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

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Abstract

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 m^2 quadrats in an 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 cespitose 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.

Keywords: 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 and Hadley, 1983). They are dynamic communities, which vary in space and time, and where long- and short-term changes are constantly modifying 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., Coutinho, 1990; Eiten, 1979; Ribeiro and 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

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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 the 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 km^2 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) first related the 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 includes 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 and 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 in the rainy season. Waterlogging is due to the soil saturation by rainfall, generally associated with impermeable and poorly structured clay horizons (Sarmiento and Monasterio, 1975). It 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 and Drew, 1984).

Batalha et al. (in press) sampled in 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 (Fig. 1). Annual rainfall and mean temperature lie around 1745 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 and 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

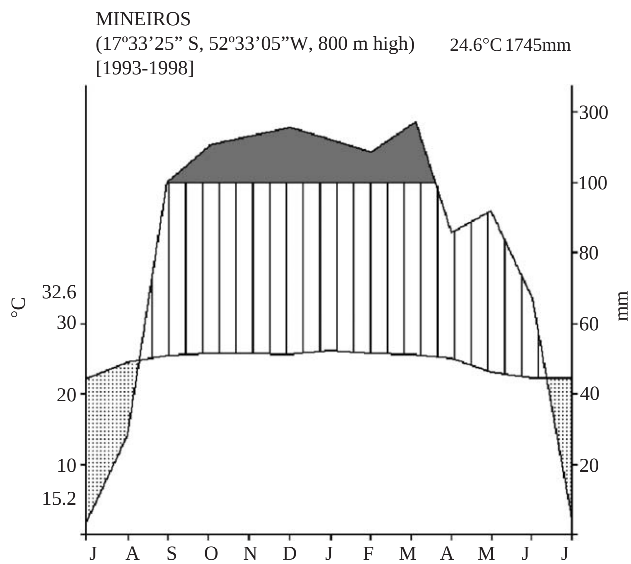

Fig. 1. Climatic diagram (Walter, 1976), constructed from data obtained at the Benedictine Monks Monastery, Mineiros, Goiás State, central Brazil. Absolute minimum and maximum temperatures were not available in the original data (from Batalha and Martins, 2004).

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 m^2 quadrats, in which we sampled all vascular plants except seedlings. We measured height and diameter at soil level of each individual, 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 and 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 deposited 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 ($m^2\,m^{-2}$); and cylindrical volume as the volume occupied by each species ($m^3\,m^{-2}$), according to Mueller-Dombois and Ellenberg (1974). We tested all these variables for normality (Shapiro and 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 and Weaver, 1949), using the natural logarithmic base (Zar, 1999; Krebs, 1999) 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 and 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 ith 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

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

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 and 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 and 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 and 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 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). 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 and Pivello, 2000).

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

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 and 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.

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

In a hyperseasonal savanna in Venezuela, Sarmiento et al. (2004), also using ten 1-m^2 quadrats per site, observed that species density during 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 to waterlogged conditions of most species belonging to the cerrado flora. 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). This is 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 of vegetation begins with a growing phase with a 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 when 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 phase 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, as it is typical of tropical savannas during dry season (Baruch, 1994). The drought-depending water deficit in the plants affects metabolism and morphology, reduces growth and arrests plant 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

Table 4. Number of individuals, basal area (m^2), 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 (%)
Andropogon leucostachyus Kunth	199	0.6443	54.10
Poaceae sp. 3	181	0.0003	10.87
Tristachya leiostachya Nees	78	0.0449	7.61
Ocimum sp.	125	0.0012	7.58
Eugenia angustissima O. Berg	46	< 0.0001	2.76
Axonopus derbyanus Black	5	0.0256	1.98
Melinis minutiflora P. Beauv.	30	0.0022	1.94
Syagrus flexuosa (Mart.) Becc.	17	0.0099	1.67
Loudetiopsis chrysothrix (Nees) Conert	8	0.0157	1.51
Myrciaria delicatula (DC.) O. Berg.	23	< 0.0001	1.38
Galactia martii A. DC.	18	< 0.0001	1.08
Eugenia complicata O. Berg	17	0.0002	1.04
Acosmium subelegans (Mohl.) Yakovlev	14	0.0023	0.99
Hyptis adpressa A. St-Hil. ex Benth.	15	< 0.0001	0.90
Allagoptera campestris (Mart.) Kuntze	3	0.0092	0.78
Erythroxylum campestre A. St-Hil.	8	< 0.0001	0.48
Psidium australe Camb.	7	0.0001	0.42
Myrcia torta A. DC.	7	< 0.0001	0.42
Paspalum pectinatum Nees	4	0.0020	0.37
Rynchelytrum repens (Nees) C.E.Hubb.	1	0.0042	0.34
Sisyrinchium vaginatum Spreng.	3	0.0004	0.21
Byttneria oblongata Pohl	3	0.0004	0.21
Mimosa gracilis Benth.	3	< 0.0001	0.18
Cuphea carthagenensis (Jacq.) Macbr.	3	< 0.0001	0.18
Panicum rudgei Roem. & Schult.	2	0.0006	0.16
Chromolaena squalida (A. DC.) King & H.Rob.	2	< 0.0001	0.12
Gymnopogon foliosus (Willd.) Nees	2	< 0.0001	0.12
Croton pohlianus Müll.Arg.	1	< 0.0001	0.06
Eragrostis articulata (Schrank) Nees	1	< 0.0001	0.06
Casearia sp.	1	< 0.0001	0.06
Froelichia procera (Seub.) Pedersen	1	< 0.0001	0.06
Unknown sp. 1	1	< 0.0001	0.06
Pfaffia helichrysoides (Moq.) Kuntze	1	< 0.0001	0.06
Annona crassiflora Mart.	1	< 0.0001	0.06
Eupatorium campestre A. DC.	1	< 0.0001	0.06
Ipomea procurrens Meins.	1	< 0.0001	0.06
Peltaea edouardii (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 (m^2 m^{-2}) and cylindrical volume (m^3 m^{-2}) in the hyperseasonal cerrado, Emas National Park (approximately, 18°18′07″S, 52°57′56″W), central Brazil

Descriptor	February	May	August	November	P	$1-\beta$
Species density	5.900 $^{a}\pm$2.025	9.200 $^{b}\pm$2.271	8.400 $^{ab}\pm$2.458	11.400 $^{b}\pm$3.864	<0.001	100%
Diversity	1.922 $^{b}\pm$0.006	1.940 $^{b}\pm$0.003	1.340 $^{a}\pm$0.004	2.399 $^{c}\pm$0.002	—	—
Evenness	0.66	0.55	0.41	0.66	—	—
Plant density	27.200 $^{a}\pm$14.382	77.100 $^{ab}\pm$81.281	67.700 $^{ab}\pm$68.962	83.400 $^{b}\pm$22.312	<0.001	74%
Basal area	0.093 $^{bc}\pm$0.031	0.114 $^{c}\pm$0.028	0.024 $^{a}\pm$0.007	0.076 $^{b}\pm$0.004	<0.001	100%
Cylindrical volume	0.058 $^{bc}\pm$0.027	0.083 $^{c}\pm$0.047	0.014 $^{a}\pm$0.005	0.043 $^{b}\pm$0.012	<0.001	100%

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, $1-\beta$ is the power of the test. Different letters indicate significant differences between means ($\alpha = 0.05$).

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, during 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.

Various 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 within certain boundaries 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, strictly determine the community structure.

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