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RELAÇÕES ENTRE AS VARIÁVEIS EDÁFICAS E VEGETACIONAIS EM CERRADO HIPERESTACIONAL, CERRADO ESTACIONAL E CAMPO ÚMIDO NO PARQUE NACIONAL DAS EMAS (GO)

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Relações entre as variáveis edáficas e vegetacionais em cerrado hiperestacional, cerrado estacional e campo úmido no Parque Nacional das Emas (GO)

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"Eu não tenho filosofia:

tenho sentidos...

Se falo da Natureza não é porque saiba o que ela é,

Mas porque a amo, e amo-a por isso,

Porque quem ama nunca sabe o que ama,

Nem sabe porque ama,

Nem o que é amar."

Fernando Pessoa

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Resumo

O Domínio do Cerrado ocupava aproximadamente dois milhões de km^2 do território brasileiro, especialmente no Planalto Central. A vegetação de cerrado não é uniforme em sua fisionomia, pois varia desde o campo limpo até o cerradão, mas a maior parte de suas fisionomias podem ser definidas como savana. Em algumas raras áreas de cerrado, a drenagem do solo é muito baixa, provocando o seu alagamento na estação chuvosa e favorecendo o surgimento de cerrados hiperestacionais, em que há dois períodos de estresse, um induzido pela seca e pelo fogo no inverno, e outro induzido pelo alagamento no verão.

Como o solo é um dos principais fatores que controlam a distribuição do cerrado, além de ser determinante para a ocorrência das diferentes fisionomias que o compõem, nosso objetivo neste trabalho foi estudar a relação solo-vegetação em uma área nuclear de cerrado, no Parque Nacional das Emas (GO), em três ambientes: cerrado hiperestacional, cerrado estacional e campo úmido. Amostramos o solo e a vegetação desses três ambientes e comparamos algumas variáveis edáficas e vegetacionais por meio de análise de correspondência canônica. Nossos resultados apresentaram uma distinção florística entre o cerrado hiperestacional, o cerrado estacional e o campo úmido. As variáveis edáficas mais relacionadas com os cerrados hiperestacional e estacional foram porcentagem de areia, saturação por bases, pH e magnésio, enquanto que com o campo úmido foram argila, matéria orgânica, alumínio, saturação por alumínio e potássio. Também relacionamos o número de espécies em cada parcela com algumas variáveis edáficas, por meio de análises de regressão, e encontramos que o pH foi relacionado negativamente, e o alumínio, positivamente, com o número de espécies.

Palavras-chave: alagamento, análise de correspondência canônica, cerrado, hiperestacionalidade, savana, solo.

Abstract

The Cerrado Domain occupied formerly 2 million km^2 of the Brazilian territory, especially in the Central Plateau. The cerrado vegetation is not uniform in physiognomy, ranging from grassland to tall woodland, but with most of its physiognomies within the range defined as tropical savanna. In cerrado, there are few areas that become waterlogged during the rainy season due to the poor drainage of the soil, allowing the appearance of a hyperseasonal cerrado, characterized by two contrasting stresses, one induced by drought and fire during the winter, the other by soil saturation in the summer.

As long as soil is important in the ecology of the cerrado, limiting the cerrado distribution and the occurrence of its physiognomies, we investigated the soil-vegetation relationships in a cerrado core area in Emas National Park, 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. We also investigated the relationships between number of species and soil characteristics, with simple multiple linear regressions, and found that aluminium and pH were the best predictors of species density, the former positively related to species density and the latter negatively related.

Key words: canonical correspondence analysis, cerrado, hyperseasonality, savanna, soil, waterlogging

Sumário

I – Introdução Geral

Introdução geral

As savanas são formações tropicais e subtropicais em que o componente herbáceo-subarbustivo é quase contínuo, interrompido apenas por arbustos em densidades variáveis, e em que os principais padrões de crescimento estão fortemente associados às estações secas (Bourlière e Hadley, 1983). Baseando-se nessa estacionalidade, Sarmiento (1984) propôs uma classificação ecológica das savanas, dividindo-as em quatro grupos: i) savanas semi-estacionais, sob clima úmido na maior parte do tempo, com uma ou duas pequenas estações secas; ii) savanas estacionais, em que uma estação maior sem chuvas faz com que o fogo e a seca definam a ritmicidade de seu funcionamento; iii) savanas hiperestacionais, nas quais ocorre alternância de dois estresses contrastantes durante o ciclo anual, um induzido pela seca e o outro induzido pela saturação do solo; e iv) esteros, nos quais o período de excedente hídrico persiste pela maior parte do ano.

A maior região de savana nas Américas é o cerrado, que ocupava originalmente cerca de 2 milhões de quilômetros quadrados, especialmente no Planalto Central Brasileiro, sob clima estacional, com verão chuvoso e inverno seco (Ratter et al., 1997). Ainda que nem todas as fisionomias de cerrado sejam consideradas savanas (Coutinho, 1990), o cerrado caracteriza-se por sua estacionalidade e pode ser também subdividido segundo a classificação de Sarmiento (1984). Assim, quase toda a área de cerrado é estacional, sem excedente hídrico no verão, mas com uma seca no inverno. Há áreas de cerrado semi-estacional, como manchas dentro do Domínio Amazônico, nas quais a estação seca é menos pronunciada (Sarmiento, 1983).

Áreas de cerrado hiperestacional devem ocupar áreas muito restritas dentro do Domínio do Cerrado, em regiões de interflúvio, mas com drenagem muito baixa ou lenta (Sarmiento 1983). Castro et al. (1998) citaram áreas no Piauí como possíveis cerrados hiperestacionais devido à grande flutuação do lençol freático, mas, já que não há alagamento lá, essas áreas devem ser classificadas como cerrados estacionais. O Parque Nacional das Emas (PNE), criado em 1961, é uma das principais reservas de cerrado no Brasil, já que é uma das maiores e mais bem preservadas

(Conservation International, 1999). Recentemente, 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. No PNE, há uma pequena área, composta por espécies de cerrado, em que há alagamento no verão e seca no inverno, e que, portanto, deve ser classificada como um cerrado hiperestacional (Batalha et al., no prelo).

O alagamento dos solos limita a difusão do oxigênio pelas raízes das plantas (Ponnamperuma, 1984). Hipoxia ou anoxia são os principais fatores que reduzem a absorção de minerais e água pelas raízes (Baruch, 1994) e também alteram o ambiente físico-químico na região das raízes: o pH tende a ser neutro e a disponibilidade de nutrientes é alterada (Gopal and Masing, 1990). Como em solos alagados podem ocorrer mudanças nas características químicas do solo (Ponnamperuma, 1984; Gambrell et al., 1991) e como o solo é um dos principais fatores que podem determinar a ocorrência do cerrado e sua variação fisionômica (Haridasan, 2000), é possível que o alagamento no cerrado hiperestacional implique diferenças nas variáveis edáficas quando comparado com o cerrado estacional, que não alaga, e com o campo úmido, que permanece alagado durante todo o ano, e, conseqüentemente, pode haver diferenças na estrutura da comunidade entre esses três ambientes.

No primeiro capítulo, ao avaliarmos as variáveis edáficas e vegetacionais de um cerrado hiperestacional, cerrado estacional e campo úmido, procuramos responder às seguintes perguntas: de que modo as três formas de vegetação estão relacionadas com as características do solo? A fertilidade do solo e a concentração de alumínio trocável estão relacionadas com a composição florística? As características do solo são importantes na distribuição das formas de vegetação e podem influenciar no número de espécies (Janssens et al., 1998; Roem and Berendse, 2000; Critchley et al., 2002). Sendo assim, no segundo capítulo, ao avaliarmos o número de espécies e as características edáficas nesses mesmos três ambientes, procuramos responder às seguintes perguntas: há alguma relação entre as variáveis edáficas e o número de espécies? Quais as variáveis do solo mais importantes para explicar a variação no número de espécies nesses ambientes?

Escolhemos a apresentação em capítulos no formato de artigos porque facilita o envio para a

publicação dos mesmos. Como esses capítulos estão formatados nos moldes das revistas a que esses artigos foram e serão submetidos, que exigem redação em inglês, eles foram escritos nesse idioma. O artigo do primeiro capítulo foi submetido à Plant Ecology e o segundo será submetido à Brazilian Archives of Biology and Technology.

