°28'S and 52°39'-53°10'W), in the cerrado core region, and is one of the largest and most important reserves in the cerrado region, with ca. 133.000 ha. Recently, ENP was included by UNESCO (2001) in the World Natural Heritage List as one of the sites containing fauna, flora, and key habitats that characterize the cerrado. Regional climate is tropical and humid, with wet summer and dry winter, classified as Aw following Köppen (1931). The dry season goes from June to August and the wet season, from September to May (Figure 1). Annual rainfall and mean temperature lie around 1,745 mm and 24.6°C, respectively. The cerrado in ENP comprises almost all physiognomies found in this vegetation type, from *campo limpo* (a grassland) to *cerrado sensu stricto* (a woodland). In the reserve, the cerrado vegetation prevails, covering 93.2% of the total area (RAMOS-NETO & PIVELLO 2000). In the southwestern part of the reserve, there is a 300 ha area covered by a hyperseasonal cerrado (BATALHA et al. in press). Physiognomically, the hyperseasonal cerrado in PNE is a grassland, but it remains waterlogged at middle of the rainy season (from February to April), whereas in the dry season (from June to August), there is a water shortage in the upper soil layers.

We carried out four surveys: in February 2003, at mid rainy season, when the hyperseasonal cerrado was waterlogged; in May 2003, at late rainy season; in August 2003, at dry season; and in November 2003, at early rainy season. We established a 1 ha area (approximately, 18°18'S and 52°57'W), and, in each field trip, we placed randomly ten 1 m² quadrats, in which we sampled all vascular plants except seedlings. We measured height and diameter of each individual at soil level, and counted the number of individuals belonging to each species. In the case of cespitose grasses, we considered as an individual the whole tuft. We identified the species by comparing the collected material to lodged vouchers, mainly the ENP's reference material collected by BATALHA & MARTINS (2002), but also vouchers lodged at São Paulo State Botanical Institute and Brazilian Institute of Geography and Statistics herbaria. When identification at species level was not possible, we or taxonomists classified them as morphospecies. We lodged the collected material at the Federal University of São Carlos herbarium.

We analyzed the following variables: species density, plant density, basal area, cylindrical volume, and diversity. We defined species density as the number of species per area (spp m⁻²); plant density as the number of individuals per area (ind m⁻²); basal area as the area covered by each species (m² m⁻²); and cylindrical volume as the volume occupied by each species (m³ m⁻²), according to MUELLER-DOMBOIS & ELLENBERG (1974). We tested all these variables for normality (SHAPIRO & WILK 1965) and homocedasticity (HARTLEY 1950). When necessary, we log-transformed our data. We used one-way analyses of variance and Tukey multiple comparison test (ZAR 1999) to test for significant differences ($\alpha = 0.05$) among the seasons. We also calculated the power of the test (ZAR 1999) to estimate the probability of committing type II error. We estimated diversity with Shannon index (SHANNON & WEAVER 1949), using the natural logarithmic base, and employed Hutcheson's test (ZAR 1999) to compare diversity index values between all possible pairs. We also calculated evenness (PIELOU 1975), floristic similarity among the seasons with Sørensen index (Magurran 1996), and species cover value (MUELLER-DOMBOIS & ELLENBERG 1974) with the formula: $CV_i = (RD_i + RDo_i)/2$, in which CV is the cover value, RD is the relative density, RDo is the relative dominance, and i is the i th species.

Results

In February, at mid rainy season, when the hyperseasonal cerrado was waterlogged, we sampled 272 individuals and 18 species (Table 1); in May, at late rainy season, we sampled 771 individuals and 32 species (Table 2); in August, at dry season, we sampled 677 individuals and 26 species (Table 3); and in November, at early rainy season, we sampled 834 individuals and 37 species (Table 4). The floristic similarity indices varied from 0.364 (between February and November) to 0.586 (between May and August). The grass *Andropogon leucostachyus* Kunth presented the highest species cover values throughout the

year, with values ranging from 54.10% in early rainy season (November) to 75.63% in dry season (August).

As long as species density, plant density, and cylindrical volume were not normally distributed, we log-transformed them prior to the analyses. We found significant differences among the seasons for species density, lower at mid rainy season, when the hyperseasonal cerrado was waterlogged, and higher at early rainy season (Table 5). Diversity was lower at the dry season, higher at early rainy season, and intermediate at mid and late rainy seasons (Table 5). Evenness was higher at early and mid rainy seasons (Table 5). We found a significant difference for plant density only between early and mid rainy seasons, lower in the latter (Table 5). Both basal area and cylindrical volume were higher at mid and late rainy seasons and lower at dry season (Table 5). For species density, basal area, and cylindrical volume, the ten quadrats we placed were sufficient to give us a power of 100%; whereas, for plant density, they gave us a power of 74% (Table 5).

Discussion

Even if usually cerrado species occur only in well-drained soils (RATTER et al. 1997), the species found in the hyperseasonal cerrado are typical cerrado species (BATALHA & MARTINS 2002, BATALHA et al. in press). One of the crucial ecological limitations for the growth of savanna plants is the soil water availability (SARMIENTO 1996a). Savanna plant communities primarily respond to plant-available moisture (PAM) regime (MEDINA AND SILVA 1990, SOLBRIG 1991, TEAGUE & SMIT 1992), which varies both spatially, in depth, and temporally, as a result of seasonal rainfall (SARMIENTO 1996a).

The hyperseasonal cerrado in ENP is physiognomically a savanna grassland, without trees and with few scattered shrubs (BATALHA et al. in press). In hyperseasonal savannas, woody species cannot successfully compete with herbs, since most trees are unable to survive alternating periods of soil water saturation and soil drought (SARMIENTO & MONASTERIO

1975). Graminoids species, with an intensive root system, exploit the upper soil layers and strictly follow a growth cycle associated with seasonality of rainfall, whereas trees, with extensive, less efficient root systems, are able to exploit both water and nutrients from deeper soil layers (MEDINA & SILVA 1990).

Short-term changes and period pulsation of plant-available moisture and plant-available nutrients may alter species composition and diversity (SARMIENTO 1996a), since individuals from different species react differently to changes in their environment and affect survival and fertility at population level (SILVA 1996). In the hyperseasonal cerrado, we found the lowest floristic similarity between early and mid rainy seasons and the highest floristic similarity between late rainy and dry seasons. Thus, waterlogging seems to be a more restrictive stressing factor for the hyperseasonal cerrado plant species, since the alteration of floristic composition was higher after waterlogging than after drought.

In highly stressed communities, resource availability limits the number of co-occurring species with similar ecological requirements; therefore, only those species highly adapted to the stressing factor survive (BARUCH et al. 1996). Dominance spectra in the grassland layer of tropical savannas show frequently a high degree of dominance by a few grass species (SARMIENTO 1983a). Although this is rarely observed in cerrado herbaceous communities (FILGUEIRAS 2002), there are some exceptions, like the dominance of *Tristachya leiostachya* Nees in ENP's seasonal cerrado grassland physiognomies (FILGUEIRAS 2002), probably due to frequent fires that burn large portions of the reserve (RAMOS-NETO & PIVELLO 2000).

We found in all seasons high cover values of the cespitose grass *Andropogon leucostachyus*, which is the dominant species in the hyperseasonal cerrado. Thus, in ENP, not only the seasonal cerrado grasslands are monodominant, but the hyperseasonal cerrado as well. The genus *Andropogon* also prevails in hyperseasonal savannas from Colombian and Venezuelan llanos (BLYDENSTEIN 1967, SARMIENTO 1996b). As a matter of fact, A.

leucostachyus is also the most frequent species in a Colombian hyperseasonal savanna (RIPPSTEIN et al. 2001).

In hyperseasonal savannas, a PAM-limited dry season alternates with a rainy season during which soil is saturated and waterlogged. Consequently, plants experience anoxic soil conditions derived from excess of water that induce not only functional stresses but also a high mortality of fine roots (JOLY 1991). In ENP, waterlogging caused a decrease in species density, diversity, and plant density, but not in evenness, basal area, and cylindrical volume. SILVA & SARMIENTO (1976) found the maximum richness in savanna plant communities under soils free from waterlogging but with a long PAM season, concluding that maximum diversity corresponds to lowest water stress. Similar results were found in a more extensive study on a wide range of Venezuelan seasonal savannas (SARMIENTO 1983b).

Species richness also peaks towards the more mesic conditions and decreases towards both extremes: dry soils and wet, seasonally saturated soils (SARMIENTO 1983b). SARMIENTO et al. (2004) found a drastical reduction on richness in a year of exceptional waterlogging in a Venezuelan hyperseasonal savanna. Indeed, we found lower values of species density under waterlogging (February) and drought (August), and higher values under mesic conditions of PAM (May and November). Plant density responded in a similar way, with the lowest value in waterlogged soil conditions and the highest one at early rainy season.

In a hyperseasonal savanna in Venezuela, SARMIENTO et al. (2004), also using ten 1-m² quadrats per site, observed that species density at the rainy season was around 22 species per square meter, almost twice more species than found by us in the hyperseasonal cerrado. The low values of species and plant densities in the waterlogging period may indicate the non-adaptation of most cerrado species to waterlogged conditions. Waterlogging may act as an environmental filter (CHASE 2003), restricting the number of cerrado species able to stand that condition.

Diversity values found in seasonal cerrado plant communities may range from 2.5 to 3.6 nats ind⁻¹ (MANTOVANI 1996). SARMIENTO et al. (2004) found values ranging from 2.44 to 3.26 nats ind⁻¹ in Venezuelan hyperseasonal savannas. In ENP's hyperseasonal cerrado, in all seasons, the diversity values were lower than the lowest limit for seasonal cerrados (MANTOVANI 1996) and hyperseasonal savannas (SARMIENTO et al. 2004), as a consequence of the low number of species and the dominance of *A. leucostachyus*. We found the lowest diversity value in August, at the dry season, when the dominance of *A. leucostachyus* was higher and evenness, lower.

