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Original article

Soil-vegetation relationships in hyperseasonal cerrado, seasonal cerrado, and wet grassland in Emas National Park (central Brazil)

Priscilla Kobayashi Amorim*, Marco Antônio Batalha

Department of Botany, Federal University of São Carlos, PO Box 676, 13565-905, São Carlos, SP, Brazil

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ABSTRACT

In South America, the largest savanna region is the Brazilian cerrado, in which there are few areas that become waterlogged in the rainy season. However, we found a small cerrado area in which the soil is poorly drained and becomes waterlogged at the end of the rainy season, allowing the appearance of a hyperseasonal cerrado. We investigated the soil-vegetation relationships in three vegetation forms: hyperseasonal cerrado, seasonal cerrado, and wet grassland. We collected vegetation and soil samples in these three vegetation forms and submitted obtained data to a canonical correspondence analysis. Our results showed a distinction among hyperseasonal cerrado, seasonal cerrado and wet grassland, which presented different floristic compositions and species abundances. The edaphic variables best related to the hyperseasonal and seasonal cerrados were sand, base saturation, pH, and magnesium. The wet grassland was related to higher concentrations of clay, organic matter, aluminium saturation, aluminium, phosphorus, and potassium. Although it is not possible to infer causal relationships based on our results, we hypothesize that the duration of waterlogging in the hyperseasonal cerrado may not be long enough to alter most of its soil characteristics, such as organic matter, phosphorus, and potassium, but may be long enough to alter some, such as pH and base saturation, as the soils under both cerrados were more similar to one another than to the soil under the wet grassland. Since waterlogging may alter soil characteristics and since these characteristics were enough to explain the plant community variation, we may conclude that water excess—permanent or seasonal—is one of the main factors to distinguish the three vegetation forms, which presented different floristic compositions and species abundances.

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1. Introduction

Savannas are tropical and subtropical formations characterized by an almost continuous grass layer, interrupted only by shrubs and trees in varying proportions, and in which the

main growth patterns are closely associated with alternating wet and dry seasons (Bourlière and Hadley, 1983). Based on this seasonality, Sarmiento (1983) suggested an ecological classification of the savannas, dividing them into four groups: (i) semi-seasonal savannas, with a constantly or mostly wet

* Corresponding author: Fax: +55 16 3351 8308.

E-mail address: prikobarim@yahoo.com.br (P.K. Amorim).

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climate, characterized by one or two short dry seasons; (ii) seasonal savannas, characterized by an extended rainless season, in which drought and fire induce a pronounced rhythmicity in their functioning; (iii) hyperseasonal savannas, characterized by the alternation of two contrasting stresses during each annual cycle, one induced by drought and fire, the other by soil saturation; and (iv) marshy savannas, in which the water excess may last most of the year, whereas a period of acute water shortage either does not exist or is very brief.

The Brazilian cerrado is the major savanna region in America and once covered about 2 million km², mainly in the Brazilian Central Plateau, under seasonal climate, with wet summer and dry winter (Ratter et al., 1997). Even if some cerrado physiognomies are not considered savannas (Coutinho, 1990), seasonality is one of the essential features of the cerrado, which, thus, may also be divided according to Sarmiento's (1983) classification. Seasonal cerrados are by far the most widespread type, whereas hyperseasonal cerrados areas are rather restricted (Sarmiento, 1983). In some cerrado areas, there are lateritic layers that may be the cause of poor drainage and, possibly, of waterlogging (Lopes and Cox, 1977). Castro et al. (1998) reported some areas in north-eastern Brazil as possible hyperseasonal cerrados due to great water-table variation throughout the year, but as long as there is no waterlogging there, these areas shall be classified as seasonal cerrados. In the Emas National Park (ENP), central Brazil, there is a small area, composed of cerrado species, in which waterlogging occurs in summer and drought in winter. Thus, it should be classified as a hyperseasonal cerrado (Batalha et al., 2005).

Several explanations for the occurrence of savannas, in general, and of the cerrado, in particular, involve soil either as a primary cause or as an indirect factor (Askew and Montgomery, 1983). Cerrado soils are generally oxisols, with low nutrient reserves and high aluminium levels (Haridasan, 2000). Soil factors, such as effective depth, presence of concretions, drainage, exchangeable aluminium, and fertility, are determinants for the occurrence of cerrado physiognomies (Haridasan, 2000). Variations in physiognomy may be accompanied by changes in floristic composition, structure, and productivity due to variations in chemical and physical soil characteristics (Haridasan, 2000). Goodland and Pollard (1973) found that the cerrado physiognomic gradient was correlated with soil fertility. In a core cerrado area Ruggiero et al. (2002), however, found no significant correlation between a physiognomic gradient and soil fertility in a disjunct southern cerrado area.

Soil waterlogging limits oxygen diffusion to the roots (Ponnamperuma, 1984), and the resulting hypoxia or anoxia reduces mineral and water absorption by the plants (Baruch, 1994). In ENP, the soils under hyperseasonal and seasonal cerrados were chemically and physically similar, suggesting that the duration of waterlogging in the hyperseasonal cerrado is not long enough to alter its soil characteristics (Amorim and Batalha, 2006). So, it is possible that the waterlogging of a hyperseasonal cerrado implies differences in soil characteristics when compared to a seasonal cerrado, never waterlogged, and the wet grassland, waterlogged throughout most of the year, and, consequently, differences in plant community structure among these three vegetation forms.