Referências bibliográficas

Baruch Z 1994 Responses to drought and flooding in tropical forage grasses: II. - Leaf and water potential, photosynthesis rate and alcohol dehydrogenase activity. Plant Soil 164, 97-105.

Batalha M A, Silva I A, Cianciaruso M V e Delitti W B C In press Hyperseasonal cerrado, a new Brazilian vegetation form. Braz. J. Biol.

Bourlière F e Hadley M 1983 Present-day savannas: an overview. In Ecosystems of the world – tropical savannas. Ed. D W Goodall. pp. 1-17. Elsevier, Amsterdam.

Castro A A J ., Martins F R e Fernandes G 1998. The woody flora of cerrado vegetation in the State of Piauí, northeastern Brazil. Edinb. J. Bot. 55, 455-472.

Conservation International 1999 Ações prioritárias para a conservação do Cerrado e do Pantanal. Conservation International, Brasília.

Coutinho L M 1990 Fire in the ecology of the Brazilian cerrado. In Fire in the tropical biota. Ed. J G Goldammer. pp. 81-103. Springer, Berlin.

Critchley C N R, Chambers B J, Fowbert J A, Sanderson R A, Bhogal A and Rose S C 2002a Association between lowland grassland plant communities and soil properties. Biol.Conserv. 105, 199-215.

Gambrell R P, DeLaune R D and Patrick W H 1991 Redox processes in soils following oxygen depletion. In Plant Life Under Oxygen Deprivation: Ecology, Physioloy and Biochemistry. Eds. M B Jackson, D D Davies and H Lambers. pp.101-117. SPB Academic Publishing BV, The Hague.

Gopal B, Masing V 1990 Biology and Ecology. In Wetlands and shallow continental water bodies. Ed. B C Patten. pp. 91-239. SPB Academic Publishing, The Hague.

Haridasan M 2000 Nutrição mineral de plantas nativas do cerrado. Revta. Bras. Fisiol. Veg. 12, 54-64.

Janssens F, Peters A, Tallowin J R B, Bakker J P, Bekker R M, Fillat F and Oomes M J M 1998 Relationship between soil chemical factors and grassland diversity. Plant Soil 202, 69-78.

Ponnamperuma E N 1984. Effects of flooding on soils. In Flooding and plant growth. Ed. T T Koslowski. pp. 265-294. Academic, New York.

Ratter J A, Ribeiro J F, Bridgewater S 1997 The Brazilian cerrado vegetation and threats to its biodiversity. Ann. Bot. 80, 223-230.

Roem W J and Berendse F 2000 Soil acidity and nutrient supply ratio as possible factors determining changes in plant species diversity in grassland and heathland communities. Biol. Conserv. 92, 151-161.

Sarmiento G 1983 The savannas of tropical America. In Ecosystems of the world – tropical savannas. Ed. D W Goodall. pp. 245-288. Elsevier, Berlin.

Sarmiento G 1984 The ecology of neotropical savannas. Harvard University, Cambridge.

Unesco. United Nations Educational, Scientific, and Cultural Organization 2001 Cerrado protected areas: Chapada dos Veadeiros and Emas National Parks. Unesco, Paris. http://www.unesco.org/whc/sites/1035.htm.

II - Capítulo 1

Relação solo-vegetação em cerrado hiperestacional, cerrado estacional e campo úmido no Parque Nacional das Emas (Brasil central)[1]

Soil-vegetation relationships in hyperseasonal cerrado, seasonal cerrado, and wet grassland in Emas National Park (central 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. The cerrado soils are generally well drained, but we found, in central Brazil, a small cerrado area in which the soil is poorly drained. The poor drainage causes waterlogging at the end of the rainy season, from February to April, allowing the appearance of a hyperseasonal cerrado. As long as soil is important in the ecology of the cerrado, limiting the cerrado distribution and the occurrence of its physiognomies, 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. Since the soil under both cerrados was more similar than the soil under the wet grassland, the duration of waterlogging in the hyperseasonal cerrado was not long enough to alter most of its soil characteristics, such as organic matter, phosphorus, and potassium. We found high species-environment correlation, which pointed out that these plant communities are structured predominantly by edaphic factors. Since waterlogging may alter soils 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. The two contransting stresses in the hyperseasonal cerrado act as environmental filters and limit the number of species able to grow in these conditions.

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 climate, characterized by one or two short dry seasons; ii) seasonal savannas, characterized by an extended rainless season, in which drought and fire provide a neat rhythmicity in its 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 km^2, mainly in the Brazilian Central Plateau, under seasonal climate, with wet summer and dry winter (Ratter *et al*. 1997). Even if some cerrado physiognomies may not be considered savannas (Coutinho 1990), seasonality is also one of the essential features of the cerrado, which, therefore, may be divided according to Sarmiento's (1983) classification as well. Seasonal cerrados are by far the most widespread type, but semi-seasonal cerrados appear as small patches within the Amazonian region (Sarmiento 1983). Hyperseasonal cerrado areas must be rather restricted within the Cerrado Domain, on interfluvial regions with poorly drained soils (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 northeastern 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 Emas National Park (ENP), central Brazil, there is a small area, composed of cerrado species, in which

there is waterlogging in summer and drought in winter, and, thus, shall be classified as a hyperseasonal cerrado (Batalha *et al.* in press).

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), in a core cerrado area, found that the cerrado physiognomic gradient was correlated with soil fertility. Ruggiero *et al.* (2002), however, found no significant correlation between 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 chemichally 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 in press). Since in waterlogged soils there may be changes in chemical soil features (Ponnamperuma 1984; Gambrell *et al.* 1991) and since soil is one of the main factors that determine the occurrence of the cerrado and its physiognomic variation (Haridasan 2000), it is possible that the waterlogging of a hyperseasonal cerrado implies differences in soils characteristics when compared to a seasonal cerrado, never waterlogged, and a the wet grassland, waterlogged throughout the whole year, and, consequently, differences in plant community structure among these three vegetation forms. Analyzing species density and some chemical and physical soil characteristics, we adressed 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?

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's (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. There is, in the southwestern part of the reserve, 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 1 ha 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°17'347"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 the whole 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 m^2 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 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 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 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 presence of sulfuric acid and a subsequent titration with ammonic 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 CaCl$_2$ (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 analysis of gradient. We

used a canonical correspondence analysis (CCA) (Jongman *et al.* 1995) to investigate relationships between soil characteristics and species density in sample quadrats with the MVSP software (Kovach 1999). 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). We tested significance of the overall CCA ordination with a Monte Carlo permutation procedure and 500 runs (Manly 1998).

Results

We sampled 272 individuals belonging to 18 species in the hyperseasonal cerrado, 575 individuals belonging to 55 species in the seasonal cerrado, and 2,276 individuals belonging to 32 species in the wet grassland (Table 1). The richest families 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 ($P < 0.01$).

The sum of all unconstrained eigenvalues was 7.69; the sum of canonical eigenvalues using surface soil data was 1.91. In this CCA, species cumulative percentages of variance in the first four axes were 16.6%, 27.2%, 31.9%, and 36.6%, respectively. For the species-environment correlation, these percentages were, respectively, 99.9%, 87.8%, 87.5% and 84.3%. Considering both the canonical coefficient and intraset correlation coefficient in this CCA, the soil variables best related to the first axis were clay, sand, organic matter, phosphorus, aluminium saturation, aluminium, and

potassium, all of them positively correlated, with the exception of sand (Table 3, Figure 1). The soil variables best related to the second axis were pH and base saturation, positively related, and magnesium, negatively related (Table 3, Figure 1).

The ordination diagram (Figure 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 (Figure 1). In the second axis, the hyperseasonal cerrado presented positive scores, related with higher values of pH and base saturation, and the seasonal cerrado presented negative scores, related with higher values of magnesium, aluminium saturation, and cation exchange capacity (Figure 1).

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. Species-environment correlation was high, showing a high degree of association between plant species and measured soil characteristics.

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 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*. (in press). 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*. in press).

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 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).