After a disturbance, the successional sequence of changing composition and structure begins with a growing phase with net increase in the number of individuals and basal area (HALLÉ et al. 1978). This phase is followed by a homeostatic phase with accumulation of basal area due to growth, but in which mortality and recruitment are balanced (HALLÉ et al. 1978). Development of seasonal herbaceous communities reaches its biomass peak at the end of the rainy season (SARMIENTO 1984), which is related with the soil PAM (SARMIENTO 1983a, SARMIENTO et al. 2004). Despite the waterlogging at mid rainy season, the hyperseasonal cerrado reached its biomass peak at late rainy season as well.

Plant growth is severely limited by drought, which results from restricted water supply and high evaporation rate, typical of tropical savannas during dry season (BARUCH 1994). Drought causes water deficit in the plant that affects its metabolism and morphology, reduces its growth and arrests its development (BARUCH 1994). In a hyperseasonal savanna, the behaviour of grasses during the dry season reflects these facts, since the daily minimum leaf water potential in grass species reaches values as low as -2.8 to -3.7 MPa, a hard enough stress to transform the above-ground biomass to dry straw (SARMIENTO et al. 2004). We found the lowest basal area and cylindrical volume values in August, at the dry season, reflecting the consequences of drought upon community structure. Death of shoots due to drought reduced

soil cover, reflected by lower basal area values, and, consequently, plant volume, reflected by lower cylindrical volume values.

The many savanna plant responses to environmental perturbations may explain the persistence of savanna communities within a broad range of environmental variation (SILVA 1996). Current knowledge suggests that savanna persists under seasonal climates, fluctuating with certain bounds as the result of the occurrence of climatic disturbances and its concatenated effects on fire, grazing, and other factors (SILVA 1996). In a hyperseasonal cerrado, the two stressing moments, drought and waterlogging, determine the community structure.

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Table 1. Number of individuals, basal area (m²), and cover value (%) for the species sampled at mid rainy season (February 2003) in the hyperseasonal cerrado, Emas National Park (approximately, 18°18'07"S and 52°57'56"W), Goiás, central Brazil.

species	individuals	basal area	cover value
<i>Andropogon leucostachyus</i> Kunth	122	0.9107	71.49
<i>Eugenia complicata</i> O. Berg	50	0.0004	9.21
<i>Psidium australe</i> Camb.	23	0.0001	4.24
<i>Andira laurifolia</i> Benth.	16	0.0001	2.95
<i>Panicum parvifolium</i> Lam.	9	0.0131	2.36
<i>Acosmium subelegans</i> (Mohl.) Yakovlev	11	0.0004	2.04
<i>Panicum rudgei</i> Roem. & Schult.	7	0.0011	1.34
<i>Galactia martii</i> A. DC.	6	< 0.0001	1.10
<i>Brachiaria decumbens</i> Stapf	5	0.0003	0.94
<i>Tonateleia micrantha</i> (Mart.) A. C. Smith	5	< 0.0001	0.92
<i>Byttneria oblongata</i> Pohl	4	< 0.0001	0.74
<i>Ocimum</i> sp.	4	< 0.0001	0.74
<i>Allagoptera campestris</i> (Mart.) Kuntze	3	0.0009	0.60
<i>Erechtites hieracifolia</i> (L.) Raf. ex A. DC.	2	< 0.0001	0.37
<i>Myrcia rhodosepala</i> Kiaersk.	2	< 0.0001	0.37
<i>Sisyrinchium vaginatum</i> Spreng.	1	0.0011	0.25
<i>Eugenia livida</i> O. Berg	1	< 0.0001	0.18
<i>Myrcia uberavensis</i> O. Berg	1	< 0.0001	0.18
Total	272	0.9284	100.00

Table 2. Number of individuals, basal area (m²), and cover value (%) for the species sampled at late rainy season (May 2003) in the hyperseasonal cerrado, Emas National Park (approximately, 18°18'07"S and 52°57'56"W), Goiás, central Brazil.

species	individuals	basal area	cover value
<i>Andropogon leucostachyus</i> Kunth	421	0.8193	63.08
<i>Hyparrhenia rufa</i> Stapf	1	0.1451	6.40
<i>Myrciaria delicatula</i> (A. DC.) O. Berg	69	0.0001	4.48
<i>Panicum rudgei</i> Roem. & Schult.	28	0.0421	3.65
<i>Paspalum pectinatum</i> Nees	4	0.0655	3.12
<i>Loudetiopsis chrysothrix</i> (Nees) Conert	17	0.0371	2.72
<i>Andira laurifolia</i> Benth.	41	0.0012	2.71
<i>Eugenia calycina</i> Cambess.	33	0.0013	2.20
<i>Acosmium subelegans</i> (Mohl.) Yakovlev	28	0.0031	1.95
<i>Hyptis adpressa</i> A. St-Hil. ex Benth.	28	0.0001	1.82
<i>Panicum parvifolium</i> Lam.	15	0.0065	1.26
<i>Galactia dimorpha</i> Burk.	13	0.0002	0.85
<i>Andropogon bicornis</i> L.	8	0.0065	0.80
<i>Syagrus flexuosa</i> (Mart.) Becc.	6	0.0071	0.70
<i>Galactia martii</i> A. DC.	9	< 0.0001	0.59
<i>Eugenia angustissima</i> O. Berg	9	< 0.0001	0.58
<i>Allagoptera campestris</i> (Mart.) Kuntze	6	0.0009	0.52
<i>Melinis minutiflora</i> P. Beauv.	7	0.0002	0.46
<i>Sisyrinchium vaginatum</i> Spreng.	1	0.0062	0.34
<i>Byttneria oblongata</i> Pohl	5	0.0002	0.33
<i>Chromolaena squalida</i> (A. DC.) King & H. Rob.	5	< 0.0001	0.32
<i>Axonopus derbyanus</i> Black	4	< 0.0001	0.26
<i>Eugenia cristaensis</i> O. Berg	3	< 0.0001	0.20
<i>Cuphea</i> sp.	2	< 0.0001	0.13
<i>Brachiaria decumbens</i> Stapf	1	0.0003	0.08
<i>Ichnanthus procurrens</i> (Nees) Sw.	1	< 0.0001	0.07
<i>Paspalum geminiflorum</i> Steud.	1	< 0.0001	0.07
<i>Eragrostis articulata</i> (Schrank) Nees	1	< 0.0001	0.07
<i>Eriope crassipes</i> Benth.	1	< 0.0001	0.07
<i>Myrcia rhodosepala</i> Kiaersk.	1	< 0.0001	0.07
<i>Emilia coccinea</i> (Sims.) Sweet	1	< 0.0001	0.06
<i>Erechtites hieracifolia</i> (L.) Raf. ex A. DC.	1	< 0.0001	0.06
Total	771	1.1452	100.00

Table 3. Number of individuals, basal area (m²), and cover value (%) for the species sampled at dry season (August 2003) in the hyperseasonal cerrado, Emas National Park (approximately, 18°18'07"S and 52°57'56"W), Goiás, central Brazil

species	individuals	basal area	cover value (%)
<i>Andropogon leucostachyus</i> Kunth	477	0.1939	75.63
<i>Loudetiopsis chrysothrix</i> (Nees) Conert	47	0.0307	9.87
<i>Eugenia calycina</i> Cambess.	48	0.0011	3.77
<i>Panicum rudgei</i> Roem. & Schult.	20	0.0020	1.90
<i>Schizachyrium condensatum</i> (Kunth) Nees	5	0.0071	1.84
Asteraceae sp. 1	13	< 0.0001	0.96
<i>Syagrus flexuosa</i> (Mart.) Becc.	4	0.0022	0.76
<i>Panicum parvifolium</i> Lam.	7	0.0005	0.63
<i>Acosmium subelegans</i> (Mohl.) Yakovlev	7	0.0005	0.62
Poaceae sp. 1	5	0.0010	0.58
<i>Gymnopogon foliosus</i> (Willd.) Nees	7	< 0.0001	0.52
<i>Psidium australe</i> Camb.	6	< 0.0001	0.45
<i>Allagoptera campestris</i> (Mart.) Kuntze	3	0.0010	0.43
<i>Myrcia rhodeosepala</i> Kiaersk.	5	< 0.0001	0.37
<i>Galactia martii</i> A. DC.	4	< 0.0001	0.30
<i>Eugenia angustissima</i> O. Berg	4	< 0.0001	0.30
<i>Brachiaria decumbens</i> Stapf	2	0.0001	0.17
<i>Diospyros hispida</i> A. DC.	2	< 0.0001	0.16
<i>Byttneria oblongata</i> Pohl	2	< 0.0001	0.15
<i>Melinis minutiflora</i> P. Beauv.	2	< 0.0001	0.15
Myrtaceae sp. 1	2	< 0.0001	0.15
<i>Ichnanthus procurrens</i> (Nees) Sw.	1	0.0001	0.09
Poaceae sp. 2	1	< 0.0001	0.08
<i>Sisyinchium vaginatum</i> Spreng.	1	< 0.0001	0.08
<i>Scoparia dulcis</i> L.	1	< 0.0001	0.07
<i>Myrciaria delicatula</i> (DC.) O. Berg.	1	< 0.0001	0.07
Total	677	0.2416	100.00

Table 4. Number of individuals, basal area (m²), and cover value (%) for the species sampled at early rainy season (November 2003) in the hyperseasonal cerrado, Emas National Park (approximately, 18°18'07"S and 52°57'56"W), Goiás, central Brazil.