Analyzing species density and some chemical and physical soil characteristics, we addressed the following questions: Do the three vegetation forms present different floristic composition and species abundances? Are the three vegetation forms related to soil characteristics? Are soil fertility and content of exchangeable aluminium related to floristic composition?

2. Material and methods

The Emas National Park (ENP), created in 1961, is one of the largest and most important cerrado reserves in Brazil (Conservation International, 1999). Recently, ENP was included by Unesco (2001) in the World Natural Heritage List as one of the sites containing flora, fauna, and key habitats that characterize the cerrado. The ENP is located on the Brazilian Central Plateau, in the cerrado core region, under tropical warm climate, with three dry months in the winter, classified as Aw according to Köppen (1931). The cerrado in ENP exhibits almost all physiognomies found in this vegetation type, from *campo limpo* (a grassland) to *cerrado sensu stricto* (a woodland). Open cerrado physiognomies prevail in the reserve—*campo limpo*, *campo sujo* (a shrub savanna), and *campo cerrado* (a savanna woodland)—occupying 78.5% of the total area. Other vegetation types, such as wet grassland, riparian forest, and seasonal forest, also exist within the park. In the southwestern part of the reserve, there is a hyperseasonal cerrado area that occupies about 300 ha, waterlogged from February to April, when the water-table rises 0.2 m above soil level.

We sampled three areas in the southwestern portion of the reserve, one composed of hyperseasonal cerrado (approximately, 18°18'07"S and 52°57'56"W), one composed of seasonal cerrado (approximately, 18°17'34"S and 52°58'12"W) and one composed of wet grassland (approximately, 18°15'40"S and 53°01'08"W). These three vegetation forms are physiognomically similar, with a continuous grass layer, scattered shrubs, and without trees. In the hyperseasonal cerrado, there are two contrasting stresses during the year, waterlogging in summer and drought in winter; in the seasonal cerrado, there is drought in winter, but no waterlogging; and in the wet grassland, there is water excess throughout most of the year.

We collected vegetation and soil samples in February 2003, at mid-rainy season, when the hyperseasonal cerrado was waterlogged. In each vegetation form, we placed randomly ten 1 m² quadrats and counted the number of individuals of each vascular plant species. We avoided sampling seedlings, defined here as those plants still with cotyledons, due to their being dynamic throughout the year. In the case of caespitose herbs, we considered as an individual the whole tuft. We collected botanical material and identified it to species level by comparison with reference vouchers collected by Batalha and Martins (2002), by using an identification key based on vegetative characters (Batalha and Mantovani, 1999), or by comparison with lodged vouchers in the São Paulo Botanical Institute herbarium. When we could not identify the collected vouchers to species level, we classified them as morphospecies. We lodged the collected material at the Federal University of São Carlos herbarium.

In each sampling point, we also collected soil samples at four depths (0–0.05, 0.05–0.25, 0.4–0.6, and 0.8–1.0 m) for chemical and granulometric analyses. Chemical and granulometric analyses were conducted at the Soil Sciences Laboratory of the University of São Paulo. We analyzed soil characteristics, according to the procedures described by van Raij et al. (1987): air dried soil samples were sieved (2.0 mm) and analyzed for total organic matter (OM) by spectrophotometry after oxidation with sodium dichromate in the presence of sulfuric acid and a subsequent titration with ammoniac ferrous sulfate; phosphorus (P) was determined by spectrophotometry after anion exchange resin extraction; exchangeable aluminium (Al) and basic cations (K, Ca, Mg) were extracted with 1 mol_c l⁻¹ KCl, cation exchange resin, and buffer SMP, respectively; cation exchange capacity (CEC) was determined based on the sum of K, Ca, and Mg; base saturation (V) was calculated as a percentage of the total CEC; aluminium saturation (m) was calculated based on effective cation exchange capacity; sum of bases (SB) was represented as the sum of Ca, Mg, and K; and soil pH was determined in CaCl₂ (0.01 M) solution. Granulometric analysis followed Boyoucus's method, described by Camargo et al. (1986), to determine the percentages of sand, silt, and clay.

We ordinated soil characteristics and density of plant species by direct gradient analysis. We used a canonical correspondence analysis (CCA) (Jongman et al., 1995) to investigate relationships between soil characteristics, centered and standardized, and species density in sample quadrats with the MVSP software (Kovach, 1999). As the lengths of the ordination axes were more than 2 SD, most of the response curves were unimodal and a CCA was appropriate (Jongman et al., 1995). Furthermore, tests of real data showed that the CCA is extremely robust when the assumption of unimodal responses do not hold (Jongman et al., 1995). In the vegetation matrix, we had the density of all sampled species and, in the environmental matrix, we had all soil characteristics; with separate environmental matrices for each soil depth. We transformed the data expressed in percentages, such as clay, sand, silt, V, and m, to their arcsines prior to the analyses (Zar, 1999).

After a preliminary analysis, we eliminated variables with high multicollinearity, detected by high inflation values, and variables poorly correlated with ordination axes, indicated by low intraset correlation coefficients and non-significant canonical coefficients (t values <2.1). The intraset correlations are the correlations of the environmental variables with the site scores that are a linear combination of these variables, differing from the interset correlations, which are weighted averages of the species scores (Jongman et al., 1995). We tested significance of the overall CCA ordination with a Monte Carlo permutation procedure and 500 runs (Manly, 1998). Results were very similar when rare species were downweighted, so we present only the results without species weighting.