Arens (1963) presented his "aluminium-toxic scleromorphism theory", which stated that high amounts of soluble aluminium in the soil are toxic to cerrado plants. There is a negative correlation between the amount of aluminium and soil pH, and since aluminium solubility and concentration in the exchangeable form are controlled by soil acidity (Ellis and Mellor 1995) and H^+ (hydrogen ions) competes with essential nutrients for the same chemical sites, aluminium promotes soil impoverishment and, indirectly, scleromorphism of cerrado species (Arens 1963). Exchangeable aluminium decreases the nutrient availability to the plants, decreasing phosphorus absorption or its precipitation in intercellular spaces (Malavolta *et al.* 1977) and, usually, causing a decrease in 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 long 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 rizosphere 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 (Niinemets and Kull 2003).

Contrary to the wet grassland, the hyperseasonal and seasonal cerrados seem to be limited by phoshorus 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, in which there is a high root to shoot ratio (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 in press).

As long as the soil under both cerrados was more similar between one another than between the soil under the wet grassland, the duration of waterlogging in the hyperseasonal cerrado is not long enough to alter most of its soil characteristics, such as organic matter, phosphorus, and potassium, but is long enough to alter some, such as pH and base saturation. 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 soils 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.

References

Amorim P.K. and Batalha M.A. In press. Soil characteristic of a hyperseasonal cerrado compared to a seasonal cerrado and a floodplain grassland: implications for plant community structure. Brazilian Journal of Biology.

Arens K. 1963. As plantas lenhosas dos campos cerrados como vegetação adaptada às deficiencias minerais do solo. In: Ferri M.G. (ed.), III Simpósio Sobre o Cerrado. Edusp, São Paulo, pp. 13-115.

Askew G.P. and Montgomery R.F. 1983. Soils of tropical savannas. In: Goodall D.W. (ed.), Ecosystems of the world – tropical savannas. Elsevier, Berlin, pp.63-77.

Baruch Z. 1994. Responses to drought and flooding in tropical forage grasses: I. – Production and allocation of biomass, leaf growth and mineral nutrients. Plant and Soil 164: 87-96.

Batalha M.A., Silva I.A., Cianciaruso M.V. and Delitti W.B.C. In press. Hyperseasonal cerrado, a new Brazilian vegetation form. Brazilian Journal of Bioloy.

Batalha M.A. and Martins F.R. 2002. The vascular flora of the cerrado in Emas National Park (Goiás, Central Brazil). Sida 20: 295-311.

Batalha M.A. and Mantovani W. 1999. Chaves de identificação das espécies vegetais vasculares baseada em caracteres vegetativos para a ARIE Cerrado Pé-de-Gigante (Santa Rita do Passa Quatro, SP). Revista do Instituto Florestal 11: 137-158.

Bodelier P.L.E., Duyts H., Blom C.W.P.M. and Laanbroek H.J. 1998. Interactions between nitrifying and denitrifying bacteria in gnotobiotic microcosms planted with the emergent macrophyte *Glyceria maxima*. FEMS Microbiology Ecology 25: 63-78.

Boeye D., Verhagen B., Van Haesebroeck V. and Verheyen R.F. 1997. Nutrient limitation in species-rich lowland fens. Journal of Vegetation Science 8: 415-424.

Bourlière F. and Hadley M. 1983. Present-day savannas: an overview. In: Goodall D.W. (ed.), Ecosystems of the world – tropical savannas. Elsevier, Amsterdam, pp. 1-17.

Bridgewater S., Ibáñez A., Ratter J.A and Furley P. 2002. Vegetation classification and floristic of the savannas and associated wetlands of the Rio Bravo Conservation and Management Area, Belize. Edinburgh Journal of Botany 59(3): 421-442.

Brinkman R. and Diepen C.A. 1990. Mineral soils. In: Patten B.C. (ed.), Wetlands and shallow continental water bodies. SPB Academic Publishing, The Hague, pp. 37-59.

Camargo O.A., Moniz A.C., Jorge J.A and Valadares J.M.A.S. 1986. Métodos de análise química e física de solos do Instituto Agronômico de São Paulo. Boletim Técnico do Instituto Agronômico de São Paulo 106: 1-94.

Castro A.A.J., Martins F.R. and Fernandes G. 1998. The woody flora of cerrado vegetation in the State of Piauí, northeastern Brazil. Edinburgh Journal of Botany 55: 455-472.

Chase J.M. 2003. Community assembly: when should history matter? Oecologia 136: 489-498.

Conservation International 1999. Ações prioritárias para a conservação do Cerrado e do Pantanal. Conservation International, Brasília.

Coutinho L.M. 1990. Fire in the ecology of the Brazilian cerrado. In: Goldammer J.G. (ed.),

Fire in the tropical biota. Springer, Berlin, pp. 81-103.

Crawley M.J. 1997. Plant Ecology. Blackwell Science, London.

Critchley C.N.R., Chambers B.J., Fowbert J.A., Sanderson R.A., Bhogal A. and Rose S.C. 2002. Association between lowland grassland plant communities and soil properties. Biological Conservation 105: 199-215.

Elisseou G.C., Veresoglou D.S. and Mamolos A.P. 1995. Vegetation productivity and diversity of acid grasslands in northern Greece as influenced by winter rainfall and limiting nutrients. Acta Oecologica 16: 687-702.

Ellis S. and Mellor A. 1995. Soils and Environment. Routledge, New York.

Furley P.A. 1976. Soil-slope-plant relationships in the northern Maya mountains, Belize, central America. Journal of Biogeography 3: 303-319.

Gambrell R.P., DeLaune R.D. and Patrick W.H. 1991. Redox processes in soils following oxygen depletion. In: Jackson M.B., Davies D.D. and Lambers H. (eds.), Plant Life Under Oxygen Deprivation: Ecology, Physioloy and Biochemistry. SPB Academic Publishing BV, The Hague, pp.101-117.

Goodland R. and Pollard R. 1973. The Brazilian cerrado vegetation: a fertility gradient. Journal of Ecology 61: 219-224.

Gopal B., Masing V. 1990. Biology and Ecology. In: Patten B.C. (ed.), Wetlands and shallow continental water bodies. SPB Academic Publishing, The Hague, pp. 91-239.

Haridasan M. 2000. Nutrição mineral de plantas nativas do cerrado. Revista Brasileira de Fisiologia Vegetal 12: 54-64.

Janssens F., Peters A., Tallowin J.R.B., Bakker J.P., Bekker R.M., Fillat F and Oomes M.J.M. 1998. Relationship between soil chemical factors and grassland diversity. Plant and Soil 202: 69-78.

Jongman R.H.G., ter Braak C.J.F. and Van Tongeren O.F.R. 1995 Data analysis in community and landscape ecology. Cambridge University, Cambridge.

Köppen W. 1931. Grundriss der Klimakunde. Gruyter, Berlin.

Kovach 1999. Multivariate Statistical Package v.3.1. Kovach Computing Services, Anglesey.

Lenssen J., Menting F., van der Putten W. and Blom K. 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. Oikos 86: 523-534.

Lopes A.S. and Cox F.R. 1977. Cerrado vegetation in Brazil: an edaphic gradient. Agronomy Journal 69: 828-831.

Malavolta E., Sarruge J.R. and Bittencourt V.C. 1977. Toxidez de alumínio e manganês. In: Ferri M.G. (ed.), IV Simpósio Sobre o Cerrado. Itatiaia, Belo Horizonte, pp. 275-301.

Manly B.F.J. 1998. Randomization, Bootstrap and Monte Carlo Methods in Biology. Chapman & Hall, London.

Marschner H. 1989. Effect of soil acidification on root growth, nutrient and water uptake. In: Ulrich B. (ed.), .Internat. Congr. Fores Decline Res. State of Knowledge and Perspectives. Universität Hohenheim, Stuttgart, pp. 381-404.

Niinemets U. and Kull K. 2003. Leaf structure vs. nutrient relationships vary with soil conditions in temperate shrubs and trees. Acta Oecologica 24: 209-219.

Ponnamperuma E.N. 1984. Effects of flooding on soils. In: Koslowski T.T. Flooding and plant growth. Academic, New York, pp. 265-294

van Raij B., Quaggio J.A., Cantarella H., Ferreira M.E., Lopes A.S. and Bataglia O.C. 1987. Análise química de solos para fins de fertilidade. Fundação Cargill, Campinas.