species	individuals	basal area	cover value (%)
<i>Andropogon leucostachyus</i> Kunth	199	0.6443	54.10
Poaceae sp. 3	181	0.0003	10.87
<i>Tristachya leiostachya</i> Nees	78	0.0449	7.61
<i>Ocimum</i> sp.	125	0.0012	7.58
<i>Eugenia angustissima</i> O. Berg	46	< 0.0001	2.76
<i>Axonopus derbyanus</i> Black	5	0.0256	1.98
<i>Melinis minutiflora</i> P. Beauv.	30	0.0022	1.94
<i>Syagrus flexuosa</i> (Mart.) Becc.	17	0.0099	1.67
<i>Loudetiopsis chrysothrix</i> (Nees) Conert	8	0.0157	1.51
<i>Myrciaria delicatula</i> (DC.) O. Berg.	23	< 0.0001	1.38
<i>Galactia martii</i> A. DC.	18	< 0.0001	1.08
<i>Eugenia complicata</i> O. Berg	17	0.0002	1.04
<i>Acosmium subelegans</i> (Mohl.) Yakovlev	14	0.0023	0.99
<i>Hyptis adpressa</i> A. St-Hil. ex Benth.	15	< 0.0001	0.90
<i>Allagoptera campestris</i> (Mart.) Kuntze	3	0.0092	0.78
<i>Erythroxylum campestre</i> A. St-Hil.	8	< 0.0001	0.48
<i>Psidium australe</i> Camb.	7	0.0001	0.42
<i>Myrcia torta</i> A. DC.	7	< 0.0001	0.42
<i>Paspalum pectinatum</i> Nees	4	0.0020	0.37
<i>Rynchelytrum repens</i> (Nees) C.E.Hubb.	1	0.0042	0.34
<i>Sisyrinchium vaginatum</i> Spreng.	3	0.0004	0.21
<i>Byttneria oblongata</i> Pohl	3	0.0004	0.21
<i>Mimosa gracilis</i> Benth.	3	< 0.0001	0.18
<i>Cuphea carthagenensis</i> (Jacq.) Macbr.	3	< 0.0001	0.18
<i>Panicum rudgei</i> Roem. & Schult.	2	0.0006	0.16
<i>Chromolaena squalida</i> (A. DC.) King & H.Rob.	2	< 0.0001	0.12
<i>Gymnopogon foliosus</i> (Willd.) Nees	2	< 0.0001	0.12
<i>Croton pohlianus</i> Müll.Arg.	1	< 0.0001	0.06
<i>Eragrostis articulata</i> (Schränk) Nees	1	< 0.0001	0.06
<i>Casearia</i> sp.	1	< 0.0001	0.06
<i>Froelichia procera</i> (Seub.) Pedersen	1	< 0.0001	0.06
Unknown sp. 1	1	< 0.0001	0.06
<i>Pfaffia helichrysoides</i> (Moq.) Kuntze	1	< 0.0001	0.06
<i>Annona crassiflora</i> Mart.	1	< 0.0001	0.06
<i>Eupatorium campestre</i> A. DC.	1	< 0.0001	0.06
<i>Ipomea procurrens</i> Meins.	1	< 0.0001	0.06
<i>Peltaea edouardii</i> (Hochr.) Krapov. & Cristóbal	1	< 0.0001	0.06
Total	834	0.7636	100.00

Table 5. Species density (number of species m⁻²), diversity (nats ind⁻¹), plant density (ind m⁻²), basal area (m² m⁻²) and cylindrical volume (m³ m⁻²) in the hyperseasonal cerrado, Emas National Park (approximately, 18°18'07"S, 52°57'56"W), central Brazil. February corresponds to mid rainy season, when the hyperseasonal cerrado was waterlogged; May corresponds to late rainy season; August corresponds to dry season; and November corresponds to early rainy season. The values are means ± standard deviations, 1 - β is the power of the test. Different letters indicate significative differences between means (α = 0,05).

descriptor	February	May	August	November	P	1 - β
species density	5.900 ^a ± 2.025	9.200 ^b ± 2.271	8.400 ^{ab} ± 2.458	11.400 ^b ± 3.864	< 0.001	100%
diversity	1.922 ^b ± 0.006	1.940 ^b ± 0.003	1.340 ^a ± 0.004	2.399 ^c ± 0.002	—	—
evenness	0.66	0.55	0.41	0.66	—	—
plant density	27.200 ^a ± 14.382	77.100 ^{ab} ± 81.281	67.700 ^{ab} ± 68.962	83.400 ^b ± 22.312	< 0.001	74%
basal area	0.093 ^{bc} ± 0.031	0.114 ^c ± 0.028	0.024 ^a ± 0.007	0.076 ^b ± 0.004	< 0.001	100%
cylindrical volume	0.058 ^{bc} ± 0.027	0.083 ^c ± 0.047	0.014 ^a ± 0.005	0.043 ^b ± 0.012	< 0.001	100%

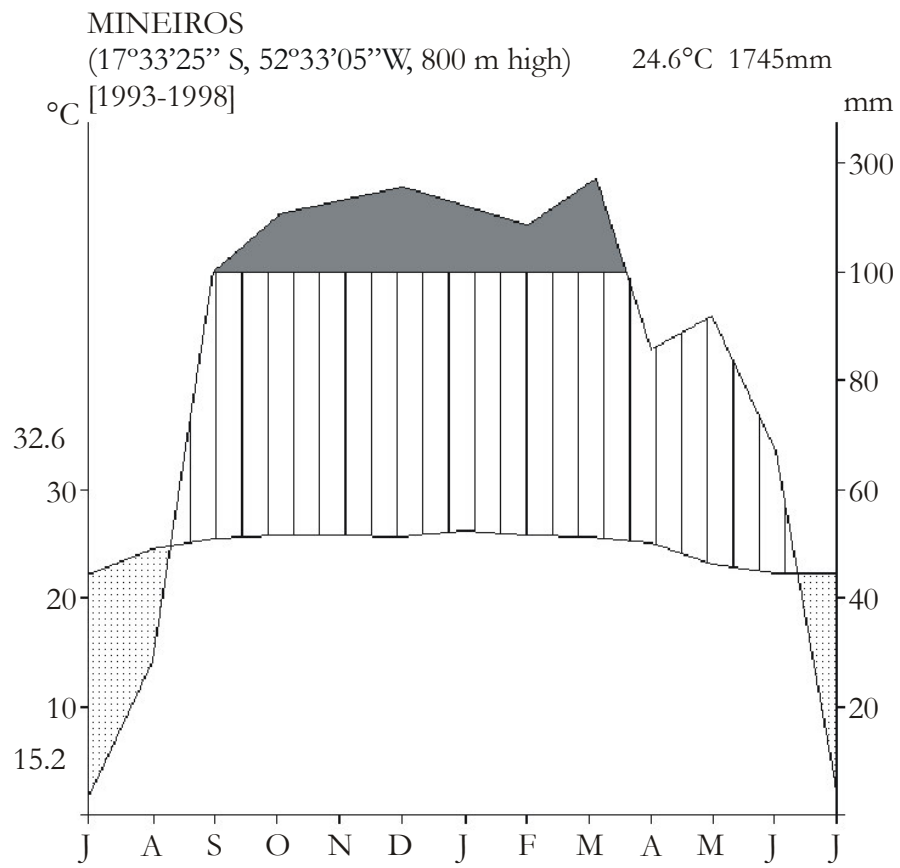


Fig. 1.

Figure 1. Climatic diagram (WALTER 1976), constructed from data obtained at the Benedictine Monks Monastery, Mineiros, Goiás State, central Brazil. Absolute minimum and maximum temperatures were not available in the original data (from BATALHA & MARTINS 2004).

III- Capítulo 2

“A maior das propriedades do homem é a mente intranquãla”.

(Isaac Asimov)

Variações estacionais na composição florística e na estrutura da comunidade em cerrados hiperestacional e estacional no Parque Nacional das Emas, Goiás²

² Trabalho submetido ao periódico *Plant Ecology* com o título “Seasonal changes in floristic composition and community structure in hyperseasonal and seasonal cerrados in Emas National Park, central Brazil”.

Seasonal changes in floristic composition and community structure of hyperseasonal and seasonal cerrados in Emas National Park, central Brazil

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Key words: Hyperseasonality, Savanna, Seasonality, Waterlogging

Abstract

In South America, the largest savanna region is the Brazilian cerrado, in which there are few hyperseasonal areas, characterized by the alternation of two contrasting stresses, drought and waterlogging. Our aim was to study temporal changes in some community descriptors, such as floristic composition, species density, plant density, cylindrical volume, and diversity, in a hyperseasonal cerrado, comparing it to a nearby seasonal cerrado, in Emas National Park, central Brazil. At four different seasons, we placed randomly ten 1 m² quadrats in each vegetation form and sampled the vascular plants. Seasonal changes in floristic composition, species density, and plant density were more pronounced in the hyperseasonal cerrado. Floristic similarity between the vegetation forms was lower when the hyperseasonal cerrado was waterlogged. Species density and diversity were always higher in seasonal cerrado. In the hyperseasonal cerrado, waterlogging probably acts as an environmental filter, restricting the number of cerrado species able to withstand it, since most cerrado species are dryland ones. The seasonal cerrado in ENP reached its biomass peak at mid rainy season, maintaining it until late rainy season, whereas the hyperseasonal cerrado reached its peak at early rainy season and, despite the waterlogging, maintained it until late rainy season. Thus, the hyperseasonal cerrado may be as productive as the seasonal cerrado, contrary to what was found in Venezuelan llanos. In general, the hyperseasonal cerrado community was more dynamic – in terms of floristic and structural changes – than the seasonal cerrado. Our results corroborated the idea that changes in the short-term determinants of savannas will affect its floristic composition and community structure.

