SOIL CHARACTERISTICS OF A HYPERSEASONAL CERRADO COMPARED TO A SEASONAL CERRADO AND A FLOODPLAIN GRASSLAND: IMPLICATIONS FOR PLANT COMMUNITY STRUCTURE

AMORIM, P. K. and BATALHA, M. A.

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

Correspondence to: Priscilla Kobayashi Amorim, Departamento de Botânica, Universidade Federal de São Carlos, C. P. 676, CEP 13565-905, São Carlos, SP, Brazil, e-mail: prikobarim@yahoo.com.br

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ABSTRACT

Savannas may be divided according to their seasonality into semi-seasonal, seasonal, hyperseasonal, or marshy savannas. Hyperseasonal savannas are characterized by the alternation of two contrasting stresses during each annual cycle, one induced by drought and fire and the other, by waterlogging. In South America, the largest savanna region is the Brazilian cerrado, in which there are few hyperseasonal areas that become waterlogged in the rainy season. The cerrado soils are generally well drained, but in central Brazil there is a small cerrado area in which the soil is poorly drained and which becomes waterlogged in the middle of the rainy season, allowing the appearance of a hyperseasonal cerrado. As long as soil is important in the ecology of the cerrado vegetation, we asked whether the waterlogging in this hyperseasonal cerrado implied that there were differences in soil characteristics in relation to a seasonal cerrado, which is not waterlogged in the rainy season, and to a floodplain grassland, which remains waterlogged throughout the year. In each environment, we randomly selected ten points, in which we collected soil samples in the mid-rainy season for chemical and granulometric analyses. For all variables, we found significant differences among the three environments, at least at one of the depths. Nevertheless, when we took into account all the variables together, we observed that the soils under the hyperseasonal and seasonal cerrados were similar and both were different to the soil under the floodplain grassland. The soil under the floodplain grassland was related to larger amounts of clay, silt, organic matter, phosphorus, aluminium, aluminium saturation, cation exchange capacity, and sum of bases, whereas soils under hyperseasonal and seasonal cerrados were related to higher pH values, base saturation, calcium, magnesium, and sand. As long as the soil under both cerrados was chemically and physically similar, the duration of waterlogging in the hyperseasonal cerrado is not long enough to alter its soil characteristics. Limitations to the plants growing on the hyperseasonal cerrado soil must be a consequence of the direct effects of flooding. Since cerrado plant species are dryland ones, the hypoxia caused by waterlogging may limit the number of cerrado species able to withstand these conditions.

Keywords: central Brazil, cerrado, hyperseasonality, savanna, waterlogging.

RESUMO

Características edáficas de um cerrado hiperestacional em comparação com um cerrado estacional e um campo úmido: implicações para a estrutura da comunidade vegetal

As savanas podem ser divididas de acordo com a sua estacionalidade em savanas semi-estacionais, savanas estacionais, savanas hiperestacionais ou esteros. Savanas hiperestacionais são caracterizadas pela alternância de dois estresses contrastantes durante cada ciclo anual, um induzido pela seca e fogo e outro, pelo alagamento. A maior região de savana na América do Sul é o cerrado brasileiro, que apresenta poucas áreas hiperestacionais, que se tornam alagadas durante a estação chuvosa. Os solos de cerrado são geralmente bem drenados, mas há, no Brasil central, uma pequena área de cerrado em que o solo é pobremente drenado e que se torna alagada no meio da estação úmida, possibilitando o aparecimento de um cerrado hiperestacional. Como o solo é importante para a ecologia da vegetação do cerrado, nós nos perguntamos se o alagamento no cerrado hiperestacional implicava diferenças nas características edáficas em relação ao cerrado estacional, que não alaga durante a estação chuvosa, e ao campo úmido, que permanece alagado durante o ano todo. Em cada ambiente, nós sorteamos dez pontos, em que coletamos amostras de solo, no meio da estação chuvosa, para análises químicas e granulométricas. Para todas as variáveis, encontramos diferenças significativas entre os três ambientes, ao menos em uma profundidade. Não obstante, quando analisamos todas as variáveis edáficas conjuntamente, observamos que os solos sob os cerrados hiperestacional e estacional foram semelhantes e ambos foram diferentes do solo sob o campo úmido. O solo sob campo úmido relacionou-se a maiores quantidades de argila, silte, matéria orgânica, fósforo, alumínio, saturação por alumínio, capacidade de troca catiônica e soma de bases, enquanto que os solos sob cerrados hiperestacional e estacional relacionaram-se a maiores valores de pH, areia, saturação por bases, cálcio e magnésio. Uma vez que os solos sob os dois tipos de cerrado foram similares química e fisicamente, a duração do alagamento no cerrado hiperestacional não é suficiente para alterar as suas características edáficas. Limitações para as plantas crescendo no cerrado hiperestacional devem ser conseqüência dos efeitos diretos do alagamento. Como as espécies vegetais de cerrado são espécies de áreas secas, a hipoxia causada pelo alagamento pode limitar o número de espécies de cerrado que são capazes de suportar essa condição.