Ratter J.A., Ribeiro J.F. and Bridgewater S. 1997. The Brazilian cerrado vegetation and threats to its biodiversity. Annals of Botany 80: 223-230.

Ruggiero P.G.C., Batalha M.A., Pivello V.R. and Meirelles S.T. 2002. Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeasthern Brazil. Plant Ecology 160: 1-16.

Sarmiento G. 1983. The savannas of tropical America. In: Goodall D.W. (ed.), Ecosystems of the world – tropical savannas. Elsevier, Berlin, pp. 245-288.

Sistani K.R., Mays D.A. and Taylor R.W. 1999. Development of natural conditions in constructed

wetlands: Biological and chemical changes. Ecological Engineering 12: 125-131.

Tyler G. and Falkengren-Grerup U. 1998. Soil Chemistry and Plant Performance – Ecological considerations. Progress in Botany. Springer-Verlag, Berlin.

Unesco. United Nations Educational, Scientific, and Cultural Organization 2001. Cerrado protected areas: Chapada dos Veadeiros and Emas National Parks. Unesco, Paris. http://www.unesco.org/whc/sites/1035.htm.

Usuda H. 1995. Phosphate deficiency in maize. V. Mobilization of nitrogen and phosphorus within shoots of young plants and its relationship to senescence. Plant and Cell Physiology 36: 1041-1049.

Zar J. 1999. Biostatistical analysis. Prentice Hall, New Jersey.

Table 1. – Plant species sampled in ENP, according to families, in hypersseasonal 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. hsc = hyperseasonal cerrado, sc = seasonal cerrado, wg = wet grassland.

Family/species	hsc	sc	wg
Amaranthaceae			
Froelichia procera (Seub.) Pedersen		x	
Annonaceae			
Annona crassiflora Mart.		x	
Annona warmingiana Mello-Silva & Pirani		x	
Arecaceae			
Allagoptera campestris (Mart.) Kuntze	x	x	
Syagrus flexuosa (Mart.) Becc.		x	
Asteraceae			
Aspilia leucoglossa Malme		x	
Erechtites hieracifolia (L.) Raf.	x		
Wedelia macedoi H. Rob.		x	
Bignoniaceae			
Tabebuia ochracea (Cham.) Standl.		x	
Celastraceae			
Tontelea micrantha (Mart.) A.C.Sm.	x	x	
Connaraceae			
Rourea induta Planch.		x	
Cyperaceae			
Exochogyne amazonica C.B. Clarke			x
Rhynchospora diamantina (C.B.Clarke) Kükenth			x
Rhynchospora globosa (Kunth) Roem. & Schult			x
Dilleniaceae			
Davilla eliptica A.St-Hil.		x	
Droseraceae			
Drosera communis A.St-Hil			x
Ebenaceae			
Diospyros hispida A. DC.		x	
Ericaceae			
Gaylussacia brasiliensis C.F.W. Meissn.			x
Eriocaulaceae			
Singonanthus xeranthemoides Ruhland			x
Erythroxylaceae			
Erythroxylum deciduum A. St-Hill		x	
Erythroxylum suberosum A. St-Hill		x	

	C1	C2	C3
Euphorbiaceae			
Croton antisyphiliticus Mart.		x	
Croton glandulosus Müll. Arg.	x		x
Phyllanthus niruri L.			x
Fabaceae			
Acosmium subelegans (Mohl.) Yakovlev	x	x	
Andira laurifolia Benth.	x		
Camptosema ellipticum (Desv.) Burkart		x	
Eriosema crinitum (Kunth) Gardner		x	
Eriosema longifolium Benth.		x	
Galactia decumbens (Benth.) Chodat & Hassl.		x	
Galactia martii A. DC.	x	x	
Mimosa gracilis Benth.		x	
Flacourtiaceae			
Casearia sp.		x	
Gentianaceae			
Irlbachia caerulescens (Aubl.) Griseb.			x
Hypoxidaceae			
Hypoxis sp.			x
Iridaceae			
Sisyrinchium vaginatum Spreng	x		x
Lamiaceae			
Hyptis adpressa A. St-Hill		x	
Hyptis pulchella Briq.			x
Hyptis villosa Pohl ex Benth.		x	
Ocimum sp.	x	x	
Lycopodiaceae			
Lycopodiella cernua (L.) Pic.Serm.			x
Lythraceae			
Cuphea carthagenensis (Jacq.) Macbr.		x	
Cuphea sp.			x
Malpighiaceae			
Byrsonima guilleminiana A. Juss.		x	
Malvaceae			
Byttneria oblongata Pohl	x	x	
Peltaea edouardii (Hochr.) Krapov. & Cristóbal		x	
Waltheria douradinha A. St-Hill		x	
Melastomataceae			
Pterolepsis repanda Triana			x
Myrtaceae			
Campomanesia pubescens (A. D.C.) O. Berg		x	
Eugenia angustissima O. Berg		x	
Eugenia calycina Cambess.		x	
Eugenia complicata O. Berg	x		

Species			
Eugenia livida O. Berg.	x		
Myrcia rhodeosepala Kiaersk.	x	x	
Myrcia uberavensis O. Berg	x	x	
Myrtaceae sp.1		x	
Myrtaceae sp.2		x	
Psidium australe Cambess.	x	x	
Psidium cinereum Mart.		x	
Psidium laruotteanum Cambess.		x	
Psidium rufum Mart. ex A. DC.		x	
Ochnaceae			
Ouratea nana (A. St-Hil.) Engl.		x	
Ouratea spectabillis (Mart.) Engl.		x	
Poaceae			
Andropogon leucostachys Kunth	x		
Anthaenantiopsis perforata (Nees) Parodi		x	
Aristidia riparia Trin.		x	
Axonopus comans (Trin.) Kuhlm.			x
Axonopus derbyanus Black		x	
Brachiaria decumbens Stapf	x		
Elionurus latiflorus Nees		x	x
Eragrostis articulata (Schrank) Nees		x	
Eragrostis bahiensis Schrad ex. Schult			x
Panicum hians Elliot.			x
Panicum parvifolium Lam.	x		
Panicum rudgei Roem. & Shult	x	x	
Paspalum dedeccae Quarin			x
Paspalum maculosum Trin.			x
Paspalum pectinatum Nees		x	
Rhynchelitrum repens (Nees) C.E. Hubb		x	
Schizachyrium tenerum Nees			x
Trachypogon sp.			x
Tristachya leiostachya Nees		x	
Poaceae sp. 1			x
Poaceae sp. 2			x
Poaceae sp. 3			x
Poaceae sp. 4			x
Poaceae sp. 5			x
Poaceae sp. 6			x
Rubiaceae			
Coccocypselum lyman-smithii Standl.			x
Sapindaceae			
Serjania cissoides Radlk.		x	
Sapotaceae			
Pradosia brevipes (Pierre) Penn.		x	
Verbenaceae			
Stachytarpheta linearis Moldenke			x
Xyridaceae			
Xyris sp.1			x

Table 2. – Soil chemical and physical characteristics (mean ± standard deviation) at four depths in hypersseasonal 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. 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.

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 $(mmolc\ kg^{-1})$	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 $(mmolc\ kg^{-1})$	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 $(mmolc\ kg^{-1})$	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 $(mmolc\ kg^{-1})$	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 $(mmolc\ kg^{-1})$	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 $(mmolc\ kg^{-1})$	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

variable	depth (m)	hsc	sc	wg
	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
	0-0.05	10.6 ± 1.2	9.8 ± 1.7	6.2 ± 1.7
V	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
	0-0.05	31.9 ± 2.3	26.9 ± 2.6	77.2 ± 2.8
clay	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
	0-0.05	6.5 ± 1.3	5.0 ± 2.2	12.2 ± 3.3
silt	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
	0-0.05	61.6 ± 2.8	68.1 ± 3.1	10.6 ± 2.8
sand	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

Table 3. Canonical coefficients and intraset correlation coefficients for axes 1and 2 for the edaphic variables supplied in the CCA using 0-0.05 m depth soil data. 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.

	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

Figure 1. Canonical correspondence analyses, 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.