Introduction

Savannas are tropical and subtropical seasonal communities with a continuous herbaceous layer and a discontinuous layer of trees and shrubs (Frost et al. 1986). They are highly dynamic on all temporal and spatial scales, in which long- and short-term changes are constantly modifying its physiognomy, composition, and ecological processes (Hopkins 1983; Walker 1987). Seasonality represents one of the most essential features to define a savanna, whether the cyclic changes in the environmental during the year are considered or the biological rhythms of plant species that accompany those external fluctuations (Sarmiento 1983).

Savannas may be divided according to their seasonality into semi-seasonal, seasonal, hyperseasonal, and marshy savannas (Sarmiento 1984). In tropical America, the most widespread savanna type are seasonal savannas, with an extended rainless season that increases fire frequency; in them, both factors, drought and burning, provide a neat rhythmicity in community functioning (Sarmiento 1984). Hyperseasonal savannas, on its turn, are characterized by the alternation of two contrasting stresses during each annual cycle – one induced by drought and fire and the other, by waterlogging – and normally occur on poorly drained bottomlands or depressed regions with slow and ill-defined drainage, especially in the Bolivian and Venezuelan llanos (Sarmiento 1984).

The cerrado is by far the largest savanna region in South America, originally covering about two million km², or 23%, of the Brazilian territory (Ratter et al. 1997), especially in the Central Plateau. The climate is seasonal, with wet summers and dry winters, classified either as Aw or Cwa following Köppen's (1931) system. The dry season is quite pronounced and, in some cases, may last six months (Eiten 1972). Temporary waterlogging is very restricted in the cerrado vegetation, which is basically seasonal (Sarmiento 1983). Nevertheless, we related the first occurrence of a hyperseasonal cerrado recently, in Emas National Park (ENP), central

Brazil (Batalha et al. in press).

Plant-available moisture (PAM) is one of the crucial ecological limitations for the growth of savanna plants, varying both spatially, according to depth, and temporally, as a result of seasonal rainfall (Sarmiento 1996a). In seasonal savannas, soil water potentials are above the permanent wilting point during the rainy season and, consequently, moisture is available for any plant species (Sarmiento 1996a). During the dry season, soil water potentials may remain in some months at values as low as the permanent wilting point, still within the reach of woody plants but not of herbaceous ones (Sarmiento and Acevedo 1991; Sarmiento 1996a). Drought causes water deficit in the plant that affects its metabolism and morphology, reduces its growth, and arrests its development (Baruch 1994). Thus, drought represents one marked stressing moment to several cerrado plants, since it drastically affects the herbaceous vegetation with superficial roots (Sarmiento 1996a).

In hyperseasonal savannas, a PAM-limited dry season alternates with a rainy season during which the soil is saturated and even waterlogged (Sarmiento 1996a). The waterlogging is due to the soil saturation by rainfall, generally associated with impermeable and poorly structured clay horizons (Sarmiento and Monasterio 1975). The overriding effect of waterlogging is to limit the diffusion of oxygen to the root zone (Ponnamperuma 1984). Hypoxia or anoxia are the main limiting factors that reduce aerobic respiration and the absorption of minerals and water by roots (Baruch 1994). In intolerant plants, ethanol and acetaldehyde, products of anaerobic respiration, may damage the general metabolism (Crawford 1982; Jackson and Drew 1984).

As a consequence of these two contrasting stresses, the hyperseasonal cerrado in ENP is an impoverished form of cerrado, with fewer species and lower diversity than seasonal cerrado communities (Batalha et al. in press). But how do the plant communities vary throughout the year in these two vegetation forms? Our aim was to study temporal changes in some community descriptors of a hyperseasonal cerrado, comparing it with a nearby seasonal

cerrado and taking into account three main ideas: a) savanna plant communities are dynamic (Hopkins 1983); b) the biological rhythms of savanna plant species accompany the climatic seasonality (Sarmiento 1984); and c) in hyperseasonal savannas, herbaceous plants are subjected to two contrasting forms of stress, drought and waterlogging, and, in seasonal savannas, only to drought (Sarmiento 1992).

We were also interested in possible changes in floristic composition of the hyperseasonal and seasonal cerrados throughout the year. We tested the postulate that the relative stability of a community on the face of a perturbation depends on its floristic composition (Silva 1996). As long as there are two stresses, drought and waterlogging, in the hyperseasonal cerrado, we expected larger variation in its floristic composition throughout the year than in the seasonal cerrado. So, we tried to answer the following questions: i) does the floristic composition vary throughout the year in the hyperseasonal and seasonal cerrados?; ii) is the floristic composition of the hyperseasonal cerrado less similar to the seasonal cerrado when the former is waterlogged?; iii) do species density, plant density, cylindrical volume, and diversity vary throughout the year in the hyperseasonal cerrado?; and iv) are these patterns similar with those found in a nearby seasonal cerrado?

Methods

The Emas National Park (ENP) is located in the Brazilian Central Plateau, southwestern Goiás State (17°49'-18°28'S and 52°39'-53°10'W), in the cerrado core region, and is one of the largest and most important reserves in the cerrado region, with ca. 133.000 ha. Recently, ENP was included by Unesco (2001) in the World Natural Heritage List as one of the sites containing fauna, flora, and key habitats that characterize the cerrado. Regional climate is tropical and humid, with wet summer and dry winter, which is classified as Aw (Köppen 1931). The dry season goes from June to August and the wet season, from September to May

(Figure 1). Annual rainfall varies from 1,200 to 2,000 mm, concentrated from October to March, and mean annual temperature lies around 24.6°C (Ramos-Neto and Pivello 2000).

The cerrado in ENP comprises almost all physiognomies found in this vegetation type, from *campo limpo* (a grassland) to *cerrado sensu stricto* (a woodland). In the reserve, open cerrado physiognomies prevail, all characterized as seasonal cerrados, covering 68.1% of the total area (Ramos-Neto and Pivello 2000). However, in the southwestern portion of the reserve, there is a 300 ha area covered by a hyperseasonal cerrado (Batalha et al. in press). Physiognomically, the hyperseasonal cerrado in PNE is a grassland, but it remains waterlogged at the middle of the rainy season (from February to April), whereas in the dry season (from June to August), there is a water shortage in the upper soil layers.

We carried out four surveys in the hyperseasonal cerrado (approximately, 18°18'07"S, 52°57'56"W) and in the seasonal cerrado (approximately, 18°17'34"S, 52°58'12"W): in February 2003, at mid rainy season, when the hyperseasonal cerrado was waterlogged; in May 2003, at late rainy season; in August 2003, at dry season; and in November 2003, at early rainy season. We delimited a 1 ha area, placing randomly ten 1 m² quadrats in each field trip and counting the number of individuals of each vascular plant except seedlings. In the case of cespitose grasses and sedges, we considered as an individual the whole tuft.

We measured the height and diameter of each individual at soil level and counted the number of individuals belonging to each species. We identified the species by comparing the collected material to lodged vouchers, mainly the ENP's reference material collected by Batalha and Martins (2002), but also vouchers lodged at the São Paulo Botanical Institute, Brazilian Institute of Geography and Statistics, and University of Brasília herbaria. When identification at species level was not possible, we classified them as morphospecies. We lodged the collected material at the Federal University of São Carlos herbarium.

To compare the floristic compositions, we constructed a presence/absence matrix with the species sampled in each survey in the seasonal and hyperseasonal cerrados and did a

detrended correspondence analysis (DCA) (Jongman et al. 1995), using the MVSP software (Kovach Computing Services 1999). We calculated the similarity between the hyperseasonal and seasonal cerrado floras and among the seasons with the Sørensen index (Magurran 1996). To compare the community structure, we analyzed the following variables: species density, diversity, plant density, and cylindrical volume. We defined species density as the number of species per area (spp m⁻²); plant density as the number of individuals per area (ind m⁻²); and cylindrical volume as the volume (basal area × height) occupied by each species (m³ m⁻²), according to Mueller-Dombois and Ellenberg (1974).

We tested all variables for normality (Shapiro and Wilk 1965) and homocedasticity (Hartley 1950). As long as species density, plant density, and cylindrical volume were not normally distributed, we log-transformed these data prior to the analyses. We used two-way analyses of variance and Tukey multiple comparisons test (Zar 1999) to test for significant differences ($\alpha = 0.05$), with ‘vegetation form’ being the first factor and ‘season’, the second one. We calculated diversity with the Shannon index (Shannon and Weaver 1963), using the natural logarithmic base, and employed Hutcheson’s test (Zar 1999) to compare diversity values among the seasons and between vegetation forms. We also calculated evenness (Pielou 1975).

Results

Using the floristic data from all field trips, we found 63 species and 18 families in the hyperseasonal cerrado (Table 1) and 107 species and 31 families in the seasonal cerrado (Table 2). We found 19 species not related in the ENP’s flora (Batalha and Martins 2002), 10 in the hyperseasonal cerrado and 9 in the seasonal cerrado (Tables 1 and 2). The most representative families in both areas were Poaceae and Myrtaceae, followed by Asteraceae and Fabaceae in the hyperseasonal cerrado and Fabaceae and Asteraceae in the seasonal

cerrado. In the hyperseasonal cerrado, the grass *Andropogon leucostachyus* Kunth presented the highest percentages of the total cylindrical volume throughout the year, ranging from 65.7% at late rainy season to 98.9% at mid rainy season. In the seasonal cerrado, the grass *Tristachya leiostachya* Nees presented the highest percentages of the total community cylindrical volume throughout the year, ranging from 66.9% at late rainy season to 80.1% at early rainy season.

Overall similarity between the two vegetation forms was 0.46, with 39 species in common. In February, at mid rainy season, we sampled 18 and 55 species in the hyperseasonal and seasonal cerrados, respectively, with a similarity index of 0.27; in May, at late rainy season, we sampled 32 and 58 species in the hyperseasonal and seasonal cerrados, respectively, with a similarity index of 0.31; in August, at dry season, we sampled 26 and 51 species in the hyperseasonal and seasonal cerrados, respectively, with a similarity index of 0.34; and in November, at early rainy season, we sampled 37 and 61 species in the hyperseasonal and seasonal cerrados, respectively, with a similarity index of 0.51. The DCA eigenvalues were 0.497 and 0.314 for the first two axes, which explained 38.6% of the variation in our data. In the first axis, the hyperseasonal cerrado had lower scores, widely dispersed, whereas the seasonal cerrado had higher scores (Figure 2). In the second axis, the seasonal cerrado scores were more dispersed than the hyperseasonal cerrado ones (Figure 2).