Palavras-chave: alagamento, Brasil central, cerrado, hiperestacionalidade, savana.

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 & 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, while a period of acute water shortage either does not exist or is very brief.

The Brazilian cerrado is the main savanna region in America and once covered about 2 million km^2, mainly in the Brazilian Central Plateau, under seasonal climate with wet summers and dry winters (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 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 in interfluvial regions with poorly drained soils (Sarmiento, 1983). In some cerrado areas, there are lateritic layers (Freitas & Silveira, 1977) that may be the cause of poor drainage (Lopes & Cox, 1977) and, consequently, of waterlogging. Castro *et al*. (1998) cited some areas in the northeastern Brazil as possible hyperseasonal cerrados due to great water-table variation throughout the year, but as long as there is no waterlogging, 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 the summer and drought in the winter and thus may be classified as a hyperseasonal cerrado (Batalha *et al.*, 2005).

Several explanations for the occurrence of savannas, in general, and cerrados, in particular, involve soil either as a primary cause or as an indirect factor (Askew & Montgomery, 1983). Alvim & Araújo (1952) suggested that the cerrado distribution, contrary to forests, is more controlled by soil than by any other ecological factor. Cerrado soils are generally oxisols, with low nutrient reserves and high aluminium levels (Haridasan, 2000). Soil factors, such as the effective depth, presence of concrections, drainage, 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). In a core cerrado area, Goodland & Pollard (1973) found that the physiognomic gradient was correlated with soil fertility. However, Ruggiero *et al*. (2002) found no significant correlation between the 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, 1994b). Under these conditions, soil pH is modified (Gambrell *et al.*, 1991) and the availability of many elements, such as calcium, magnesium, phosphorus, and potassium, is increased (Ponnamperuma, 1972). Reduction of Fe^{3+} and Mn^{4+} to Fe^{2+} and Mn^{2+} increases their concentrations in the solution (Blom & Voesenek, 1996).

Since in waterlogged soils there may be changes in chemical soil characteristics (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 that there are differences in soil characteristics when compared to a seasonal cerrado, which is not waterlogged, and a floodplain grassland, which is waterlogged throughout the whole year, and, consequently, differences in plant community structure among these three environments. Analyzing some chemical and physical soil characteristics, we addressed the following questions: are soils under hyperseasonal cerrado, seasonal cerrado, and floodplain grassland different? If there are changes in soil characteristics due to waterlogging in the hyperseasonal cerrado, what are the possible implications for the plant community?

MATERIAL AND METHODS

The Emas National Park (ENP), which was founded 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 a tropical warm wet climate with three dry months in the winter, classified as Aw according to Köppen's (1931) classification.

The cerrado in ENP has almost all physiognomies found in this vegetation type from *campo limpo* (a grassland) to *cerrado sensu stricto* (a woodland). Cerrado physiognomies prevail in the reserve – *campo limpo*, *campo sujo* (a shrub savanna), *campo cerrado* (a savanna woodland), and *cerrado sensu stricto* – occupying 93.2% of the total area. Other vegetation types, such as floodplain grassland, riparian forests, and seasonal forests also exist within the park. In the southwestern part of the reserve, there is a hyperseasonal cerrado area that occupies about 300 ha (Fig. 1) which is 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 consisting of the hyperseasonal cerrado (approximately, 18°18'07" S and 52° 57' 56" W), another consisting of a seasonal cerrado (approximately, 18° 17' 347" S and 52° 58' 12" W) and another consisting of a floodplain grassland (approximately, 18° 15' 40" S and 53° 01' 08" W). These three environments are physiognomically similar with a continuous grass layer, scattered shrubs, and no trees. In the hyperseasonal cerrado, there are two contrasting stresses during the year, waterlogging in the summer and drought in the winter; in the seasonal cerrado, there are drought in the winter, but no waterlogging; in the floodplain grassland, there is an excess of water throughout the whole year.