Vector scaling: 5,81
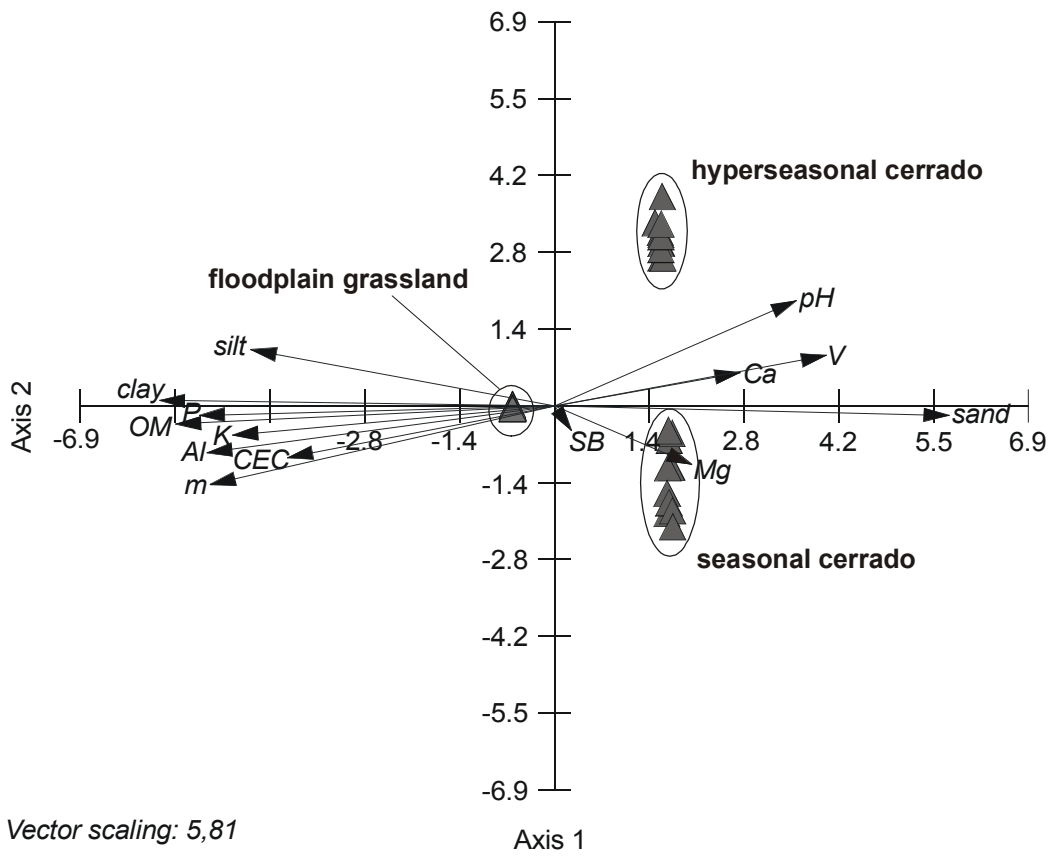
III – Capítulo 2

Variáveis edáficas e densidade de espécies em comunidades herbáceas no Parque Nacional das Emas (Brasil central)[2]

Soil chemical factors and grassland species density in Emas National Park (central Brazil)

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ABSTRACT

Studies of grasslands on specific soil types suggest that different nutrients can limit biomass production and, hence, species composition and number. As long as soil chemical factors are important in the distribution of the vegetation forms within the Cerrado Domain and may influence the number of species, we analyzed some soil characteristics in three herbaceous vegetation forms – hyperseasonal cerrado, seasonal cerrado, and wet grassland – in Emas National Park, for investigating the relationships between number of species and soil characteristics. We collected vegetation and soil samples in these three vegetation forms and submitted obtained data to simple multiple linear regression. We found that aluminium and pH were the best predictors of species density, the former positively related to species density and the latter negatively related.

Key words: aluminium, nutrient limitation, pH, soil, species density.

INTRODUCTION

In herbaceous communities, the number of species and biomass appear to present a humped-back relationship (Al-Mufti et al., 1977; Grime, 1979). Biomass, on its turn, depends on the production of the community and, thus, on the fertility of the soil (Janssens et al., 1998). Therefore, one may expect a humped-back relationship between the number of species and soil fertility as well (Janssens et al., 1998). In this case, species richness would be higher where nutrients are in short supply – and, consequently, plants do not grow tall and compete for light – and where environmental stress is not too excessive (Grime, 1979; Moore and Keddy, 1989). Nutrient limitation is, indeed, one of the most important factors affecting the structure of plant communities (Grime et al., 1997).

Individual studies of grasslands on specific soil types suggest that different nutrients can limit biomass production and, hence, species composition and number (Critchley et al., 2002a). Whereas phosphorus influences grassland biodiversity (Janssens et al., 1998; McCrea et al., 2001), the role of potassium is less clear. High potassium levels on[i] former arable land are believed to diminish species diversity (Gilbert and Andersen, 1998), although high potassium additions did not alter the floristic composition of experimental hay plots (Elberse et al., 1983). Similarly, the role of pH is also unclear: on the one hand, pH was the variable most highly correlated with species richness and diversity in the Netherlands (Roem and Berendse, 2000), but, on the other hand, in some temperate regions of western and central Europe, it was not correlated with them at all (Janssens et al., 1998).

Savannas are tropical and subtropical formations with an almost continuous grass layer, occasionally interrupted by trees and shrubs, and with the main growth patterns 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, which occur under a mostly wet climate, with one or two short dry seasons; ii) seasonal savannas, characterized by an extended rainless season, in which drought and fire provide a neat rhythmicity in its 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 waterlogging; 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 occupied formerly 2 million km[2], especially in the Brazilian Central Plateau (Ratter et al., 1997). The cerrado vegetation is not uniform in physiognomy, ranging from grassland to tall woodland (Coutinho, 1990), but with most of its physiognomies within the range defined as tropical savanna. Almost all cerrado areas are

seasonal; hyperseasonal cerrado areas are rather restricted within the Cerrado Domain, appearing in interfluvial regions with poorly drained soils (Sarmiento, 1983). Nevertheless, in Emas National Park (ENP), central Brazil, there is a small area, composed of cerrado species, characterized by waterlogging in summer and drought in winter, which, thus, shall be classified as a hyperseasonal cerrado (Batalha et al., in press).

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). As long as soil chemical factors are important in the distribution of the vegetation forms within the Cerrado Domain and may influence the number of species, we analyzed some soil characteristics in three herbaceous vegetation forms – hyperseasonal cerrado, seasonal cerrado, and wet grassland – in ENP, a core cerrado site. In ENP, number of species is higher in the wet grassland and lower in the hyperseasonal cerrado (Silva et al. submitted). But, is this pattern related to soil characteristics? That is, regardless of the vegetation form, are there relationships between soil factors and the number of species in those herbaceous communities? Which soil factors are important in explaining variation in number of species in those grasslands?

MATERIAL AND METHODS

Created in 1961, the Emas National Park (ENP) is located in the Brazilian Central Plateau, in the cerrado core region. 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. Regional climate is humid tropical with wet summer and three dry months in the winter, classified as Aw according to Köppen's (1931). The cerrado in ENP comprises 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) – covering 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 300 ha area covered by a hyperseasonal cerrado, waterlogged from February to April.

We sampled three 1 ha 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 the wet grassland is waterlogged throughout most of the year.

We collected vegetation and soil samples in February 2003, at mid-rainy season. In each vegetation form, we placed randomly ten 1 m^2 quadrats and counted the number of individuals of each vascular plant species, except seedlings, due to their 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 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 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 analyses, which were conducted at the Soil Sciences Laboratory of the University of São Paulo. We analyzed soil factors according to the procedures described by 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 presence of sulfuric acid and a subsequent titration with

ammonic ferrous sulfate; phosphorus (P) was determined by spectrophotometry after anion exchange resin extraction; exchangeable aluminium (Al) and potassium (K) were extracted with 1 mol_c l^{-1} KCl, cation exchange resin, and buffer SMP, respectively; and soil pH was determined in $CaCl_2$ (0.01 M) solution.

For each quadrat, we counted the number of species, which gave us the species density. Thus, we had a matrix with the number of species and soil chemical factors for each one of the 30 quadrats and for each one of the four depths. To test the relationships between species density and soil chemical factors at each depth, we used linear multiple regressions (Jongman et al., 1995). In these analyses, species density was the response variable and the soil chemical factors – pH, organic matter, phosphorus, aluminium, and potassium – were the explanatory variables. We used analyses of variance to test whether the partial regression coeficients were equal to zero.

