

Soil–vegetation relationships in cerrados under different fire frequencies

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Abstract Fire is an important ecological factor that structures savannas, such as the cerrado, by selecting plant species and altering soil nutrient content. In Emas National Park, central Brazil, we compared soils under three different fire regimes and their relationship to the cerrado species they support. We collected 25 soil and vegetation samples at each site. We found differences in soil characteristics ($p < 0.05$), with fertility and fire frequency positively related: in the annually burned site we found higher values of organic matter, nitrogen, and clay, whereas in the protected site we detected lower values of pH and higher values of aluminum. We also observed differences in plant community structure, with distinct floristic compositions in each site. Floristic composition was more related to sand proportion (intra-set correlation = 0.834). Different fire frequencies increase environmental heterogeneity and beta diversity in the Brazilian cerrado.

Keywords Cerrado · Fire · Savanna · Soil–vegetation relationships

Abbreviations

OM	organic matter
SB	sum of bases
CEC	cation exchange capacity
V	base saturation
m	aluminum saturation
CCA	canonical correspondence analysis

Introduction

Fire plays an important role in the ecology of savannas, such as in the Brazilian cerrado, structuring vegetation by selecting plant species throughout thousands of years (Coutinho 1990; Bond et al. 2005). Burning has a direct negative effect on plant growth rate and seedlings mortality; however, it also has an indirect positive effect, possibly due to release of nutrients to the soil (Hoffmann 1996, 1998, 2002; Setterfield 2002). Many cerrado plant species are adapted to fire and some depend on it to complete their natural life cycles and maintain their populations (Coutinho 1990; Hoffman 1998; Gottsberger and Silberbauer-Gottsberger 2006). Besides, attempts to avoid fire in cerrado patches resulted in catastrophic burnings due to accumulation of plant dry matter (Ramos-Neto and Pivello 2000). So, it is not possible neither desirable to exclude fire completely from cerrado reserve areas. However, cerrado reserves are also subjected to anthropogenic fires that burn larger areas and can be detrimental to the vegetation (Ramos-Neto and Pivello 2000). To

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control fire extension and frequency, managers are using prescribed burnings, that is, establishing a net of firebreaks, burning large predetermined areas periodically (“burning blocks”), or simply allowing lightning fires to burn freely (Ramos-Neto and Pivello 2000; van Wilgen et al. 2004).

Fire management may result in changes of environmental characteristics of target natural areas, since fires are expected to alter the concentration of some chemicals and organic matter in soils (Brye 2006). The change on each soil nutrient quantity depends on fire intensity and frequency and can result from ash deposition or mineralization of organic forms (Kennard and Gholz 2001). During a fire, some of the plant nutrients are released to the atmosphere as gaseous compounds and some are deposited on the soil as ash (Pivello-Pompéia and Coutinho 1992). Soil pH tends to increase after a fire due to the release of basic ions (Knicker 2007). The effect of fire on organic matter content is highly variable, ranging from total destruction to increasing (González-Pérez et al. 2004). Fire also affects mycorrhizal symbiosis and soil microbial activity, which can alter soil nutrients dynamics (Nardoto and Bustamante 2003; Hartnett et al. 2004; Yong-Mei et al. 2005). Burnings may either increase or not change soil nitrogen content (Nardoto and Bustamante 2003; Brye 2006).

Cerrado soils are usually acidic, deep, well-drained and nutrient-poor, with low cation exchange capacity, low organic matter content, and high aluminum saturation and are among the most important factors to determine the occurrence of the cerrado and its physiognomy variation (Montgomery and Askew 1983; Gottsberger and Silberbauer-Gottsberger 2006). Plant and soil have a dependence interrelationship, in a way that they are influenced by alterations in each other (Montgomery and Askew 1983). If fire alters soil features, then it will be reflected in changes in the cerrado plant communities adapted to those soil conditions.

Poor attention has been paid to how fire frequency and soil properties can interact with the cerrado vegetation. Although there are many studies about fire effects on both cerrado vegetation (e.g., Hoffmann 1996, 1998, 2002) and cerrado soil (e.g., Pivello-Pompéia and Coutinho 1992; Nardoto and Bustamante 2003), and there are some studies considering the effect of soil upon cerrado vegetation (e.g., Haridasan 2000; Amorim and Batalha 2007) there was no study relating soil

properties, floristic composition, and fire frequency in cerrado sites.

Here we compared chemical and physical soil features in three nearby cerrado sites under different fire frequency, relating them to the vegetation they support. We looked for differences in soil features according to fire frequency, particularly at the highest fire frequency. We aimed to relate soil features and floristic composition, which should have a strict relation due to the interdependence of soil and vegetation. The soil feature more related to the vegetation should be the one that has an influence in both nutrient and water availability to plants. Higher fire frequencies should lead to more severe changes in soil characteristics and, as a consequence, to more severe modifications in plant communities, maybe resulting in loss of diversity in firebreaks.