We found significant differences between vegetation forms and among seasons for all community descriptors (Table 3). Species density was always higher in the seasonal cerrado, and we found seasonal changes only in the hyperseasonal cerrado (Table 3 and Figure 3). We did not find interaction between the two factors for plant density (Table 3). Plant density changed seasonally only in the hyperseasonal cerrado and was significantly different between the vegetation forms only at mid rainy season (Figure 3). We did not find interaction between the two factors for cylindrical volume (Table 3), which varied seasonally in both vegetation forms (Table 3 and Figure 3). In the hyperseasonal cerrado, cylindrical volume was higher

throughout the rainy season and, in the seasonal cerrado, at mid and late rainy seasons (Figure 3).

Diversity was higher in the seasonal cerrado than in the hyperseasonal cerrado at all seasons (Table 4). We found the highest diversity at different moments in each vegetation form – at early rainy season in the hyperseasonal cerrado and at mid rainy season in the seasonal cerrado (Table 4). Evenness was lower in the seasonal cerrado, ranging from 0.37 at early rainy season to 0.50 at mid rainy season, and higher in the hyperseasonal cerrado, ranging from 0.41 at dry season to 0.66 at early and mid rainy season (Table 4).

Discussion

The floristic similarity between the hyperseasonal and seasonal cerrados was relatively low, showing that the two contrasting stresses in the hyperseasonal cerrado limit the number and the distribution of species able to grow in those conditions and reflecting the physiological incapacity of most cerrado species in tolerating waterlogging (Batalha et al. in press). We found 19 species not related in the ENP's flora (Batalha and Martins 2002). Batalha and Martins (2002) had already stated that the number of species in ENP could be increased by species not found in that survey, since floristic surveys certainly miss a number of species in a given area, especially those that are not at reproductive stage at the time of the visit, flower sporadically, are ephemeral, or are inconspicuous, problems that particularly affect the herbaceous component of the vegetation.

Savanna plant communities primarily respond to plant-available moisture (PAM) regime (Medina and Silva 1990; Solbrig 1990; Teague and Smit 1992), which varies both spatially, in depth, and temporally, as a result of seasonal rainfall (Sarmiento 1996a). Graminoids species, with an intensive root system, exploit the upper soil layers and strictly follow a growth cycle associated with seasonality of rainfall, whereas trees, with extensive, less efficient root

systems, are able to exploit both water and nutrients from deeper soil layers (Medina and Silva 1990). Short-term changes and period pulsation of plant-available moisture and plant-available nutrients may alter species composition and diversity (Sarmiento 1996a), since individuals from different species react differently to changes in their environment and affect survival and fertility at population level (Silva 1996).

The magnitude of the connection from individual to population will depend on the species life story traits, which is another reason why community responses to perturbations depend heavily on the floristic structure (Silva 1996). Seasonal changes in floristic composition were more pronounced in the hyperseasonal cerrado, highlighted by the wide dispersion of its scores in the first axis of the correspondence analysis. As expected, the hyperseasonal cerrado was less similar to the nearby seasonal cerrado at mid rainy season, when the former was waterlogged, and more similar at early rainy season. Sarmiento and Vera (1979) also found a large variation in species composition in nearby seasonal and hyperseasonal savannas in the Venezuelan llanos.

Species density was always higher in the seasonal cerrado than in the hyperseasonal cerrado. Sarmiento and Vera (1979) found that seasonal savannas are richer in species than hyperseasonal ones. Whereas we found seasonal changes for species density in the hyperseasonal cerrado, higher at early rainy season and lower when it was waterlogged, we did not find it in the seasonal cerrado, highlighting the increased seasonality in the hyperseasonal cerrado as a consequence of its two contrasting stresses (Sarmiento 1984). Similarly, we found seasonal changes for plant density only in the hyperseasonal cerrado.

The lower values of species density in the hyperseasonal cerrado and of plant density when it was waterlogged also indicate the non-adaptation of most cerrado species in tolerating waterlogging (Batalha et al. in press). In highly stressed communities, resource availability limits the number of co-occurring species with similar ecological requirements, therefore, only those species highly adapted to the stressing factor survive (Baruch et al. 1996). Thus,

waterlogging may act as an environmental filter (Chase 2003), restricting the number of cerrado species, on the one hand, and favoring those few species able to withstand it, such as *A. leucostachyus*, on the other hand.

Dominance spectra in herbaceous layer of tropical savannas show frequently a high degree of dominance by a few grass species (Sarmiento 1983). Although this is rarely observed in cerrado herbaceous communities (Filgueiras 2002), there are some exceptions as the dominance of *T. leiostachya* in ENP's seasonal cerrado grassland physiognomies (Filgueiras 2002), probably due to frequent fires that usually burn large portions of the reserve (Ramos-Neto and Pivello 2000). We found in all seasons high cylindrical volume percentages of the perennial grasses *A. leucostachyus* in the hyperseasonal cerrado and *T. leiostachya* in the seasonal cerrado. Thus, in ENP, not only the seasonal cerrado grasslands are monodominants, but the hyperseasonal cerrado as well. The genus *Andropogon* also prevails in hyperseasonal savannas of the Colombian and Venezuelan llanos (Blydenstein 1967; Sarmiento 1996b). For instance, *A. leucostachyus* is also the most abundant species in a Colombian hyperseasonal savanna (Rippstein et al. 2001).

The herbaceous component should present its largest development at late rainy season and lowest at dry season (Sarmiento 1984; Sarmiento et al. 2004), which is related with the soil PAM (Sarmiento 1983; Sarmiento et al. 2004). Considering the cylindrical volume as a good biomass estimator for cerrado plants (Batalha et al. 2001), the seasonal cerrado in ENP reached its biomass peak at mid rainy season, maintaining it until late rainy season, whereas the hyperseasonal cerrado reached its peak at early rainy season and, despite the waterlogging, maintained it until late rainy season. So, the hyperseasonal cerrado may be as productive as the seasonal cerrado, contrary to what was found in Venezuelan llanos, where hyperseasonal savannas are 30% more productive than seasonal ones (Sarmiento and Vera 1979).

We found diversity values ranging from 2.51 to 3.17 nats ind⁻¹ in the seasonal cerrado, within the range found by Mantovani (1996), from 2.5 to 3.6 nats ind⁻¹, for seasonal cerrado

plant communities. In the hyperseasonal cerrado, diversity values were always lower than in the seasonal cerrado, as a consequence of the low number of species. There is a hierarchy of determinants, some of them correlated to others, that affects species composition and diversity of savanna communities (Solbrig 1991). At the top of the hierarchy, there is the annual regime of PAM, but other determinants, such as available nutrients, fire, and herbivory, must be considered (Solbrig 1991). Short-term changes and period pulsation of these determinants may alter species composition and diversity, but species within functional groups are not entirely equivalent and, hence, they have different tolerances to environmental pulsation (Sarmiento 1996a). Therefore, changing conditions may result in a certain degree of floristic replacement, without major changes in the functioning of the system. This means that savannas should be more stable in functional than in floristic terms (Sarmiento 1996a).

Structural variations in savanna communities may be described as a *continuum* that follows the main environmental factors, especially soil moisture gradient (Silva and Sarmiento 1976). Amorim and Batalha (in press) studied, at mid rainy season, the soil features in the same seasonal and hyperseasonal cerrados, concluding that the duration of waterlogging in the latter is not long enough to alter its soil characteristics and limitations to the plants growing on it must be a consequence of the direct effects of flooding. Thus, in the hyperseasonal cerrado, the two stressing moments, drought and waterlogging, determined the community structure. The hyperseasonal cerrado was more dynamic – in terms of floristic and structural changes – than the seasonal cerrado. Our results corroborated the idea proposed by Sarmiento (1996) and Silva (1996) that changes in the short-term determinants of savannas will affect its floristic composition and community structure.

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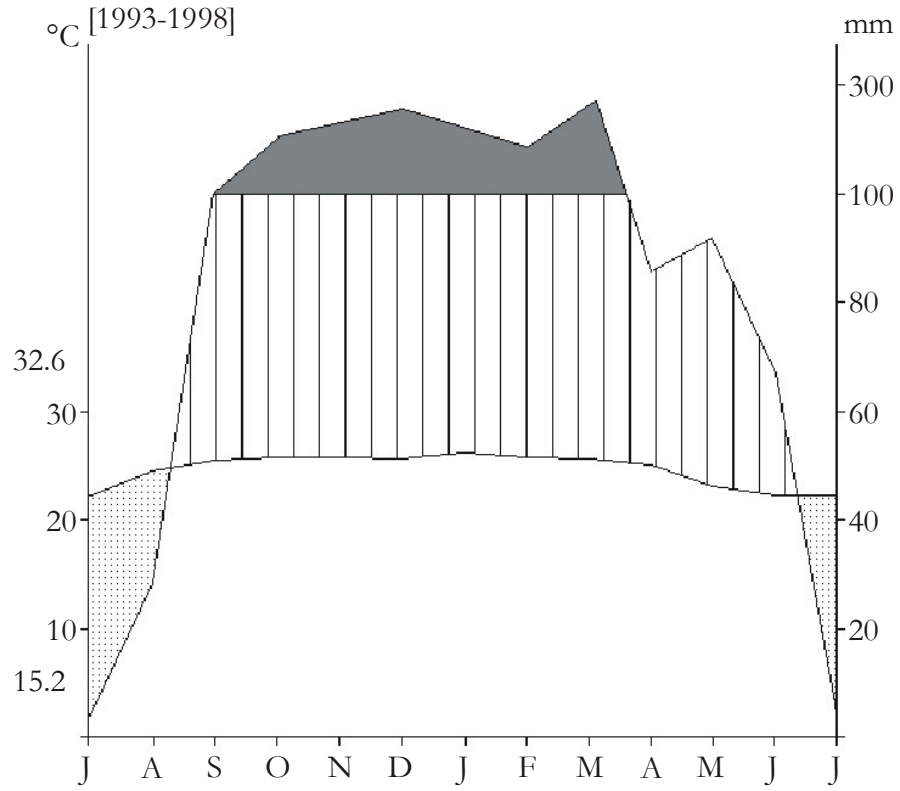
Figure 1. Climatic diagram (Walter 1970), constructed from data obtained at the Benedictine Monks Monastery, Mineiros, Goiás State, central Brazil. Absolute minimum and maximum temperatures were not available in the original data (after Batalha and Martins 2004).