RESULTS

Contrary to the expected, we did not find humped-back relationships for none of the analyzed soil chemical factors (Figures 1 through 5 – only data for surface soil are shown). Species density varied from three to 24 spp m^{-2} (Table 1). We found significant relationships between the number of species and soil chemical factors for all depths. The depth with the highest coefficient of determination was the superficial one ($R^2 = 0.68$, $F = 10.179$, $P < 0.001$). In this depth, aluminium and pH were the best predictors of species density, the former positively related to species density and the latter negatively related (Table 2).

DISCUSSION

Humped-back relationships between species density and soil factors may be expected, at least for major soil nutrients, such as phosphorus and potassium (Janssens et al., 1998). Contrary to temperate grasslands (Janssens et al., 1998), relationships between species density and major soil nutrients may be more complex in tropical grasslands, as those grasslands within the Cerrado Domain. Since we did not find humped-back relationships between species density and soil factors, we cannot expect humped-back

relationships between species density and biomass in the grasslands we studied as well, contrary to what was found in other herbaceous communities by Al-Mufti et al. (1977) and Grime (1979).

Differences among species in their abilities to exploit limiting resources affect the coexistence of species (Tilman, 1982). Since some plant species have special adaptations to low nitrogen availability and others, to low phosphorus availability, the type of nutrient limitation may affect species composition and richness through its effect on productivity (Venterink et al., 2003). The nutrient mosaic theory states that the mechanism that could help to maintain high plant species density involves differentiation in the use of various materials, such as nitrogen, phosphorus, potassium, calcium, and so on; according to this argument, each plant species has its own peculiar set of requirements (Pianka, 1994).

Even if there were significant relationships between species density and soil at all depths, we found a higher correspondence with surface soil, as expected (Amorim & Batalha, in press; Ruggiero et al., 2002). There is an intimate relationship between the properties of the surface soil horizons and the nature and abundance of plant species, which affects nutrients, as well as water absorption, and retention in the biomass and upper rhizosphere (Furley, 1976). The vegetation itself influences soil characteristics at upper layers, by, for example, transferring organic matter through nutrient cycling (Ruggiero et al., 2002).

In the grasslands we studied, aluminium and pH were the best predictors of species density, as The Netherlands (Venterink et al., 2003). In temperate regions, grassland plant species density is generally higher on neutral or basic soils than in acidic soil (Marrs, 1993). For instance, Roem and Berendse (2000) and Critchley et al. (2002b) found a positive relationship between pH and species density in Europe. Low pH reduces the mineralization of soil organic matter and other nutrient reserves, inhibiting root growth and, consequently, adsorption of nutrients (Vermeer and Berendse, 1983). In tropical grasslands, such as in Australia, on the other hand, plant species density is negatively correlated with soil pH (Morgan, 1998), corroborating our results. Local relationships between plant species number and

soil pH are related to evolutionary history, thus, the relationship between them should be positive in those floristic regions where the evolutionary center is on high pH soil – that is, higher latitudes – and negative where the evolutionary center is on low pH soil – that is, lower latitudes (Pärtel, 2002).

Exchangeable aluminium decreases the nutrient availability to the plants by lowering phosphorus absorption or its precipitation in intercellular spaces (Malavolta et al., 1977). Aluminium also causes a decrease in magnesium and calcium absorption (Marschner, 1989) and induces a larger decrease in anion uptake – particularly NO^{-3} – by plant roots (Calba and Jaillard, 1997). Thus, we could expect a negative relationship between aluminium and species density. However, we found a positive relationship in the grasslands we studied. Braakhekke (1980) and Tilman (1982) suggested that species number is greater in sites where plant growth is limited by several nutrients. Since aluminium decreases nutrient availability, plant growth would be limited by several nutrients in aluminium-rich soils. Thus, we may postulate that the positive relationship aluminium and species density we found is because the grassland species in ENP are limited by several nutrients. This positive relationship between aluminium and species density does not mean that high concentration of aluminium in soil implies in high species density, since this high concentration of aluminium can be toxic to the plants and decrease the species density.

Although phosphorus may influence grassland biodiversity (Janssens et al., 1998; McCrea et al., 2001) in temperate regions, it was not significantly related to species density in ENP's grasslands. Since the influence of phosphorus could be indirect by its control on the soil available nitrogen quantities (Janssens et al., 1998), it is possible that others factors were influencing the available nitrogen quantities in ENP. Low quantities of organic matter, for instance, reduce phosphorus limiting effect (Janssens et al., 1998) and may explain our results. Whereas high potassium levels diminished species diversity on former arable land (Gilbert and Andersen, 1998), potassium additions did not alter the floristic composition of hay plots (Elberse et al., 1983), what was corroborated by our results. The influence of organic matter on species density, on its turn, could be indirect by its control of the soil available nitrogen, primarily determined by the mineralization of organic nitrogen in the soil, which depends on the amount of soil organic matter (Roem and Berendse, 2000). Nitrogen is one of the main limiting factors of grassland richness (Janssens et al, 1998) and may be a good predictor of species density in tropical grasslands.

Vegetation and soils are dynamic systems, and relationships between particular vegetation characteristics and soil factors at one time may not always reflect the suitability of plant species present to that set of soil conditions (Critchley et al., 2002b). Our study is limited in time and there may be variations in soil characteristics and number of species in the three environments throughout the year due to the seasonal variations, such as the temporary waterlogging in the hyperseasonal cerrado that would result in changes of chemical soil features (Gopal and Masing, 1990). These changes may imply differences in species density during the waterlogging when compared to the other seasons of the year. Nevertheless, even taking into account these limitations, species density in ENP's grasslands may be predicted by two soil factors: pH and aluminium. Since the predictable variation in species density is important to determining areas of conservation (Pärtel, 2002), we may postulate that these two soil factors are indicators of high species density areas in tropical grasslands, which could be used for assigning priority sites for conservation.

ACKNOWLEDGMENTS

RESUMO

Estudos em comunidades herbáceas em diferentes tipos de solo sugerem que diferentes nutrientes podem limitar a produção de biomassa e, por isso, a composição e o número de espécies. Como as características químicas do

solo influenciam na distribuição da vegetação no Domínio do Cerrado e pode influenciar no número de espécies, nós analisamos algumas variáveis edáficas em três comunidades herbáceas – cerrado hiperestacional, cerrado estacional e campo úmido – para investigar as relações entre o número de espécies e as características do solo. Nós coletamos amostras da vegetação e do solo nessas três formas de vegetação e com os dados obtidos nós realizamos uma regressão linear múltipla simples. Nós observamos que o alumínio e o pH foram as variáveis que melhor previam a densidade de espécies, sendo o primeiro relacionado positivamente com a densidade de espécies, e o segundo, negativamente.

REFERENCES

Al-Mufti, M. M.; Sydes, C. L.; Furness, S. B.; Grime, J. P. and Band, S. R. (1977), A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J. Ecol.,* **65**, 759-791.

Amorim, P. K. and Batalha, M. A. (in press), Soil characteristic of a hyperseasonal cerrado compared to a seasonal cerrado and a floodplain grassland: implications for plant community structure. *Braz. J. Biol.*

Askew, G. P. and Montgomery, R. F. (1983), Soils of tropical savannas. In *Ecosystems of the world – tropical savannas*, ed. D. W. Goodall. Elsevier, Berlin, pp.63-77.

Batalha, M. A.; Silva, I. A.; Cianciaruso, M. V. and Delitti, W. B. C. (in press), Hyperseasonal cerrado, a new Brazilian vegetation form. *Braz. J. Biol.*

Batalha, M. A. and Martins, F. R. (2002), The vascular flora of the cerrado in Emas National Park (Goiás, Central Brazil). *Sida*, **20**, 295-311.

Batalha, M. A. and Mantovani, W. (1999), Chaves de identificação das espécies vegetais vasculares baseada em caracteres vegetativos para a ARIE Cerrado Pé-de-Gigante (Santa Rita do Passa Quatro, SP). *Revista do Instituto Florestal,* **11**, 137-158.