3. Results

We sampled 272 individuals belonging to 18 species in the hyperseasonal cerrado, 575 individuals belonging to 55 species in the seasonal cerrado, and 2276 individuals belonging to 32 species in the wet grassland (Table 1). The richest families

Table 1 – Plant species sampled in ENP and abundance in hyperseasonal cerrado (approximately 18° 18' 07" S and 52° 57' 56" W), seasonal cerrado (approximately 18° 17' 34" S and 52° 58' 12" W) and wet grassland (approximately 18° 15' 40" S and 53° 01' 08" W), Emas National Park, central Brazil, February 2003

| Family/species | hsc | sc | wg |
|--|-----|----|-----|
| Amaranthaceae | | | |
| <i>Froelichia procera</i> (Seub.) Pedersen | | 9 | |
| Annonaceae | | | |
| <i>Annona crassiflora</i> Mart. | | 9 | |
| <i>Annona warmingiana</i> Mello-Silva & Pirani | | 4 | |
| Arecaceae | | | |
| <i>Allagoptera campestris</i> (Mart.) Kuntze | 3 | 5 | |
| <i>Syagrus flexuosa</i> (Mart.) Becc. | | | 12 |
| Asteraceae | | | |
| <i>Aspilia leucoglossa</i> Malme | | | 1 |
| <i>Erechtites hieracifolia</i> (L.) Raf. | 2 | | |
| <i>Wedelia macedoi</i> H. Rob. | | | 2 |
| Bignoniaceae | | | |
| <i>Tabebuia ochracea</i> (Cham.) Standl. | | | 5 |
| Celastraceae | | | |
| <i>Tontelea micrantha</i> (Mart.) A.C.Sm. | 5 | 1 | |
| Connaraceae | | | |
| <i>Rourea induta</i> Planch. | | | 1 |
| Cyperaceae | | | |
| <i>Exochogyne amazonica</i> C.B. Clarke | | | 1 |
| <i>Rhynchospora diamantina</i> (C.B. Clarke) Kükenth | | | 31 |
| <i>Rhynchospora globosa</i> (Kunth) Roem. & Schult | | | 14 |
| Dilleniaceae | | | |
| <i>Davilla elliptica</i> A.St-Hil. | | | 1 |
| Droseraceae | | | |
| <i>Drosera communis</i> A.St-Hil | | | 3 |
| Ebenaceae | | | |
| <i>Diospyros hispida</i> A. DC. | | | 9 |
| Ericaceae | | | |
| <i>Gaylussacia brasiliensis</i> C.F.W. Meissn. | | | 58 |
| Eriocaulaceae | | | |
| <i>Singonanthus xeranthemoides</i> Ruhland | | | 83 |
| Erythroxylaceae | | | |
| <i>Erythroxylum deciduum</i> A. St-Hill | | | 6 |
| <i>Erythroxylum suberosum</i> A. St-Hill | | | 5 |
| Euphorbiaceae | | | |
| <i>Croton antisiphiliticus</i> Mart. | | | 16 |
| <i>Croton glandulosus</i> Müll. Arg. | | | 200 |
| <i>Phyllanthus niruri</i> L. | | | 28 |
| Fabaceae | | | |
| <i>Acosmium subelegans</i> (Mohl.) Yakovlev | 11 | 4 | |
| <i>Andira laurifolia</i> Benth. | 16 | | |
| <i>Camptosema ellipticum</i> (Desv.) Burkart | | | 2 |
| <i>Eriosema crinitum</i> (Kunth) Gardner | | | 2 |
| <i>Eriosema longifolium</i> Benth. | | | 3 |
| <i>Galactia decumbens</i> (Benth.) Chodat & Hassl. | | | 4 |
| <i>Galactia martii</i> A. DC. | 6 | 2 | |
| <i>Mimosa gracilis</i> Benth. | | | 3 |
| Flacourtiaceae | | | |
| <i>Casearia</i> sp. | | | 3 |

(continued on next page)

Table 1 (continued)