We collected soil samples in February 2003 in the mid-rainy season, when the hyperseasonal cerrado was waterlogged. In each environment, we

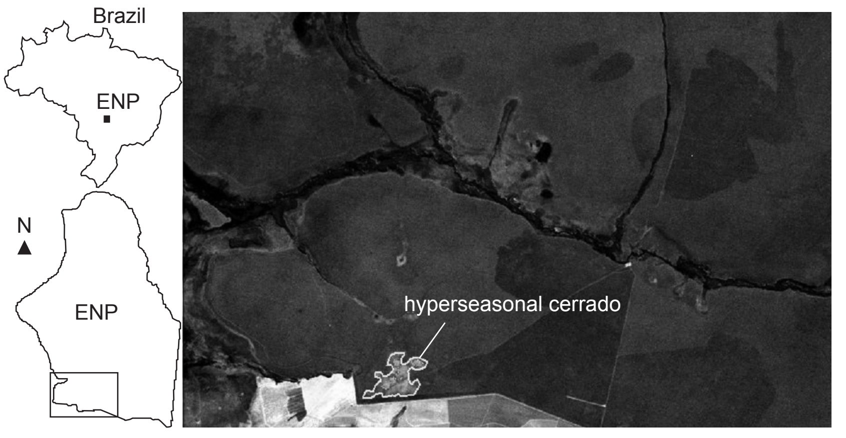

Fig. 1 — Location of Emas National Park in Brazil and the area covered by the hyperseasonal cerrado in the southwestern portion of the reserve.

randomly selected ten points. We used a Global Position System receiver to obtain these points. At each point, we 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. During the soil sampling in the hyperseasonal cerrado, we also checked whether there was a lateritic layer up to 2 m deep. Chemical and granulometric analyses were conducted at the Soil Sciences Laboratory at 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 the presence of sulphuric acid and a subsequent titration with ammonic ferrous sulphate; 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; the cation exchange capacity (CEC) was determined based on the sum of K, Ca, and Mg; the base saturation (V) was calculated as a percentage of the total CEC; the aluminium saturation (m) was calculated based on effective cation exchange capacity; the sum of bases (SB) was represented as the sum of Ca, Mg, and K; and the pH soil was determined in $CaCl_2$ (0.01 M) solution. A granulometric analysis was carried out according to Boyoucus's method described by Camargo *et al.* (1986) to determine the percentages of sand, silt, and clay.

We used analyses of variance (Zar, 1999) to test for significant differences ($\alpha = 0.05$) among the soils of the three environments. We used parametric statistical analyses even when data were not normally distributed and variances were heterogenous, because the analysis of variance is robust enough for possible deviations in normality when, as in our case, the number of replicates are equal (Zar, 1999). We transformed the data shown in percentages, such as clay, sand, silt, CEC, V, and m, to their arcsines prior to the analyses (Zar, 1999). We used the Principal Component Analysis (PCA) (Jongman *et al.*, 1995) to analyze all soil variables simultaneously using data from the four depths (centralized and standardized) with the MVSP software (Kovach, 1999). We presented the results for the depth with the largest eigenvalues in the first two axes and we constructed a joint plot of sites and soil characteristics.

RESULTS

We did not find a lateritic layer in the hyperseasonal soil profile, at least until the depth of 2 m. We classified the soil under the hyperseasonal and seasonal cerrados as Latosol, according to the Brazilian system (Embrapa, 1999), or Oxisol, according to the US Taxonomy system (Soil Survey Staff, 1999), and the soil under floodplain grassland as Gleysol (Embrapa, 1999) or Fluvent Entisol (Soil Survey Staff, 1999).

For all chemical variables, we found significant differences among the three environments, at least at one of the depths (Table 1). For pH, there were significant differences among the three environments at the first depth (0-0.05 m), between hyperseasonal cerrado and the other two environments at the third depth (0.4-0.6 m), and between both cerrados and the floodplain grassland at the fourth depth (0.8-1.0 m). In relation to OM, Al, CEC, and m, we found significant differences

TABLE 1

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 floodplain grassland (approximately, 18° 15' 40" S and 53° 01' 08" W) in Emas National Park, central Brazil. Means significantly different (α = 0.05) are indicated by different letters. hsc = hyperseasonal cerrado; sc = seasonal cerradol; fg = floodplain grassland; OM = organic matter; P = phsophorus; K = potassium; Ca = calcium; Mg = magnesium; Al = aluminium; m = aluminium saturation; SB = sum of bases; CEC = cation exchange capacity; and V = base saturation; $^{NS}P > 0.05$; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$