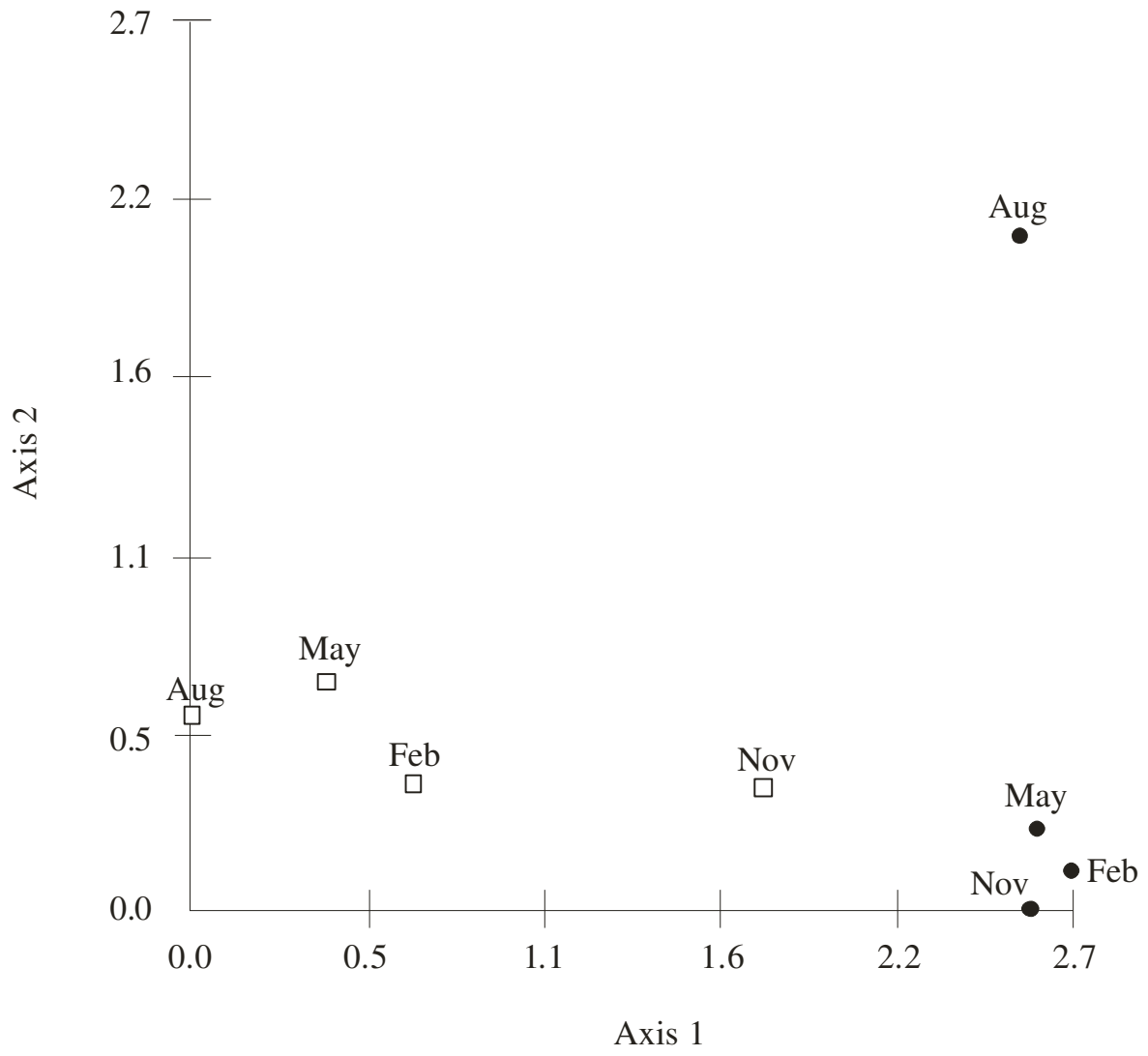
Figure 2. Detrended correspondence analysis ordination diagram of floristic composition of the hyperseasonal cerrado (□) and seasonal cerrado (●), in Emas National Park, central Brazil, at four seasons. February, mid rainy season; May = late rainy season; Aug = August, dry season; and Nov = November, early rainy season.

Figure 3. Logarithms of species density (A), plant density (B), and cylindrical volume (C) in the hyperseasonal cerrado (□) and seasonal cerrado (●), in Emas National Park, central Brazil, at four seasons. Feb = February, mid rainy season; May = late rainy season; Aug = August, dry season; and Nov = November, early rainy season. Values are means \pm 95% confidence intervals. Different letters indicate significant differences between means ($\alpha = 0.05$).

MINEIROS

(17°33'25" S, 52°33'05" W, 800 m high) 24.6°C 1745mm





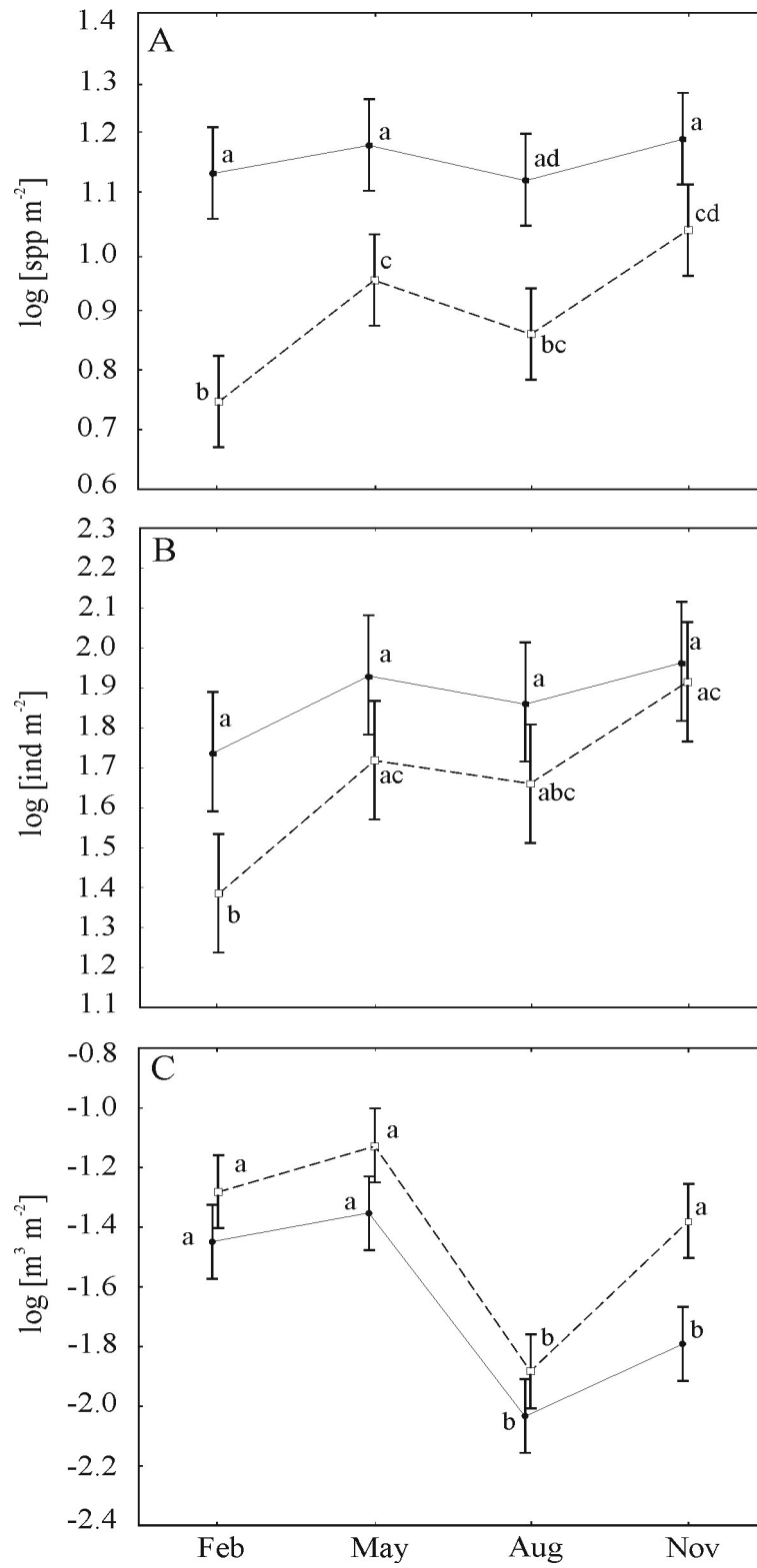


Table 1. Species and number of individuals found in the hyperseasonal cerrado (18°18'07"S, 52°57'56"W), Emas National Park, Goiás, central Brazil. February = mid rainy season, May = late rainy season; August = dry season, November = early rainy season. * = addition to ENP's flora, that is, not reported by Batalha and Martins (2002).