| Family/species | hsc | sc | wg |
|---|-----|----|-----|
| Gentianaceae | | | |
| <i>Iribachia caerulescens</i> (Aubl.) Griseb. | | 4 | |
| Hypoxidaceae | | | |
| <i>Hypoxis</i> sp. | | 5 | |
| Iridaceae | | | |
| <i>Sisyrinchium vaginatum</i> Spreng | 1 | | 19 |
| Lamiaceae | | | |
| <i>Hyptis adpressa</i> A. St-Hill | | 2 | |
| <i>Hyptis pulchella</i> Briq. | | | 11 |
| <i>Hyptis villosa</i> Pohl ex Benth. | | 3 | |
| <i>Ocimum</i> sp. | 4 | 34 | |
| Lycopodiaceae | | | |
| <i>Lycopodiella cernua</i> (L.) Pic.Serm. | | 2 | |
| Lythraceae | | | |
| <i>Cuphea carthagenensis</i> (Jacq.) Macbr. | | 1 | |
| <i>Cuphea</i> sp. | | | 7 |
| Malpighiaceae | | | |
| <i>Byrsonima guilleminiana</i> A. Juss. | | 3 | |
| Malvaceae | | | |
| <i>Byttneria oblongata</i> Pohl | 4 | 12 | |
| <i>Peltaea edouardii</i> (Hochr.) Krapov. & Cristóbal | | 4 | |
| <i>Waltheria douradinha</i> A. St-Hill | | 7 | |
| Melastomataceae | | | |
| <i>Pterolepsis repanda</i> Triana | | | 13 |
| Myrtaceae | | | |
| <i>Campomanesia pubescens</i> (A. D.C.) O. Berg | | 80 | |
| <i>Eugenia angustissima</i> O. Berg | | 44 | |
| <i>Eugenia calycina</i> Cambess. | | 7 | |
| <i>Eugenia complicata</i> O. Berg | 50 | | |
| <i>Eugenia livida</i> O. Berg. | 1 | | |
| <i>Myrcia rhodoseopala</i> Kiaersk. | 2 | 11 | |
| <i>Myrcia uberavensis</i> O. Berg | 1 | 1 | |
| Myrtaceae sp.1 | | 2 | |
| Myrtaceae sp.2 | | 19 | |
| <i>Psidium australe</i> Cambess. | 23 | 2 | |
| <i>Psidium cinereum</i> Mart. | | 3 | |
| <i>Psidium laruotteanum</i> Cambess. | | 17 | |
| <i>Psidium rufum</i> Mart. ex A. DC. | | 8 | |
| Ochnaceae | | | |
| <i>Ouratea nana</i> (A. St-Hil.) Engl. | | 4 | |
| <i>Ouratea spectabilis</i> (Mart.) Engl. | | 13 | |
| Poaceae | | | |
| <i>Andropogon leucostachys</i> Kunth | 122 | | |
| <i>Anthraenantiopsis perforata</i> (Nees) Parodi | | 2 | |
| <i>Aristida riparia</i> Trin. | | 2 | |
| <i>Axonopus comans</i> (Trin.) Kuhlman | | | 926 |
| <i>Axonopus derbyanus</i> Black | | 4 | |
| <i>Brachiaria decumbens</i> Stapf | 5 | | |
| <i>Elionurus latiflorus</i> Nees | | 69 | 1 |
| <i>Eragrostis articulata</i> (Schrank) Nees | | 5 | |
| <i>Eragrostis bahiensis</i> Schrad ex. Schult | | | 13 |
| <i>Panicum hians</i> Elliot. | | | 5 |
| <i>Panicum parvifolium</i> Lam. | 9 | | |
| <i>Panicum rudgei</i> Roem. & Shult | 7 | 2 | |
| <i>Paspalum dedecae</i> Quarin | | | 50 |
| <i>Paspalum maculosum</i> Trin. | | | 57 |
| <i>Paspalum pectinatum</i> Nees | | 7 | |
| <i>Rhynchelitrum repens</i> (Nees) C.E. Hubb | | 3 | |
| <i>Schizachyrium tenerum</i> Nees | | | 352 |

Table 1 (continued)

| Family/species | hsc | sc | wg |
|--|-----|----|-----|
| <i>Trachypogon</i> sp. | | | 5 |
| <i>Tristachya leiostachya</i> Nees | | 88 | |
| Poaceae sp. 1 | | | 12 |
| Poaceae sp. 2 | | | 1 |
| Poaceae sp. 3 | | | 4 |
| Poaceae sp. 4 | | | 7 |
| Poaceae sp. 5 | | | 100 |
| Poaceae sp. 6 | | | 92 |
| Rubiaceae | | | |
| <i>Coccocypselum lyman-smithii</i> Standl. | | | 22 |
| Sapindaceae | | | |
| <i>Serjania cissooides</i> Radlk. | | 1 | |
| Sapotaceae | | | |
| <i>Pradosia brevipes</i> (Pierre) Penn. | | 6 | |
| Verbenaceae | | | |
| <i>Stachytarpheta linearis</i> Moldenke | | | 8 |
| Xyridaceae | | | |
| <i>Xyris</i> sp.1 | | | 142 |
| hsc, hyperseasonal cerrado; sc, seasonal cerrado; wg, wet grassland. | | | |

were Poaceae (25 species), Myrtaceae (13 species) and Fabaceae (8 species), which together accounted for 49.46% of the total number of species. Soil properties according to vegetation form and soil depth (Table 2) against species density in the CCA showed significant correlations in the first axis at all soil depths ($P < 0.01$) and in the second axis at first depth ($P < 0.01$). Summary of CCA outputs for the first four axes and all soil depths are given in Table 3.

Using surface soil data, the sum of all unconstrained eigenvalues was 7.69 and the sum of canonical eigenvalues was 1.91. Cumulative percentages of variance in the first four axes were 16.61%, 27.19%, 31.86%, and 36.55%, respectively (Table 3). Species–environment correlations were 0.99, 0.87, 0.87, and 0.84 for the first four axes, respectively (Table 3). Considering both canonical coefficient and intraset correlation coefficient, the soil variables best related to the first axis were clay, organic matter, phosphorus, aluminium saturation, aluminium, and potassium, all of them negatively correlated (Table 4, Fig. 1). The soil variables best related to the second axis were pH and base saturation, positively related, and magnesium, negatively related (Table 4, Fig. 1).