Variable	Depth (m)	hsc	sc	fg	F
pH	0-0.05	$4.18^c \pm 0.09$	$4.05^b \pm 0.08$	$3.92^a \pm 0.09$	21.03***
	0.05-0.25	$4.15^a \pm 0.12$	$4.02^a \pm 0.06$	$4.04^a \pm 0.21$	2.43^{NS}
	0.4-0.6	$4.50^b \pm 0.09$	$4.29^a \pm 0.06$	$4.28^a \pm 0.20$	8.59***
	0.8-1.0	$4.95^b \pm 0.11$	$4.82^b \pm 0.10$	$4.53^a \pm 0.26$	15.56***
OM (g kg^{-1})	0-0.05	$48.1^a \pm 10.0$	$50.6^a \pm 4.9$	$170.4^b \pm 22.1$	238.31***
	0.05-0.25	$30.3^a \pm 4.6$	$41.6^a \pm 3.7$	$188.7^b \pm 48.9$	96.51***
	0.4-0.6	$19.2^a \pm 3.7$	$25.2^a \pm 2.9$	$164.5^b \pm 82.4$	29.71***
	0.8-1.0	$13.6^a \pm 3.8$	$19.3^a \pm 2.1$	$74.0^b \pm 35.9$	25.42***
P (mg kg^{-1})	0-0.05	$4.2^a \pm 0.9$	$4.0^a \pm 0.9$	$24.1^b \pm 5.8$	113.04***
	0.05-0.25	$1.8^a \pm 0.6$	$2.9^a \pm 0.5$	$20.1^b \pm 10.1$	30.66***
	0.4-0.6	$1.0^a \pm 0.0$	$1.1^a \pm 0.3$	$4.0^b \pm 2.1$	20.15***
	0.8-1.0	$1.0^a \pm 0.0$	$1.0^a \pm 0.0$	$2.1^a \pm 1.8$	3.76*
K (mmolc kg^{-1})	0-0.05	$2.11^a \pm 0.24$	$2.21^a \pm 0.25$	$3.87^b \pm 0.71$	46.62***
	0.05-0.25	$1.68^a \pm 0.27$	$1.97^a \pm 0.27$	$2.87^b \pm 0.70$	18.05***
	0.4-0.6	$1.18^a \pm 1.08$	$1.10^a \pm 0.12$	$1.38^a \pm 0.24$	0.50^{NS}
	0.8-1.0	$0.77^a \pm 0.19$	$0.93^{ab} \pm 0.11$	$1.02^b \pm 0.16$	6.38**
Ca (mmolc kg^{-1})	0-0.05	$4.1^b \pm 0.8$	$4.0^b \pm 1.2$	$2.6^a \pm 1.1$	6.07**
	0.05-0.25	$1.4^a \pm 0.6$	$1.5^a \pm 0.5$	$2.4^a \pm 1.7$	2.46^{NS}
	0.4-0.6	$1.1^a \pm 0.3$	$1.1^a \pm 0.3$	$1.3^a \pm 0.6$	0.61^{NS}
	0.8-1.0	$1.0^a \pm 0.0$	$1.1^a \pm 0.3$	$1.3^a \pm 0.6$	1.26^{NS}
Mg (mmolc kg^{-1})	0-0.05	$3.1^a \pm 0.5$	$4.1^b \pm 0.7$	$2.8^a \pm 1.1$	6.45**
	0.05-0.25	$1.5^a \pm 0.5$	$1.8^{ab} \pm 0.4$	$2.3^b \pm 0.8$	4.32*
	0.4-0.6	$1.1^a \pm 0.3$	$1.0^a \pm 0.0$	$1.2^a \pm 0.6$	0.60^{NS}
	0.8-1.0	$1.0^a \pm 0.0$	$1.0^a \pm 0.0$	$1.1^a \pm 0.1$	1.00^{NS}
Al (mmolc kg^{-1})	0-0.05	$7.2^a \pm 1.5$	$10.4^a \pm 1.1$	$28.7^b \pm 5.8$	108.75***
	0.05-0.25	$5.8^a \pm 1.3$	$8.8^a \pm 1.0$	$24.7^b \pm 7.3$	54.27***
	0.4-0.6	$2.0^a \pm 0.9$	$3.1^a \pm 2.5$	$19.6^b \pm 9.4$	30.33***
	0.8-1.0	$0.2^a \pm 0.4$	$0.6^a \pm 0.5$	$5.9^b \pm 4.9$	12.15***
m (%)	0-0.05	$43.5^a \pm 5.9$	$50.4^a \pm 6.4$	$75.4^b \pm 6.2$	71.04***
	0.05-0.25	$55.7^a \pm 10.9$	$62.6^a \pm 6.7$	$76.3^b \pm 6.6$	16.44***
	0.4-0.6	$37.0^a \pm 11.7$	$45.2^a \pm 12.3$	$78.7^b \pm 15.6$	27.44***
	0.8-1.0	$5.7^a \pm 12.1$	$15.2^a \pm 13.1$	$56.7^b \pm 19.3$	25.75***

TABLE 1
Continued...