family	species	February	May	August	November
Amaranthaceae	<i>Froelichia procera</i> (Seub.) Pedersen				1
	<i>Pfaffia helichrysoides</i> (Moq.) Kuntze				1
Annonaceae	<i>Annona crassiflora</i> Mart.				1
Arecaceae	<i>Allagoptera campestris</i> (Mart.) Kuntze	3	6	3	3
	<i>Syagrus flexuosa</i> (Mart.) Becc.		6	4	17
Asteraceae	Asteraceae sp. 1 *			13	
	<i>Chromolaena squalida</i> (A. DC.) King & H. Rob.		5		2
	<i>Emilia coccinea</i> (Sims.) Sweet		1		
	<i>Erechtites hieraciifolia</i> (L.) Raf.	2	1		
	<i>Eupatorium campestre</i> A. DC.				1
Celastraceae	<i>Tontelea micrantha</i> (Mart.) A. C. Smith	5			
Ebenaceae	<i>Diospyros hispida</i> A. DC.			2	
Erythroxylaceae	<i>Erythroxylum campestre</i> A. St-Hil.				8
Euphorbiaceae	<i>Croton pohlianus</i> Müll. Arg.				1
Fabaceae	<i>Acosmium subelegans</i> (Mohl.) Yakovlev	11	28	7	14
	<i>Andira laurifolia</i> Benth.	16	41		
	<i>Galactia dimorpha</i> Burk.		13		
	<i>Galactia martii</i> A. DC.	6	9	4	18
	<i>Ipomea procurrens</i> Meins.				1
	<i>Mimosa gracilis</i> Benth.				3
Flaucortiaceae	<i>Casearia</i> sp.				1
Iridaceae	<i>Sisyrinchium vaginatum</i> Spreng.	1	1		3
Lamiaceae	<i>Eriope crassipes</i> Benth.		1		
	<i>Hyptis adpressa</i> A. St-Hil. ex Benth.		28		15
	<i>Ocimum</i> sp.	4			125
Lythraceae	<i>Cuphea carthagenensis</i> (Jacq.) Macbr.				3
	<i>Cuphea</i> sp. *		2		
Malvaceae	<i>Byttneria oblongata</i> Pohl	4	5	2	3
	<i>Peltaea edouardii</i> (Hochr.) Krapov. & Cristóbal				1
Myrtaceae	<i>Eugenia angustissima</i> O. Berg		9	4	46
	<i>Eugenia calycina</i> Cambess.		33	48	
	<i>Eugenia complicata</i> O. Berg	50			17
	<i>Eugenia cristaensis</i> O. Berg		3		
	<i>Eugenia livida</i> O. Berg *	1			
	<i>Myrcia rhodosepala</i> Kiaersk.	2	1	5	
	<i>Myrcia torta</i> A. DC.				7
	<i>Myrcia uberavensis</i> O. Berg	1			
	<i>Myrciaria delicatula</i> (A. DC.) Berg.		69	1	23
	Myrtaceae sp. 1 *			2	
	<i>Psidium australe</i> Camb.	23		6	7
Poaceae	<i>Andropogon bicornis</i> L.		8		
	<i>Andropogon leucostachys</i> Kunth	122	421	477	199
	<i>Axonopus derbyanus</i> Black		4		5
	<i>Brachiaria decumbens</i> Stapf	5	1	2	
	<i>Eragrostis articulata</i> (Schrank) Nees		1		1
	<i>Gymnopogon foliosus</i> (Willd.) Nees			7	2
	<i>Hyparrhenia rufa</i> (Nees)		1		
	<i>Ichnanthus procurrens</i> (Nees) Sw.		1	1	
	<i>Loudetiopsis chrysothryx</i> (Nees) Conert		17	47	8

family	species	February	May	August	November
	<i>Melinis minutiflora</i> P. Beauv.		7	2	30
	<i>Panicum parvifolium</i> Lam. *	9	15	7	
	<i>Panicum rudgei</i> Roem. & Schult.	7	28	20	2
	<i>Paspalum geminiflorum</i> Steud.		1		
	<i>Paspalum pectinatum</i> Nees		4		4
	Poaceae sp. 1 *				181
	Poaceae sp. 2 *			1	
	Poaceae sp. 3 *			5	
	Poaceae sp. 4 *			1	
	<i>Rynchelytrum repens</i> (Nees) C.E.Hubb.				1
	<i>Schizachyrium condensatum</i> (Kunth) Nees			5	
	<i>Tristachya leiostachya</i> Nees				78
Scrophulariaceae	<i>Scoparia dulcis</i> L.			1	
Unknown	Unknown *				1

Table 2. Species and number of individuals found in the seasonal cerrado (18°17'34"S, 52°58'12"W), Emas National Park, Goiás, central Brazil. February = mid rainy season, May = late rainy season; August = dry season, November = early rainy season. * = addition to ENP's flora, that is, not reported by Batalha and Martins (2002).

family	species	February	May	August	November
Amaranthaceae	<i>Froelichia procera</i> (Seub.) Pedersen	9	1	1	1
	<i>Pfaffia helichrysoides</i> (Moq.) Kuntze				4
Anacardiaceae	<i>Anacardium humile</i> A. St-Hil.		2		4
Annonaceae	<i>Annona crassiflora</i> Mart.	9	4	1	2
	<i>Annona warmingiana</i> Mello-Silva & Pirani	4			1
Arecaceae	<i>Allagoptera campestris</i> (Mart.) Kuntze	5	6	1	2
	<i>Syagrus flexuosa</i> (Mart.) Becc.	12	9	9	7
Asteraceae	<i>Aspilia leucoglossa</i> Malme	1		3	1
	Asteraceae sp. 2 *		11		
	<i>Calea clausseniana</i> Baker				2
	<i>Calea cuneifolia</i> A. DC.				5
	<i>Elephantopus biflorus</i> Less.			1	
	<i>Vernonia herbacea</i> (Vell.) Rusby				2
	<i>Wedelia macedoi</i> H. Rob.	2			
Bignoniaceae	<i>Tabebuia ochracea</i> (Cham.) Standl.	5	3		
Burseraceae	<i>Protium ovatum</i> Engl.			1	1
Celastraceae	<i>Tontelea micrantha</i> (Mart.) A.C. Smith	1		2	18
Connaraceae	<i>Rourea induta</i> Planch.	1	1		3
Cyperaceae	<i>Bulbostylis junciformis</i> Kuntze		1	3	
Dilleneaceae	<i>Davilla elliptica</i> A. St-Hil.	1	10		
Ebenaceae	<i>Diospyros hispida</i> A. DC.	9	5	13	5
Erythroxylaceae	<i>Erythroxylum campestre</i> A. St-Hil.		11	8	
	<i>Erythroxylum deciduum</i> A. St-Hil.	6			
	<i>Erythroxylum suberosum</i> A. St-Hil.	5			3
Euphorbiaceae	<i>Croton antisyphiliticus</i> Mart.	16	7	1	
	<i>Croton lundianus</i> Müll. Arg.			2	
	<i>Croton pohlianus</i> Müll.Arg.		1		
	<i>Sebastiania bidentata</i> (Mart.) Pax			1	
Fabaceae	<i>Acosmium subelegans</i> (Mohl.) Yakovlev	4	7	4	13
	<i>Camptosema ellipticum</i> (Desv.) Burkart	2			
	<i>Chamaecrista nictitans</i> (L.) Moench.		1		1
	<i>Eriosema crinitum</i> (Kunth) Gardner	2			1
	<i>Eriosema longifolium</i> Benth.	3			
	<i>Galactia decumbens</i> (Benth.) Chodat & Hassl.	4	1		4
	<i>Galactia dimorpha</i> Burk.				2
	<i>Galactia martii</i> A. DC.	2	10	11	5
	<i>Mimosa gracilis</i> Benth.	3	5		
<i>Mimosa polycephala</i> Benth.		3		3	
	<i>Periandra mediterranea</i> (Vell.) Taub.		24		
Flaucortiaceae	<i>Casearia</i> sp.	3			
Iridaceae	<i>Sisyrinchium vaginatum</i> Spreng.		1	3	2
Lamiaceae	<i>Eriope crassipes</i> Benth.		4	3	
	<i>Hyptis adpressa</i> A. St-Hil. ex Benth.	2	9	2	
	<i>Hyptis villosa</i> Pohl ex Benth.	3	1	1	16
	<i>Hyptis virgata</i> Benth.			1	
	<i>Ocimum</i> sp.	34			28
Lythraceae	<i>Cuphea carthagenensis</i> (Jacq.) Macbr.	1	8	4	5
Malpighiaceae	<i>Byrsonima crassa</i> Nied.			2	
	<i>Byrsonima guillemianiana</i> A. Juss.	3	3		
Malvaceae	<i>Byttneria oblongata</i> Pohl	12	6		4
	<i>Peltaea edouardii</i> (Hochr.) Krapov. & Cristóbal	4	1		1
	<i>Waltheria douradinha</i> A. St-Hil.	7			
Melastomataceae	<i>Miconia ligustroides</i> (A. DC.) Naud.				10