The ordination diagram (Fig. 1) showed three distinct groups, each one corresponding to one of the sampled vegetation forms. The first axis separated the wet grassland from the hyperseasonal and seasonal cerrado, whereas the second axis separated the hyperseasonal cerrado from the seasonal cerrado. The wet grassland presented negative scores in the first axis, being related to larger amounts of clay, organic matter, phosphorus, aluminium saturation, aluminium, and potassium; whereas the hyperseasonal and seasonal cerrados presented positive scores in the first axis, being related to higher values of sand, pH, base saturation, and magnesium (Fig. 1). In the second axis, the hyperseasonal cerrado presented positive scores, related with higher values of pH and

Table 2 – Soil chemical and physical characteristics (mean ± standard deviation) at four depths in hyperseasonal cerrado (approximately 18° 18'07"S and 52° 57'56"W), seasonal cerrado (approximately 18° 17'34"S and 52° 58'12"W) and wet grassland (approximately 18° 15'40"S and 53° 01'08"W) in Emas National Park, central Brazil, February 2003

| Variable | Depth (m) | hsc | sc | wg |
|---|-----------|--------------|---------------|----------------|
| pH | 0–0.05 | 4.18 ± 0.09 | 4.05 ± 0.08 | 3.92 ± 0.09 |
| | 0.05–0.25 | 4.15 ± 0.12 | 4.02 ± 0.06 | 4.04 ± 0.21 |
| | 0.4–0.6 | 4.50 ± 0.09 | 4.29 ± 0.06 | 4.28 ± 0.20 |
| | 0.8–1.0 | 4.95 ± 0.11 | 4.82 ± 0.10 | 4.53 ± 0.26 |
| OM (g kg ⁻¹) | 0–0.05 | 48.1 ± 10.0 | 50.6 ± 4.9 | 170.4 ± 22.1 |
| | 0.05–0.25 | 30.3 ± 4.6 | 41.6 ± 3.7 | 188.7 ± 48.9 |
| | 0.4–0.6 | 19.2 ± 3.7 | 25.2 ± 2.9 | 164.5 ± 82.4 |
| | 0.8–1.0 | 13.6 ± 3.8 | 19.3 ± 2.1 | 74.0 ± 35.9 |
| P (mg kg ⁻¹) | 0–0.05 | 4.2 ± 0.9 | 4.0 ± 0.9 | 24.1 ± 5.8 |
| | 0.05–0.25 | 1.8 ± 0.6 | 2.9 ± 0.5 | 20.1 ± 10.1 |
| | 0.4–0.6 | 1.0 ± 0.0 | 1.1 ± 0.3 | 4.0 ± 2.1 |
| | 0.8–1.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 2.1 ± 1.8 |
| K (mmol _c kg ⁻¹) | 0–0.05 | 2.11 ± 0.24 | 2.21 ± 0.25 | 3.87 ± 0.71 |
| | 0.05–0.25 | 1.68 ± 0.27 | 1.97 ± 0.27 | 2.87 ± 0.70 |
| | 0.4–0.6 | 1.18 ± 1.08 | 1.10 ± 0.12 | 1.38 ± 0.24 |
| | 0.8–1.0 | 0.77 ± 0.19 | 0.93 ± 0.11 | 1.02 ± 0.16 |
| Ca (mmol _c kg ⁻¹) | 0–0.05 | 4.1 ± 0.8 | 4.0 ± 1.2 | 2.6 ± 1.1 |
| | 0.05–0.25 | 1.4 ± 0.6 | 1.5 ± 0.5 | 2.4 ± 1.7 |
| | 0.4–0.6 | 1.1 ± 0.3 | 1.1 ± 0.3 | 1.3 ± 0.6 |
| | 0.8–1.0 | 1.0 ± 0.0 | 1.1 ± 0.3 | 1.3 ± 0.6 |
| Mg (mmol _c kg ⁻¹) | 0–0.05 | 3.1 ± 0.5 | 4.1 ± 0.7 | 2.8 ± 1.1 |
| | 0.05–0.25 | 1.5 ± 0.5 | 1.8 ± 0.4 | 2.3 ± 0.8 |
| | 0.4–0.6 | 1.1 ± 0.3 | 1.0 ± 0.0 | 1.2 ± 0.6 |
| | 0.8–1.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 |
| Al (mmol _c kg ⁻¹) | 0–0.05 | 7.2 ± 1.5 | 10.4 ± 1.1 | 28.7 ± 5.8 |
| | 0.05–0.25 | 5.8 ± 1.3 | 8.8 ± 1.0 | 24.7 ± 7.3 |
| | 0.4–0.6 | 2.0 ± 0.9 | 3.1 ± 2.5 | 19.6 ± 9.4 |
| | 0.8–1.0 | 0.2 ± 0.4 | 0.6 ± 0.5 | 5.9 ± 4.9 |
| m (%) | 0–0.05 | 43.5 ± 5.9 | 50.4 ± 6.4 | 75.4 ± 6.2 |
| | 0.05–0.25 | 55.7 ± 10.9 | 62.6 ± 6.7 | 76.3 ± 6.6 |
| | 0.4–0.6 | 37.0 ± 11.7 | 45.2 ± 12.3 | 78.7 ± 15.6 |
| | 0.8–1.0 | 5.7 ± 12.1 | 15.2 ± 13.1 | 56.7 ± 19.3 |
| SB (mmol _c kg ⁻¹) | 0–0.05 | 9.31 ± 1.38 | 10.31 ± 1.93 | 9.27 ± 2.47 |
| | 0.05–0.25 | 4.58 ± 1.24 | 5.27 ± 0.97 | 7.57 ± 2.92 |
| | 0.4–0.6 | 3.38 ± 1.17 | 3.20 ± 0.37 | 3.88 ± 1.37 |
| | 0.8–1.0 | 2.77 ± 0.19 | 3.03 ± 0.32 | 3.42 ± 1.02 |
| CEC (mmol _c kg ⁻¹) | 0–0.05 | 86.11 ± 6.27 | 105.31 ± 4.97 | 156.37 ± 36.02 |
| | 0.05–0.25 | 62.68 ± 4.94 | 88.47 ± 4.18 | 142.57 ± 51.29 |
| | 0.4–0.6 | 36.08 ± 3.52 | 45.10 ± 4.02 | 144.48 ± 42.02 |
| | 0.8–1.0 | 25.67 ± 1.36 | 30.13 ± 1.98 | 81.62 ± 28.58 |
| V (%) | 0–0.05 | 10.6 ± 1.2 | 9.8 ± 1.7 | 6.2 ± 1.7 |
| | 0.05–0.25 | 7.3 ± 2.1 | 5.8 ± 1.1 | 6.0 ± 2.8 |
| | 0.4–0.6 | 9.6 ± 2.9 | 7.1 ± 0.8 | 3.0 ± 1.2 |
| | 0.8–1.0 | 10.9 ± 1.2 | 9.9 ± 1.2 | 4.8 ± 2.7 |
| Clay (%) | 0–0.05 | 31.9 ± 2.3 | 26.9 ± 2.6 | 77.2 ± 2.8 |
| | 0.05–0.25 | 29.8 ± 1.8 | 24.7 ± 2.1 | 75.6 ± 5.2 |
| | 0.4–0.6 | 25.2 ± 2.7 | 20.5 ± 0.8 | 66.1 ± 11.7 |
| | 0.8–1.0 | 25.7 ± 2.1 | 20.6 ± 2.7 | 66.4 ± 11.6 |
| Silt (%) | 0–0.05 | 6.5 ± 1.3 | 5.0 ± 2.2 | 12.2 ± 3.3 |
| | 0.05–0.25 | 3.8 ± 1.7 | 4.2 ± 1.9 | 13.8 ± 3.9 |
| | 0.4–0.6 | 4.1 ± 1.3 | 4.4 ± 1.4 | 18.9 ± 7.3 |
| | 0.8–1.0 | 5.9 ± 1.6 | 4.8 ± 1.9 | 18.1 ± 8.1 |
| Sand (%) | 0–0.05 | 61.6 ± 2.8 | 68.1 ± 3.1 | 10.6 ± 2.8 |
| | 0.05–0.25 | 66.4 ± 2.1 | 71.1 ± 2.3 | 10.6 ± 4.3 |
| | 0.4–0.6 | 70.7 ± 2.6 | 75.1 ± 1.5 | 15.0 ± 16.2 |
| | 0.8–1.0 | 68.4 ± 2.2 | 74.6 ± 2.5 | 15.5 ± 17.8 |