Variable	Depth (m)	hsc	sc	fg	F
SB (mmolc kg^{-1})	0-0.05	$9.31^a \pm 1.38$	$10.31^a \pm 1.93$	$9.27^a \pm 2.47$	0.88^{NS}
	0.05-0.25	$4.58^a \pm 1.24$	$5.27^a \pm 0.97$	$7.57^b \pm 2.92$	6.68**
	0.4-0.6	$3.38^a \pm 1.17$	$3.20^a \pm 0.37$	$3.88^a \pm 1.37$	1.09^{NS}
	0.8-1.0	$2.77^a \pm 0.19$	$3.03^a \pm 0.32$	$3.42^a \pm 1.02$	2.73^{NS}
CEC (mmolc kg^{-1})	0-0.05	$86.11^a \pm 6.27$	$105.3^a \pm 4.97$	$156.37^b \pm 36.02$	29.06***
	0.05-0.25	$62.68^a \pm 4.94$	$88.47^a \pm 4.18$	$142.57^b \pm 51.29$	18.66***
	0.4-0.6	$36.08^a \pm 3.52$	$45.10^a \pm 4.02$	$144.48^b \pm 42.02$	60.49***
	0.8-1.0	$25.67^a \pm 1.36$	$30.13^a \pm 1.98$	$81.62^b \pm 28.58$	35.26***
V (%)	0-0.05	$10.6^b \pm 1.2$	$9.8^b \pm 1.7$	$6.2^a \pm 1.7$	22.36***
	0.05-0.25	$7.3^a \pm 2.1$	$5.8^a \pm 1.1$	$6.0^a \pm 2.8$	1.43^{NS}
	0.4-0.6	$9.6^c \pm 2.9$	$7.1^b \pm 0.8$	$3.0^a \pm 1.2$	43.86***
	0.8-1.0	$10.9^b \pm 1.2$	$9.9^b \pm 1.2$	$4.8^a \pm 2.7$	31.00***
clay (%)	0-0.05	$31.9^b \pm 2.3$	$26.9^a \pm 2.6$	$77.2^c \pm 2.8$	22.95***
	0.05-0.25	$29.8^b \pm 1.8$	$24.7^a \pm 2.1$	$75.6^c \pm 5.2$	43.47***
	0.4-0.6	$25.2^a \pm 2.7$	$20.5^a \pm 0.8$	$66.1^b \pm 11.7$	43.59***
	0.8-1.0	$25.7^a \pm 2.1$	$20.6^a \pm 2.7$	$66.4^b \pm 11.6$	25.27***
silt (%)	0-0.05	$6.5^a \pm 1.3$	$5.0^a \pm 2.2$	$12.2^b \pm 3.3$	964.42***
	0.05-0.25	$3.8^a \pm 1.7$	$4.2^a \pm 1.9$	$13.8^b \pm 3.9$	567.93***
	0.4-0.6	$4.1^a \pm 1.3$	$4.4^a \pm 1.4$	$18.9^b \pm 7.3$	131.61***
	0.8-1.0	$5.9^a \pm 1.6$	$4.8^a \pm 1.9$	$18.1^b \pm 8.1$	126.89***
sand (%)	0-0.05	$61.6^b \pm 2.8$	$68.1^c \pm 3.1$	$10.6^a \pm 2.8$	951.49***
	0.05-0.25	$66.4^b \pm 2.1$	$71.1^c \pm 2.3$	$10.6^a \pm 4.3$	814.79***
	0.4-0.6	$70.7^b \pm 2.6$	$75.1^b \pm 1.5$	$15.0^a \pm 16.2$	105.03***
	0.8-1.0	$68.4^b \pm 2.2$	$74.6^b \pm 2.5$	$15.5^a \pm 17.8$	78.48***

between both cerrados and the floodplain grassland at all depths. For P, we found significant differences between both cerrados and the floodplain grassland at the first three depths.

In relation to K, there were significant differences between both cerrados and the floodplain grassland at the first two depths and between hyperseasonal cerrado and floodplain grassland at the fourth depth. For Ca, the only significant difference we found was between both cerrados and the floodplain grassland at the first depth. For Mg, we found significant differences between seasonal cerrado and the other two environments at the first depth and between hyperseasonal cerrado and floodplain grassland at the second one. Base saturation (V) was significantly different between both cerrados and the floodplain grassland at the first and fourth depths and among the three environments at the third one. In relation to SB, we found significant differences between both cerrados and the floodplain grassland at the second depth.

Silt content in both cerrados was significantly different to that in floodplain grassland at all depths, the same pattern found for clay and sand content at the last two depths. Clay and sand content at the first two depths were significantly different among the three environments.

In the PCA, the first depth presented the highest eigenvalues in the first two axes; the first axis explaining 60.00% of the variation and the second one explaining 25.98%. The three environments formed two distinct groups (Fig. 2): soils under floodplain grassland presented positive scores in the first axis, related to larger amounts of clay, silt, OM, P, Al, m, CEC, and SB, whereas soils under hyperseasonal and seasonal cerrados presented negative scores in the first axis related to higher values of pH, V, Ca, Mg, and sand.