Menispermaceae	<i>Cissampelos ovalifolia</i> Ruiz & Pav.			1	
Myrtaceae	<i>Campomanesia pubescens</i> (A. DC.) O. Berg	80	72	9	31
	<i>Eugenia angustissima</i> O. Berg	44	87	58	67
	<i>Eugenia aurata</i> O. Berg		2		4
	<i>Eugenia bimarginata</i> A. DC.			1	
	<i>Eugenia calycina</i> Cambess.	7	2	5	
	<i>Eugenia complicata</i> O. Berg		1		7
	<i>Eugenia piauhiensis</i> O. Berg			5	2
	<i>Eugenia puniceifolia</i> (Kunth) A. DC.		3		1
	<i>Myrcia guianensis</i> A. DC.		49	21	
	<i>Myrcia rhodosepala</i> Kiaersk.	11		8	11
	<i>Myrcia torta</i> A. DC.				1
	<i>Myrcia uberavensis</i> O. Berg	1	8		
	<i>Myrciaria delicatula</i> (DC.) O. Berg		91	246	233
	Myrtaceae sp. 2 *	2			
	Myrtaceae sp. 3 *	19			
	<i>Psidium australe</i> Camb.	2	17	15	15
	<i>Psidium cinereum</i> Mart.	3	6		
	<i>Psidium firmum</i> O. Berg		3	2	13
	<i>Psidium laruotteanum</i> Cambess.	17	4	1	8
	<i>Psidium multiflorum</i> Cambess.			1	
	<i>Psidium rufum</i> Mart. ex A. DC.	8			1
Ochnaceae	<i>Ouratea floribunda</i> (A. St-Hil.) Engl.		2	11	
	<i>Ouratea nana</i> (A. St-Hil.) Engl.	4	4	1	14
	<i>Ouratea spectabilis</i> (Mart.) Engl.	13			1
Poaceae	<i>Andropogon leucostachys</i> Kunth		1		2
	<i>Anthraenantiopsis perforata</i> (Nees) Parodi	2		17	
	<i>Aristida riparia</i> Trin.	2			
	<i>Axonopus derbyanus</i> Black	4	8	57	23
	<i>Elionurus latiflorus</i> Nees	69	8		28
	<i>Elionurus muticus</i> Kuntze			1	
	<i>Eragrostis articulata</i> (Schrank) Nees	5			
	<i>Gymnopogon foliosus</i> (Willd.) Nees		6	1	7
	<i>Leptosaccharum filiforme</i> A. Camus *		22		
	<i>Loudetiopsis chrysothryx</i> (Nees) Conert		5	32	1
	<i>Panicum olyroides</i> Kunth			1	
	<i>Panicum rudgei</i> Roem. & Schult.	2		23	1
	<i>Paspalum carinatum</i> Humb. & Bonpl. ex Fleug.		1		18
	<i>Paspalum gardnerianum</i> Nees			2	
	<i>Paspalum lineare</i> Trin. *		8		
	<i>Paspalum pectinatum</i> Nees	7	1	1	2
	Poaceae sp. 5 *		10		6
	Poaceae sp. 6 *		4		
	Poaceae sp. 7 *			1	
	<i>Rynchelytrum repens</i> (Nees) C.E.Hubb.	3	11		
	<i>Trachypogon</i> sp. *			11	2
	<i>Tristachya leiostachya</i> Nees	88	277	160	319
Rubiaceae	<i>Diodia schumanii</i> Standl.				1
	<i>Palicourea coriacea</i> (Cham.) K. Schum.			1	4
	<i>Tocoyena formosa</i> K. Schum.				1
Sapindaceae	<i>Serjania cissoides</i> Radlk.	1			
Sapotaceae	<i>Pradosia brevipes</i> (Pierre) Penn.	6	4		
Solanaceae	<i>Solanum subumbellatum</i> Vell.				3
Turneraceae	<i>Piriqueta emasensis</i> Arbo				4

Table 3. Two-way analyses of variance for species density, plant density, and cylindrical volume in hyperseasonal cerrado (18°18'07"S, 52°57'56"W) and seasonal cerrado (18°17'347"S, 52°58'12"W), in Emas National Park, central Brazil, at four seasons.

community descriptor factor	F	P
species density		
<i>vegetation form</i>	88.085	< 0.001
<i>season</i>	7.948	< 0.001
<i>interaction</i>	3.100	0.032
plant density		
<i>vegetation form</i>	14.835	< 0.001
<i>season</i>	8.826	< 0.001
<i>interaction</i>	1.400	0.090
cylindrical volume		
<i>vegetation form</i>	30.008	< 0.001
<i>season</i>	51.535	< 0.001
<i>interaction</i>	1.862	0.144

Table 4. Diversity (nats ind⁻¹) and evenness in the hyperseasonal cerrado (18°18'07"S, 52°57'56"W) and seasonal cerrado (18°17'347"S, 52°58'12"W), in Emas National Park, central Brazil. February = mid rainy season, May = late rainy season; August = dry season, November = early rainy season. Different letters indicate significant differences between values ($\alpha = 0.05$).

vegetation form	descriptor	February	May	August	November
hyperseasonal cerrado	diversity	1.922 ^b ± 0.006	1.940 ^b ± 0.003	1.340 ^a ± 0.004	2.399 ^c ± 0.002
	evenness	0.66	0.55	0.41	0.66
seasonal cerrado	diversity	3.170 ^f ± 0.055	2.810 ^e ± 0.055	2.510 ^d ± 0.055	2.570 ^d ± 0.055
	evenness	0.50	0.41	0.38	0.37

IV - Conclusão geral

Conclusão geral

Com este trabalho, chegamos às seguintes conclusões:

- A flora do cerrado hiperestacional no Parque Nacional das Emas (GO) é composta por, no mínimo, 63 espécies, pertencentes a 18 famílias. No cerrado estacional, encontramos 107 espécies, pertencentes a 31 famílias. Dessas espécies, 19 não estão relatadas em Batalha & Martins (2002) – 10 no cerrado hiperestacional e 9 no cerrado estacional, o que evidencia que levantamentos florísticos deixam de amostrar um certo número de espécies, já que as plantas podem não se encontrar em estágio reprodutivo no momento do levantamento, são efêmeras, inconspícuas ou bianuais;
- As famílias mais representativas em ambos os cerrados foram Poaceae e Myrtaceae, seguidas por Asteraceae e Fabaceae no cerrado hiperestacional e Fabaceae e Asteraceae no cerrado estacional, que, de acordo com Batalha & Martins (2002), são as famílias mais representativas na flora do cerrado do Parque Nacional das Emas (GO);
- A espécie dominante no cerrado hiperestacional é a gramínea *Andropogon leucostachyus* Kunth., sendo que no cerrado estacional, a espécie dominante é a gramínea *Tristachya leiostachya* Nees. Ambas apresentaram os maiores valores de cobertura e volume cilíndrico em todas as estações do ano. Dessa maneira, o cerrado hiperestacional e o cerrado estacional no Parque Nacional das Emas são uma das poucas formações de cerrado com fisionomia campestre que são monodominantes;
- A similaridade total entre os dois cerrados foi baixa (índice de Sørensen de 0,46). Ao longo do ano, encontramos menor similaridade em fevereiro, quando o cerrado hiperestacional estava alagado (índice de Sørensen de 0,27), e maior em novembro (índice de Sørensen de 0,51). No cerrado hiperestacional, encontramos variação estacional para a densidade de espécies, densidade de indivíduos, diversidade, área basal e volume cilíndrico. Encontramos os menores valores de densidade de espécies e indivíduos em fevereiro – quando o cerrado

hiperestacional estava alagado – e os maiores em novembro. Portanto, o alagamento parece ser um fator estressante mais restritivo para as espécies do cerrado hiperestacional;

- No cerrado hiperestacional, o alagamento provocou uma diminuição na densidade de espécies, densidade de indivíduos, diversidade, mas não na equabilidade, área basal e volume cilíndrico. No cerrado estacional, encontramos variação estacional apenas para a diversidade, menor na estação seca e início da estação chuvosa e maior no meio da estação chuvosa, e para o volume cilíndrico, menor em agosto e maior em fevereiro e novembro. Dessa forma, alagamento no cerrado hiperestacional pode ser considerado um filtro ambiental, restringindo o número da maioria de espécies de cerrado e favorecendo poucas espécies que suportam essa condição, como, por exemplo, *Andropogon leucostachyus*;
- Os valores de diversidade do cerrado estacional encontraram-se dentro dos limites previstos para o cerrado – entre 2,5 e 3,6 nats ind⁻¹, enquanto que no cerrado hiperestacional os valores sempre estiveram abaixo do limite inferior. Portanto, o cerrado hiperestacional é uma formação mais pobre e menos diversa que o cerrado estacional, o que reflete a estacionalidade reforçada nesse ambiente, resultado dos dois estresses contrastantes – a seca e o alagamento;
- O cerrado estacional apresentou a maior biomassa em fevereiro, mantendo-a em maio. O cerrado hiperestacional atingiu a maior biomassa em novembro, mantendo-a em fevereiro (apesar do alagamento) e em maio. Portanto, o cerrado hiperestacional deve ser tão produtivo quanto o estacional, diferindo das savanas hiperestacionais dos lhanos venezuelanos;
- A comunidade do cerrado hiperestacional foi mais dinâmica – em termos de mudanças florísticas e estruturais – do que a do cerrado estacional. Assim, nossos resultados corroboraram a idéia de que mudanças em curto prazo nos determinantes das savanas (e.g. umidade disponível para as plantas) afetam tanto a composição florística quanto a estrutura dessas comunidades.

Acreditamos que nosso trabalho contribuiu para o conhecimento da dinâmica da vegetação do cerrado, principalmente pela oportunidade de compararmos um tipo de cerrado raríssimo – o cerrado hiperestacional – com o cerrado estacional. Porém, esta é uma pequena contribuição tendo em vista as várias questões que surgiram durante este trabalho e que merecem ser investigadas posteriormente. Por exemplo:

- Quais as adaptações morfológicas ou fisiológicas das espécies do cerrado hiperestacional ao alagamento?
- Existem diferenças funcionais entre o cerrado hiperestacional e o estacional, como, por exemplo, nos padrões reprodutivos e no espectro biológico?
- Existem outras áreas de cerrado hiperestacional? Se sim, elas são florística e estruturalmente similares ao cerrado hiperestacional do PNE?

V - Referências bibliográficas

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