hsc, hyperseasonal cerrado; sc, seasonal cerrado; wg, wet grassland; OM, organic matter; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; Al, exchangeable aluminium; m, aluminium saturation; SB, sum of bases; CEC, cation exchange capacity; V, base saturation.

Table 3 – Summary of correspondence canonical analysis outputs for the first four axes and all soil depths

| | Depth (m) | Axis 1 | Axis 2 | Axis 3 | Axis 4 |
|---------------------------------|-----------|--------|--------|--------|--------|
| Eigenvalues | 0–0.05 | 0.99 | 0.63 | 0.28 | 0.28 |
| | 0.05–0.25 | 0.99 | 0.53 | 0.24 | 0.19 |
| | 0.4–0.6 | 0.99 | 0.73 | 0.30 | 0.18 |
| | 0.8–1.0 | 0.99 | 0.65 | 0.35 | 0.25 |
| Percentage of variance | 0–0.05 | 16.61 | 10.58 | 4.77 | 4.69 |
| | 0.05–0.25 | 16.63 | 8.89 | 4.14 | 3.30 |
| | 0.4–0.6 | 16.54 | 12.12 | 4.99 | 2.93 |
| | 0.8–1.0 | 16.56 | 10.80 | 5.78 | 4.15 |
| species–environment correlation | 0–0.05 | 0.99 | 0.87 | 0.87 | 0.84 |
| | 0.05–0.25 | 0.99 | 0.81 | 0.82 | 0.83 |
| | 0.4–0.6 | 0.99 | 0.91 | 0.86 | 0.80 |
| | 0.8–1.0 | 0.99 | 0.87 | 0.88 | 0.81 |

base saturation, and the seasonal cerrado presented negative scores, related with higher values of magnesium, aluminium saturation, and cation exchange capacity (Fig. 1).

4. Discussion

Canonical correspondence analysis showed that the edaphic variables we measured explained only part of the gradient variation, as pointed out by the low cumulative percentages of variance and by the difference between the sum of the unconstrained eigenvalues and the canonical eigenvalues. Nevertheless, this fact did not invalidate the relationships, since they were statistically significant, CCA tends to underestimate the variance explained, and the sum of the eigenvalues is an inadequate measure of compositional variation (Okland,

1999). Species–environment correlations were high, showing a high degree of association between plant species and measured soil characteristics.

The values of the soil characteristics were within the expected range for the cerrado (Lopes and Cox, 1977; Ruggiero et al., 2002; Motta et al., 2002). The correspondence between soil and vegetation was higher for surface soil data and lower for soil at 0.8–1.0 m deep, as in a southern cerrado reserve (Ruggiero et al., 2002). There is an intimate relationship between the properties of surface soil and the floristic composition and species abundance, which affects nutrient and water absorption and plant biomass (Furley, 1976). Such correspondence between plant community and surface soil characteristics may be explained by the fact that the vegetation influences soil features at upper layers by transferring organic matter through nutrient cycling (Ruggiero et al., 2002).