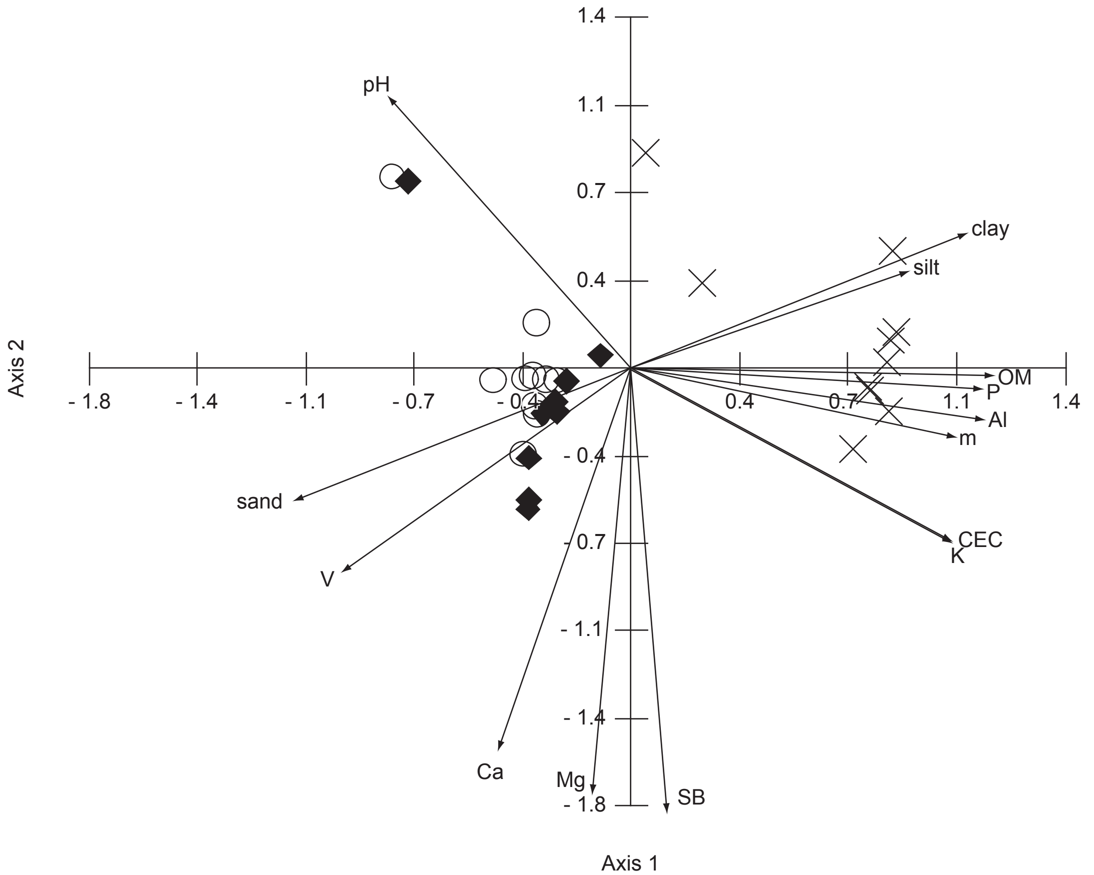

Fig. 2 — Principal Component Analysis of soil variables at 0-0.05 m deep for the hyperseasonal cerrado (○), seasonal cerrado (♦), and floodplain grassland (x) in Emas National Park, (18° 18' 07" S and 52° 57' 56" W), central Brazil. OM = organic matter; P = phsophorus; K = potassium, Ca = calcium; Mg = magnesium; Al = aluminium; m = aluminium saturation; SB = sum of bases; CEC = cation exchange capacity; and V = base saturation.

DISCUSSION

In water-saturated soils, oxygen supply is only sufficient for microbial activity in the first few millimeters of surface soil; at greater depths, oxygen disappears from the system within several days to a week after water saturation under tropical conditions (Brinkman & Diepen, 1990). Flooding drastically reduces oxygen diffusion into the soil, causing hypoxia or anoxia, which is the main limitation that reduces root aerobic respiration and the absorption of minerals and water (Baruch, 1994a). The hypoxic or anoxic conditions above and below the soil surface promote anaerobic activities (Blom & Voesenek, 1996) that result in several characteristics of the physico-chemical environment of the roots: pH tends to be neutral, toxic substances produced by the reduction of ions such as ferrous and manganous accumulation, nitrates and sulphates are reduced to ammonia and sulphides, the availability of phosphorus and other nutrients is changed, and the incomplete decomposition of organic matter produces various toxic compounds (Gopal & Masing, 1990).