Bourlière, F. and Hadley, M. (1983), Present-day savannas: an overview. In *Ecosystems of the world – tropical savannas*, ed. D. W. Goodall. Elsevier, Amsterdam, pp. 1-17.

Braakhekke, W. G. (1980), On coexistence: a causal approach to diversity and stability in grassland vegetation. Agricultural Research Reports. Wageningen, The Netherlands.

Calba, H. and Jaillard, B. (1997), Effect of aluminium on ion uptake and H^+ release by maize. *New Phytol.,* **137**, 607-616.

Conservation International (1999), Ações prioritárias para a conservação do Cerrado e do Pantanal. Conservation International, Brasília.

Coutinho, L. M. (1990). Fire in the ecology of the Brazilian cerrado. In *Fire in the tropical biota*, ed. J. G. Goldammer,.Springer, Berlin, pp. 81-103.

Critchley, C. N. R.; Chambers, B. J.; Fowbert, J. A.; Sanderson, R. A.; Bhogal, A. and Rose, S. C. (2002a), Association between lowland grassland plant communities and soil properties. *Biol.Conserv.,* **105**, 199-215.

Critchley, C. N. R.; Chambers, B. J.; Fowbert, J. A.; Bhogal, A.; Rose, S. C. and Sanderson, R. A. (2002b), Plant species richness, functional type and soil properties of grasslands and allied vegetation in English Environmentally Sensitive Areas. *Grass and Forage Science*, **57**, 82-92.

Elberse, W. T.; van der Bergh, J. P. and Dirven J. G. P. (1983), Effects of use and mineral supply on the botanical composition and yield of old grassland on heavy-clay soil. *Neth. J. Agr. Sci.,* **31**, 62-88.

Furley, P. A. (1976), Soil-slope-plant relationships in the northern Maya mountains, Belize, central America. *J. Biogeo.,* **3**, 303-319.

Gilbert, O. L. and Andersen, P. (1998), Habitat Creation and Repair. Oxford University Press, Oxford.

Gopal, B. and Masing, V. (1990), Biology and Ecology. In *Wetlands and shallow continental water bodies,* ed. B. C. Patten. SPB Academic Publishing, The Hague, pp. 91-239.

Grace, J. B. (1999), The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology, Evolution and Systematics*, **2**, 1-28.

Grime, J. P. (1979), Plant Strategies and Vegetation Processes. John Wiley and Sons, Chichester, UK.

Grime, J. P.; Thompson, K.; Hunt, R.; Hodgson, J. G.; Cornelissen, J. H. C.; Rorison, I. H.; Hendry, G. A. F.; Ashenden, T. W.; Askew, A. P.; Band, S. R.; Booth, R. E.; Bossard, C. C.; Campbell, B. D.; Cooper, J. E. L.; Davison, A. W.; Gupta, P. L.; Hall, W.; Hand, D. W.; Hannah, M. A.; Hillier, S. H.; Hodkinson, D. J.; Jalili, A.; Liu, Z.; Mackey, J. M. L.; Matthews, N.; Mowforth, M. A.; Neal, A. M.; Reader, R. J.; Reiling, K.; Ross-Fraser, W.; Spencer, R. E.; Sutton, F.; Tasker, D. E.; Thorpe, P. C. and Whitehouse, J. (1997), Integrated screening validates primary axes of specialization in plants. *Oikos*, **79**, 259-281.

Janssens, F.; Peters, A.; Tallowin, J. R. B.; Bakker, J. P.; Bekker, R. M.; Fillat, F. and Oomes, M. J. M. (1998), Relationship between soil chemical factors and grassland diversity. *Plant Soil*, **202**, 69-78.

Jongman, R. H. G.; ter Braak, C. J. F. and Van Tongeren, O. F. R. (1995), Data analysis in community and landscape ecology. Cambridge University, Cambridge.

Köppen, W. (1931), Grundriss der Klimakunde.

Gruyter, Berlin.

Malavolta, E.; Sarruge, J. R. and Bittencourt, V. C. (1977), Toxidez de alumínio e manganês. In *IV Simpósio sobre o cerrado,* ed. M. G. Ferri. Itatiaia, Belo Horizonte, pp. 275-301.

McCrea, A. R.; Trueman, I. C.; Fullen, M. A.; Atkinson, M. D. and Besenyei, L. (2001), Relationships between soil characteristics and species richness in two botanically heterogeneous created meadows in the urban English West Midlands. *Biol. Conserv.*, **97**, 171-180.

Marrs, R. H. (1993), Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. *Adv. Ecol. Res.*, **24**, 241-300.

Marschner, H. (1989), Effect of soil acidification on root growth, nutrient and water uptake. In *Internat. Congr. Fores Decline Res. State of Knowledge and Perspectives*, ed. B. Ulrich. Universität Hohenheim, Stuttgart, pp. 381-404.

Moore, D. R. J. and Keddy, P. A. (1989), Relationship between species richness and standing crop in wetlands: the importance of scale. *Vegetatio*, **79**, 99-106.

Morgan, J. W. (1998), Patterns of invasion of an urban remnant of a species-rich grassland in southeastern Australia by non-native plant species. *J. Veg. Sci.*, **9**, 181-190.

Pärtel, M. (2002), Local plant diversity patterns and evolutionary history at the regional scale. *Ecology*, **83**, 2361-2366.

Pianka, E. R. (1994), Evolutionary ecology. Harper Collins, New York.

Raij, B.; Quaggio, J. A.; Cantarella, H.; Ferreira, M. E.; Lopes, A. S. and Bataglia, O. C. (1987), Análise química de solos para fins de fertilidade. Fundação Cargill, Campinas.

Ratter, J. A.; Ribeiro, J. F. and Bridgewater, S. (1997), The Brazilian cerrado vegetation and threats to its biodiversity. *Ann. Bot.*, **80**, 223-230.

Roem, W. J. and Berendse, F. (2000), Soil acidity and nutrient supply ratio as possible factors determining changes in plant species diversity in grassland and heathland communities. *Biol. Conserv.*,

92, 151-161.

Ruggiero, P. G. C.; Batalha, M. A.; Pivello, V. R. and Meirelles, S. T. (2002), Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeasthern Brazil. *Plant Ecol.*, **160**, 1-16.

Sarmiento, G. (1983), The savannas of tropical America. In *Ecosystems of the world – tropical savannas*, ed. D. W. Goodall. Elsevier, Berlin, pp. 245-288.

Silva, I. A.; Cianciaruso, M. V. and Batalha, M. A. (Submitted), Species density and diversity of a hyperseasonal cerrado in Emas National Park, central Brazil. *Braz. Arch. Biol. Tech.*

Tilman, D. (1982), Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Unesco. United Nations Educational, Scientific, and Cultural Organization (2001), Cerrado protected areas: Chapada dos Veadeiros and Emas National Parks. Unesco, Paris. http://www.unesco.org/whc/sites/1035.htm.

Venterink, H. O.; Wassen, M. J.; Verkroost, A. W. M. and Ruiter, P. C. (2003), Species richness-productivity patterns differ between N-, P- and K-limited wetlands. *Ecology*, **84**, 2191-2199.