The three environments we sampled formed distinct groups in the ordination diagram as a consequence of different floristic composition and species abundance, corroborating Batalha et al. (2005). There was a low floristic similarity between the seasonal cerrado and the wet grassland, since there was only one species shared by these two environments, *Elionorus latiflorus*. Probably, the two contrasting stresses in the hyperseasonal cerrado act as environmental filters (Chase, 2003) and limit the number of species able to grow in these conditions, reflecting the physiological incapacity of most cerrado species, generally dryland ones, in tolerating waterlogging and of most wet grassland species, generally wetland ones, in tolerating drought (Batalha et al., 2005). There was a larger variation concerning floristic composition and species abundance between the wet grassland and both cerrados, reflected in the first ordination axis and related to larger amounts of clay, organic matter, phosphorus, aluminium saturation, aluminium, and potassium in the wet grassland. Constant waterlogging in this vegetation form causes hypoxia or anoxia, which is the main limitation that reduces root aerobic respiration and the absorption of minerals and water (Baruch, 1994), and consequently decreases decomposition rates and increases the amounts of organic matter in the soil (Crawley, 1997). Indeed, wet grasslands are generally related to larger amounts of organic matter (Critchley et al., 2002). Clay, as a colloidal component of the soil, is related to base adsorption and, consequently, is important for the vegetation (Ellis and Mellor, 1995). Wetland communities in Belize also appeared on soils with increased amounts of clay (Bridgewater et al., 2002). Under waterlogging, there is also an increase in aluminium concentration (Sistani et al., 1999) and reduction of ferrous ions that indirectly increases phosphorus and potassium concentrations (Gopal and Masing, 1990).

There was also another variation concerning plant community between the hyperseasonal and the seasonal cerrados, reflected in the second ordination axis and related to higher values of pH and base saturation in the hyperseasonal cerrado and to higher values of magnesium, aluminium saturation, and cation exchange capacity in the seasonal cerrado. The higher values of pH and base saturation in hyperseasonal cerrado may be related to the temporary waterlogging that causes hypoxia or anoxia and alters the physico-chemical environment of the roots: pH tends to be neutral and availability of nutrients is changed (Gopal and Masing, 1990).

Table 4 – Canonical coefficients and intraset correlation coefficients for axes 1 and 2 for the edaphic variables supplied in the CCA using 0–0.05 m depth soil data

| | Canonical coefficients | | Intraset correlation coefficients | |
|------|------------------------|--------|-----------------------------------|--------|
| | Axis 1 | Axis 2 | Axis 1 | Axis 2 |
| pH | 0.05 | 0.32 | 0.61 | 0.34 |
| OM | –0.06 | –0.43 | –0.95 | –0.06 |
| P | 0.13 | 0.39 | –0.89 | –0.03 |
| K | 0.06 | 0.12 | –0.81 | –0.09 |
| Ca | 0.00 | 0.00 | 0.47 | 0.12 |
| Mg | 0.15 | 0.42 | 0.34 | –0.17 |
| Al | 0.21 | 0.86 | –0.88 | –0.14 |
| SB | –0.09 | –2.11 | 0.04 | –0.06 |
| CEC | –0.26 | 0.86 | –0.67 | –0.16 |
| V | –0.14 | 0.60 | 0.70 | 0.18 |
| m | –0.18 | –3.34 | –0.87 | –0.26 |
| Clay | –0.94 | 1.83 | –0.99 | 0.02 |
| Sand | 0.00 | 0.00 | 0.99 | –0.04 |
| Silt | –0.06 | 0.55 | –0.74 | 0.12 |

OM, organic matter; P, phosphorus; K, potassium; Ca, calcium; Mg, magnesium; Al, exchangeable aluminium; m, aluminium saturation; SB, sum of bases; CEC, cation exchange capacity; V, base saturation.

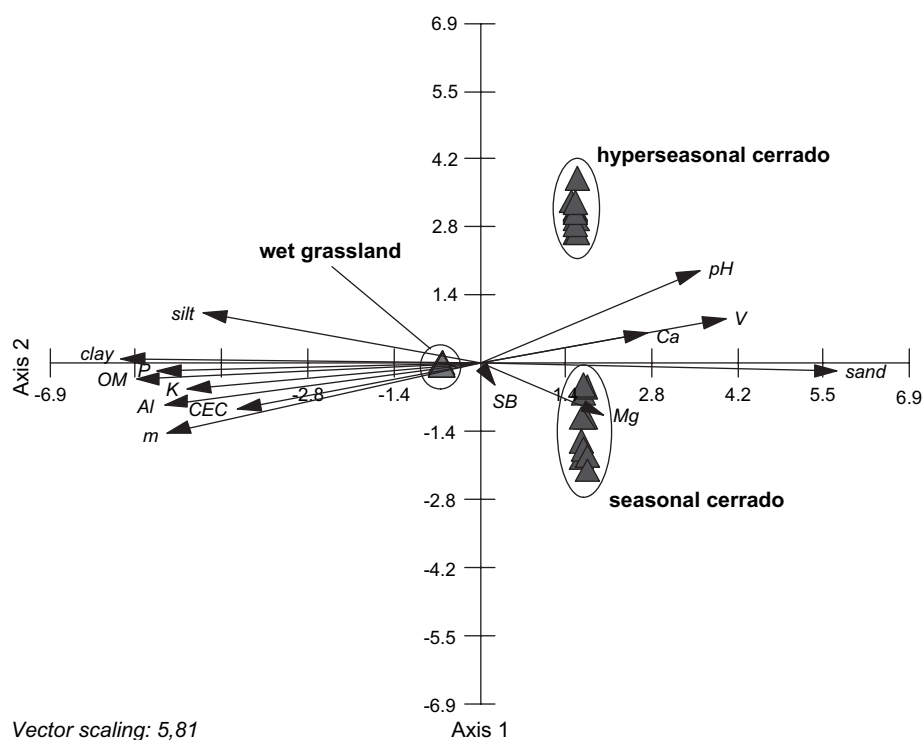


Fig. 1 – Canonical correspondence analysis, using the species density and the surface soil (0–0.05 m) data for the hyperseasonal cerrado, seasonal cerrado, and wet grassland in Emas National Park, Brazil, February 2003.