Although we found significant differences in the pH among the three environments (Table 1), its effect on the plants in all environments must be similar, since all values indicated acid soils, which are generally poor in nutrients (Embrapa, 1999). The organic matter content was different between both cerrados and the floodplain grassland (Table 1) due to the incomplete decomposition at the latter site (Gopal & Masing, 1990). Apparently, the short waterlogging period in the hyperseasonal cerrado was not long enough to promote a higher organic matter content in the soil under these environments when compared to the soil under the seasonal cerrado.

All three environments had aluminic soils, with aluminium saturation higher than 50% or a base saturation lower than 50% (Table 1). Exchangeable aluminium decreases the nutrient availability to the plants, decreasing phosphorus absorption or its precipitation in intercellular spaces (Malavolta *et al.*, 1977), and usually causes a decrease in magnesium and calcium absorption from roots (Marschner, 1989). The effects of Al and H^+ are additive in acid soils, as the sampled ones, with respect to replacement of Ca^{2+} and Mg^{2+}, contributing to the reduced availability of these nutrients to the plants (Marschner, 1989).

The soils under the three environments were nutrient-poor ones, but with different limitations: in the floodplain grassland, there were higher values of organic matter, aluminium, clay, phosphorus, and aluminium saturation, whereas in the hyperseasonal and seasonal cerrados, there were higher values of sand and base saturation. The floodplain grassland does not seem to be limited by phosphorus, contrary to the hyperseasonal and seasonal cerrados. Low levels of available phosphorus highly increases the proportion of legumes (Elisseou *et al.*, 1995; Janssens *et al.*, 1998); thus we predict a higher proportion of legumes in the hyperseasonal and seasonal cerrados than in the floodplain grassland, where grasses and sedges should be more abundant (Janssens *et al.*, 1998).

The soils under both cerrados and under the floodplain grassland differed in relation to clay and sand proportions (Table 1). Oxisols (Latosols), such as the soils under hyperseasonal and seasonal cerrados, tend to have good physical properties due to high aggregate stability, but poor chemical ones due to low nutrients, relative to plant growth (Motta *et al.*, 2002). The higher sand proportion in hyperseasonal and seasonal cerrados implies that there is a low water capacity (Morgan *et al.*, 2001).

Despite the high sand proportion in the hyperseasonal cerrado soil, it becomes waterlogged at the end of the rainy season. As stated previously, the waterlogging causes a decrease in soil oxygen content. The ability of roots to respond to variations in soil environment, such as water and oxygen content in adjustments in their physiology, form, and structure that compensate for alteration in the availability of these resources has high survival values in plants from environments that experience severe drought and waterlogging (Sarmiento, 1984). In tropical grasslands, dryland grasses respond to flooding by increasing the proportion of root aerenchyma, enhancing the diffusion of atmospheric or photosynthetic oxygen from shoot to roots, so that aerobic respiration and growth can be maintained (Baruch and Mérida, 1995). In non-wetland plants, the formation of aerenchyma is induced by soil anaerobiosis and many species present this response to flooding (Peterson, 1992).

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 & 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, which is particularly true for pH and pH-related properties, like CEC and the 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 environments. Nevertheless, even in the waterlogging period, when the soil conditions under the hyperseasonal cerrado should be closer to those under the floodplain grassland, the soil characteristics in the hyperseasonal cerrado were similar to those in the seasonal cerrado (Fig. 2).

As long as the soil under both cerrados were chemically and physically similar, the duration of waterlogging in the hyperseasonal cerrado was not long enough to alter its soil characteristics. Thus, the limitations to the plants growing on the hyperseasonal cerrado soil must be a consequence of the direct effects of flooding, *i.e.*, oxygen stress, not indirect effects with regard to nutrient supply. Since cerrado species are generally not adapted to overcome oxygen stress, the number of species and the diversity in the hyperseasonal cerrado should be lower than in the seasonal cerrado.

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REFERENCES

ALVIM, P. T. & ARAÚJO, W. A., 1952, El suelo como factor ecológico em el desarrollo de la vegetación en el centro-oeste del Brasil. *Turrialba, 2*: 153-160.

ASKEW, G. P. & MONTGOMERY, R. F., 1983, Soils of tropical savannas, pp. 63-77. *In*: D. W. Goodall (ed.), *Ecosystems of the world – tropical savannas*, Elsevier, Amsterdam.

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

BARUCH, Z., 1994b, 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.

BARUCH, Z. & MÉRIDA, T., 1995, Effects of drought and flooding on root anatomy in four tropical forage grasses. *Int. J. Plant Sci., 156*: 514-521.