Vermeer, J. G. and Berendse, F. (1983), The relationship between nutrient availability, shoot biomasa and species richness in grassland and wetland communities. *Vegetatio*, **53**, 121-126.
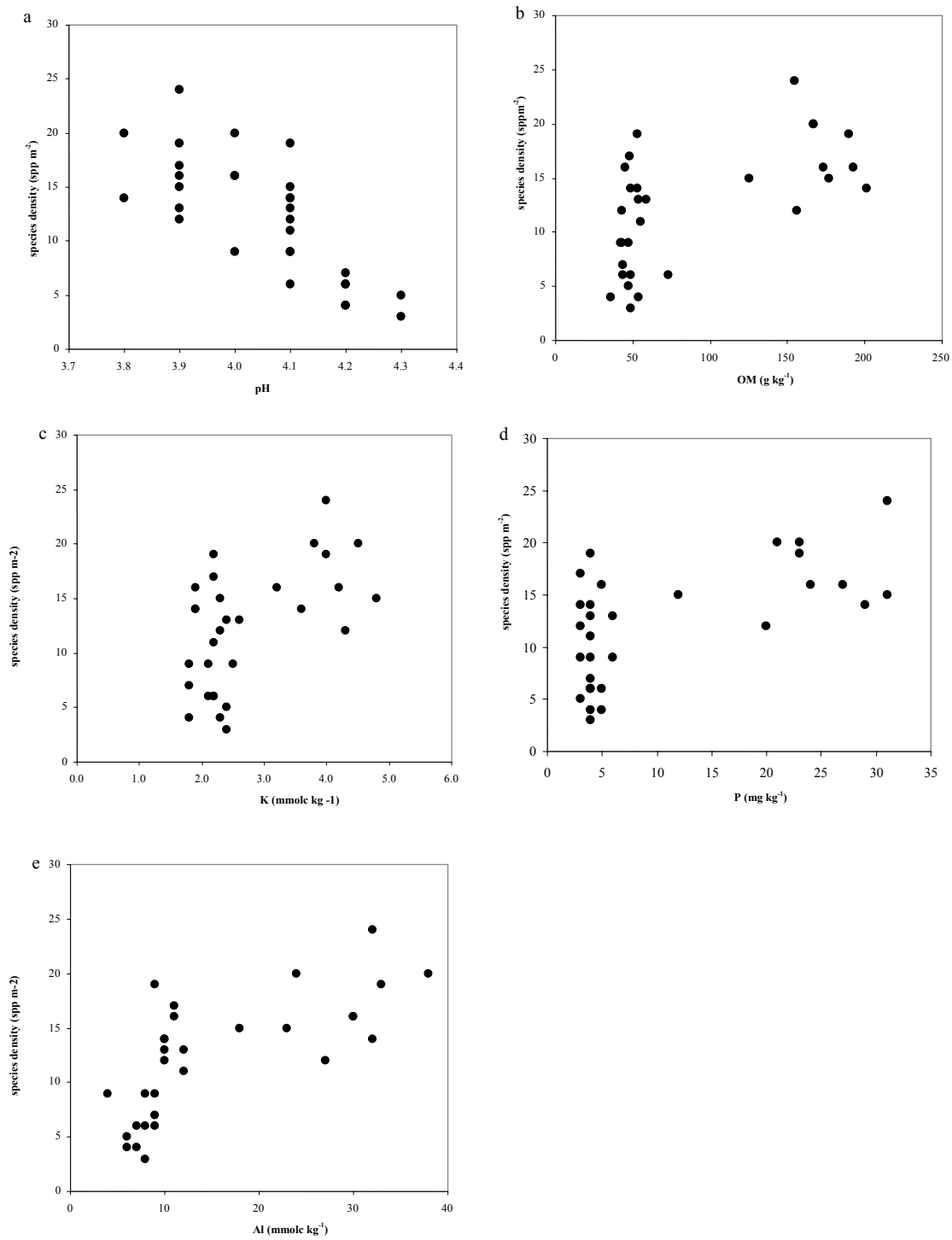
Figure 1. Relationship between pH (a), OM (b), K (c), P (d) and Al (e), at 0-0.05 m deep, and species density (spp m^{-2}) in grassland communities in Emas National Park, central Brazil (18°15'-18°18'S, 52°57-53°01'W), February 2003.

Table 1. Species density and soil chemical factors, at 0-0.5 m deep, in grassland communities in Emas National Park, central Brazil (18°15'-18°18'S, 52°57-53°01'W), February 2003; species density (sd – spp m^{-2}), pH, organic matter (OM – g kg^{-1}), phosphorus (P – mg kg^{-1}), aluminium (Al – mmolc kg^{-1}), potassium (K – mmolc kg^{-1}).

quadrat	vegetation form	sd	pH	OM	P	Al	K
1	hyperseasonal cerrado	5	4.3	47	3	6	2.4
2	hyperseasonal cerrado	6	4.2	73	5	7	2.2
3	hyperseasonal cerrado	6	4.1	44	4	8	2.1
4	hyperseasonal cerrado	9	4.1	43	6	8	2.1
5	hyperseasonal cerrado	6	4.2	49	4	9	2.2
6	hyperseasonal cerrado	3	4.3	49	4	8	2.4
7	hyperseasonal cerrado	4	4.2	36	4	6	1.8
8	hyperseasonal cerrado	9	4.0	42	3	4	1.8
9	hyperseasonal cerrado	4	4.2	54	5	7	2.3
10	hyperseasonal cerrado	7	4.2	44	4	9	1.8
11	seasonal cerrado	14	4.1	53	3	10	1.9
12	seasonal cerrado	16	4.0	45	5	11	1.9
13	seasonal cerrado	12	4.1	43	3	10	2.3
14	seasonal cerrado	17	3.9	48	3	11	2.2
15	seasonal cerrado	13	4.1	59	6	10	2.6
16	seasonal cerrado	11	4.1	55	4	12	2.2
17	seasonal cerrado	9	4.1	47	4	9	2.5
18	seasonal cerrado	14	4.1	49	4	10	1.9
19	seasonal cerrado	13	3.9	54	4	12	2.4
20	seasonal cerrado	19	4.1	53	4	9	2.2
21	wet grassland	15	4.1	125	12	18	2.3
22	wet grassland	12	3.9	156	20	27	4.3
23	wet grassland	24	3.9	155	31	32	4.0
24	wet grassland	20	4.0	167	23	38	3.8
25	wet grassland	16	4.0	193	24	30	3.2
26	wet grassland	14	3.8	201	29	32	3.6
27	wet grassland	20	3.8	167	21	24	4.5
28	wet grassland	15	3.9	177	31	23	4.8
29	wet grassland	16	3.9	173	27	30	4.2
30	wet grassland	19	3.9	190	23	33	4.0

Table 2. Standardized partial regression coefficient (β) and partial F values (t) for multiple regressions between either species density or diversity and soil chemical factors, at 0-0.05 m deep, in grassland communities in Emas National Park, central Brazil (18°15'-18°18'S, 52°57-53°01'W), February 2003; organic matter (OM), phosphorus (P), aluminium (Al), potassium (K), calcium (Ca) ; ^{NS} $P > 0,05$; * $P < 0,05$; ** $P < 0,01$.

factor	species density	
	β	t
pH	-0.57	-3.38**
OM	-0.57	-1.14^{NS}
P	-0.00	-0.01^{NS}
Al	0.96	2.55*
K	-0.25	-0.51^{NS}

IV – Conclusão Geral

Com este trabalho, chegamos às seguintes conclusões:

- os três ambientes, cerrado hiperestacional, cerrado estacional e campo úmido, formaram grupos distintos na análise ordenação; logo constituem formações vegetais distintas, com diferenças na composição florística e na abundância de espécies;

- a correlação espécies-ambiente foi alta, logo há um alto grau de associação das espécies vegetais com as variáveis que medimos;

- há uma grande variação na composição florística e abundância de espécies entre o campo úmido e os dois cerrados que é refletida no primeiro eixo de ordenação e está relacionada com maiores quantidades de argila, matéria orgânica, alumínio, saturação por alumínio, fósforo e potássio, que, portanto, deve ser conseqüência do alagamento constante que ocorre no campo úmido;

- há também uma grande variação entre os cerrados hiperestacional e estacional, refletida no segundo eixo de ordenação que está relacionada com maiores valores de pH e saturação por bases no cerrado hiperestacional e a maiores valores de magnésio, saturação por alumínio e capacidade de troca catiônica no cerrado estacional. Essas diferenças entre esses dois cerrados, pois, deve-se provavelmente ao alagamento temporário que ocorre no cerrado hiperestacional;

- como o alagamento pode alterar as características do solo e como estas foram suficientes para explicar a variação na comunidade vegetal, nós podemos concluir que o excesso de água – permanente ou temporário – é um dos principais fatores que distinguem as três formações vegetais;

• as variáveis edáficas que melhor explicaram a variação na densidade de espécies foram o alumínio e o pH, este relacionado negativamente com a densidade de espécies e aquele, positivamente;

• como a variação previsível na densidade de espécies é importante para determinar áreas de conservação, podemos postular que essas variáveis, alumínio e pH, podem ser indicadoras de áreas com alta densidade de espécies e, eventualmente, ser usadas para estabelecer áreas prioritárias de conservação.