Arens (1963) presented his “aluminium-toxic scleromorphism theory”, which stated that high amounts of soluble aluminium in the soil are toxic to cerrado plants. At soil pH values at or below five, toxic forms of Al are solubilized into the soil solution (Kochian et al., 2005). Since aluminium solubility and concentration in the exchangeable form are controlled by soil acidity and since H^+ (hydrogen ions) competes with essential nutrients for the same chemical sites (Ellis and Mellor, 1995; Kochian et al., 2005), aluminium promotes soil impoverishment and, indirectly, scleromorphism of cerrado species. Exchangeable aluminium decreases the nutrient availability to the plants, lowering phosphorus absorption or its precipitation in intercellular spaces (Malavolta et al., 1977) and magnesium and calcium absorption from roots (Marschner, 1989).

Nevertheless, even if cerrado soils are characterized by high aluminium concentration (Haridasan, 2000), we found higher amounts of aluminium in the wet grassland soil, more acid than the cerrado soils. As we did not find cerrado species of the Melastomataceae, Rubiaceae, and Vochysiaceae families, which accumulate aluminium in their leaves (Haridasan, 2000), lower levels of aluminium in hyperseasonal and seasonal cerrado soils may be a consequence of changes in the rhizosphere environment promoted by some plant species that exude a large variety of organic compounds that combine with aluminium ions in the soil solution and reduce aluminium effects (Tyler and Falkengren-Grerup, 1998).

The soils under the three environments were nutrient-poor ones, but with different limitations. The wet grassland in ENP does not seem to be limited by phosphorus, but many studies on nutrient limitation in wet grasslands reveal

N-limitation for the plant community (Boeye et al., 1997), because the anaerobic root conditions generally reduce mineralization and stimulate denitrification, lowering nitrogen supply to plants (Bodelier et al., 1998). Larger phosphorus availability may increase the content of nucleic acids, thereby enhancing the rate of protein turnover (Usuda, 1995). Such an effect of phosphorus on the rate of protein turnover may partly compensate for low soil nitrogen availability in perennials competing in the wet grassland (Niinemets and Kull, 2005).

Contrary to the wet grassland, the hyperseasonal and seasonal cerrados seem to be limited by phosphorus and potassium, which can limit plant growth, also in combination with nitrogen (Boeye et al., 1997). Low levels of available phosphorus highly increases the proportion of legumes (Elisseou et al., 1995; Janssens et al., 1998); thus, we should expect a higher proportion of legumes in the hyperseasonal and seasonal cerrados than in the wet grassland, where grasses and sedges should be more abundant (Janssens et al., 1998). In fact, none of the eight legume species we sampled appeared in the wet grassland. Also, we sampled four grasses in the hyperseasonal cerrado, nine grasses in the seasonal cerrado, and 17 grasses and sedges in the wet grassland. Phosphorus limitation may effectively be overcome by increased biomass investment in roots, a common feature in cerrado species, which have a high root to shoot ratios (Haridasan, 2000).

In soils under seasonally alternating flooded and aerated conditions, changes are generally rapid, including reversible changes, such as fluctuations in redox potential, pH, dissolved and exchangeable iron, and exchangeable aluminium (Brinkman and Diepen, 1990). A bias in our analyses is that

the properties of the soil solution in waterlogged soils are different to those of equilibrium extracts of dried soils, what is particularly true for pH and pH-related properties, like CEC and composition of exchangeable ions. Another bias is that our analysis is limited in time and there may be variations in soil characteristics throughout the year in all vegetation forms. Nevertheless, even in the waterlogging period, when the soil conditions under the hyperseasonal cerrado should be closer to those under the wet grassland, the soil characteristics in the hyperseasonal cerrado were similar to those in the seasonal cerrado (Amorim and Batalha, 2006). Moreover, fire frequency increases from the wet grassland, through the hyperseasonal cerrado, to the seasonal cerrado and may alter soil characteristics (Coutinho, 1990).

Although it is not possible to infer causal relationships based on our results, we hypothesize that the duration of waterlogging in the hyperseasonal cerrado may not be long enough to alter most of its soil characteristics, such as organic matter, phosphorus, and potassium, but may be long enough to alter some, such as pH and base saturation, as the soils under both cerrados were more similar to one another than to the soil under the wet grassland. In permanently or temporally flooded areas, plant communities are structured predominantly by abiotic factors (Lenssen et al., 1999), as pointed out by the high species–environment correlation we found. Since waterlogging may alter soil characteristics and since these characteristics were enough to explain the plant community variation, we may conclude that water excess—permanent or seasonal—is one of the main factors to distinguish the three vegetation forms, which presented different floristic compositions and species abundances.

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