BATALHA, M. A., SILVA, I. A., CIANCIARUSO, M. V. & DELITTI, W. B. C., 2005, Hyperseasonal cerrado, a new Brazilian vegetation form. *Braz. J. Biol., 65*: 735-738

BLOM, C. W. P. M. & VOESENEK, L. A. C. J., 1996, Flooding: the survival strategies of plants. *Trends Ecol. Evol, 11*: 290-295.

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

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

CAMARGO, O. A., MONIZ, A. C., JORGE, J. A. & VALADARES, J. M. A. S., 1986, Métodos de análise química e física de solos do Instituto Agronômico de São Paulo. *Bolm. Téc. Inst. Agr. S. Paulo, 106*: 1-94.

CASTRO, A. A. J. F., MARTINS, F. R. & 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, 75p.

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

ELISSEOU, G. C., VERESOGLOU, D. S. & MAMOLOS, A. P., 1995, Vegetation productivity and diversity of acid grasslands in northern Greece as influenced by winter rainfall and limiting nutrients. *Acta Oecol., 16*: 687-702.

EMBRAPA, 1999, Sistema Brasileiro de Classificação de Solos. Embrapa Produção de Informação, Brasília, 412p.

FREITAS, F. G. & SILVEIRA, C. O., 1977, Principais solos sob vegetação de cerrado e sua aptidão agrícola, pp. 155-190. *In*: M. G. Ferri (ed.), *Simpósio sobre o cerrado 4*. Itatiaia, Belo Horizonte.

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

GOODLAND, R. & POLLARD, R., 1973, The Brazilian cerrado vegetation: a fertility gradient. *J. Ecol., 61*: 219-224.

GOPAL, B. & MASING, V., 1990, Biology and Ecology, pp. 91-239. *In*: B. C. Patten (ed.), *Wetlands and shallow continental water bodies*, 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. & 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. & VAN TONGEREN, O. F. R., 1995, *Data analysis in community and landscape ecology*. Cambridge University, Cambridge, 299p.

KÖPPEN, W., 1931, *Grundriss der Klimakunde*. Gruyter, Berlin, 388p.

KOVACH, 1999, *Multivariate Statistical Package v. 3. 1*. Kovach Computing Services, Anglesey, 131p.

LOPES, A. S. & COX, F. R., 1977, Cerrado vegetation in Brazil: an edaphic gradient. *Agron. J., 69*: 828-831.

MALAVOLTA, E., SARRUGE, J. R. & BITTENCOURT, V. C., 1977, Toxidez de alumínio e manganês, pp. 275-301. *In*: M. G. Ferri (ed.), *Simpósio sobre o cerrado 4. Itatiaia*, Belo Horizonte.

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

MORGAN, K. T., LAWRENCE, R. P. & WHEATON, A., 2001, Comparison of laboratory and field-derived soil water retention curves for a fine sand soil using tensiometric, resistance and capacitance methods. *Plant Soil, 234*: 153-157.

MOTTA, P. E. F., CURI, N. & FRANZMEIER, D. P., 2002, Relation of soils and geomorphic surfaces in the Brazilian cerrado, pp. 13-32. *In*: P. S. Oliveira & R. J. Marquis (eds.), *The cerrados of Brazil*. Columbia University, New York.

PETERSON, R. L., 1992, Adaptation of root structure in relation to biotic and abiotic factors. *Can. J. Bot., 70*: 661-675.

PONNAMPERUMA, E. N., 1972, The chemical of submerged soils. *Adv. Agron., 24*: 29-96.

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

RAIJ, B., QUAGGIO, J. A., CANTARELLA, H., FERREIRA, M. E., LOPES, A. S. & BATAGLIA, O. C., 1987, *Análise química de solos para fins de fertilidade*. Fundação Cargill, Campinas, 170p.

RATTER, J. A., RIBEIRO, J. F. & BRIDGEWATER, S., 1997, The Brazilian cerrado vegetation and threats to its biodiversity. *Ann. Bot., 80*: 223-230.

RUGGIERO, P. G. C., BATALHA, M. A., PIVELLO, V. R. & 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, pp. 245-288. *In*: D. W. Goodall (ed.), *Ecosystems of the world – tropical savannas*, 730p., Elsevier, Amsterdam.

SARMIENTO, G., 1984, *The ecology of neotropical savannas*. Harvard University, Cambridge, 235p.

SOIL SURVEY STAFF, 1999, S*oil Taxonomy. A basic system of soil classification for making and interpreting soil surveys*. US Government Printing Office, Washington, 871p.

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.

ZAR, J. H., 1999, *Biostatiscal analysis*. Prentice Hall, Upper Saddle River, 663p.