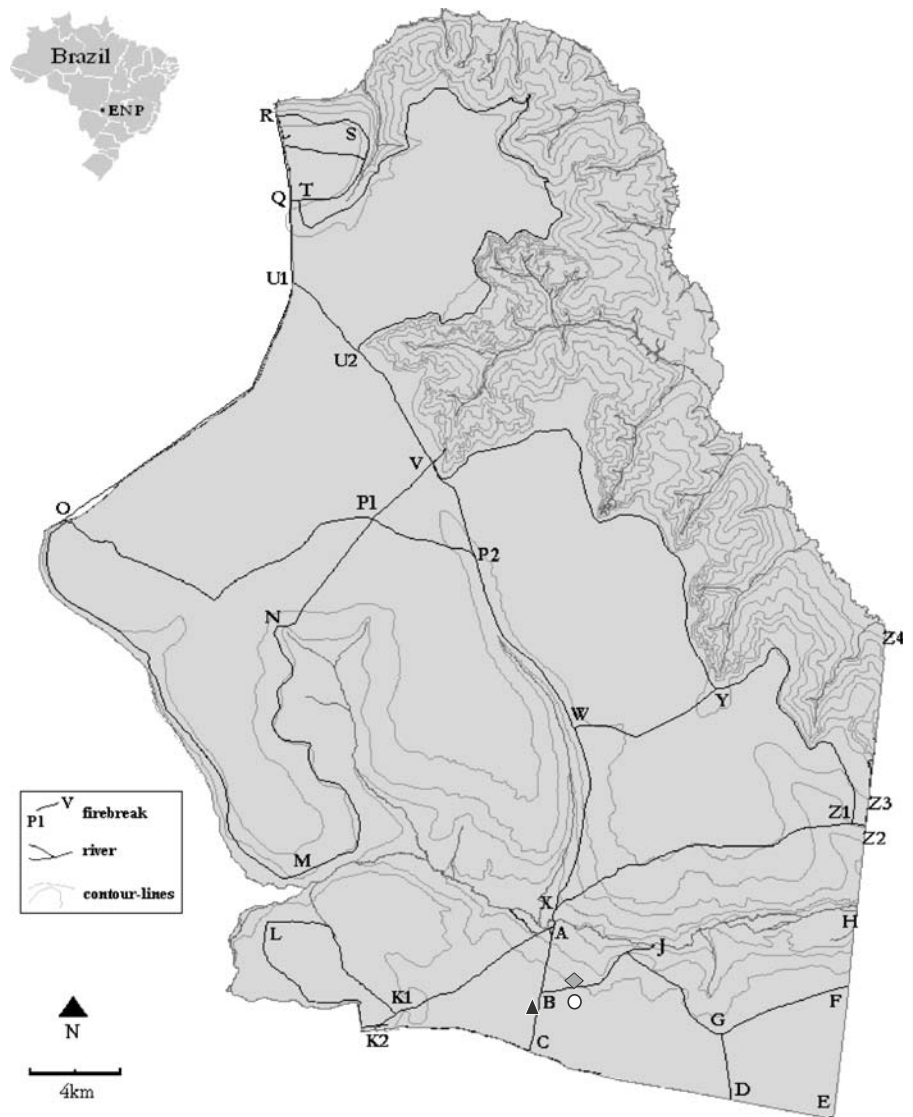
Materials and methods

Study area

We conducted our study in Emas National Park (ENP), located in the Brazilian Central Plateau (approximately 17°49′–18°28′S and 52°39′–53°10′ W), under a tropical warm wet climate, with at least three dry months during the winter. Annual rainfall varies from 1200 to 2000 mm, concentrated from October to March (Ramos-Neto and Pivello 2000). Soils in ENP are mainly Oxisols (Scardua 2004).

Inside ENP, annual prescribed burnings are applied in firebreaks to remove plant dry mass and to avoid the spreading of fires, which in the past resulted in catastrophic burnings every three years (Ramos-Neto and Pivello 2000). In 2006, at late rainy season, we sampled three savanna woodland (*campo cerrado*) sites distant less than 2 km one from the other, all located in the southeastern portion of the reserve, subjected to different fire frequencies: two firebreaks, one burned annually for the last ten years (approximately 18°18′50″S and 52°54′00″W), other burned in 1996, 1999, 2001, 2002, and 2003 (approximately 18°19′01″S and 52°54′10″W), and a site without burnings since 1994 (approximately 18°17′28″S and 52°53′41″W) (Fig. 1). In 1994, a great fire burned out the whole park, after which fire management inside the reserve was changed (França et al. 2007). Prior to 1994, a policy of complete fire exclusion inside ENP

Fig. 1 Firebreak net in Emas National Park ($17^{\circ}49'-18^{\circ}28'S$, $52^{\circ}39'-53^{\circ}10'W$), Brazil (after Ramos-Neto and Pivello 2000). Annually burned (\blacktriangle), intermediate burned (\blacklozenge), unburned since 1994 (\circ). Letters represent reference points inside ENP



lead, paradoxically, to catastrophic burnings every three years due to the accumulation of dry biomass; after 1994, natural fires were allowed inside ENP and, since then, with a periodic reduction of dry biomass, no catastrophic burning occurred (França et al. 2007). So, this year represents a turning point in ENP's fire regime: before 1994, a given point was burned every three years on average; after 1994, every seven years (França et al. 2007).

Sampling

At each site, we delimited a 2.5 km line, in which we placed sampling points every 10 m, comprising 250

points per site. At each point, we collected a soil sample at 5 cm depth, since this layer is the most correlated to the cerrado vegetation (Ruggiero et al. 2002; Amorim and Batalha 2007). We took a composite sample comprising 10 sampling points. Thus, we had 25 soil samples for each site.

At each point, with the point-quarter method (Müller-Dombois and Ellenberg 1974), we sampled four individuals belonging to the woody component, that is, woody individuals with stem diameter at soil level equal to or higher than 3 cm (SMA 1997). We identified them to species level, by using identification keys based on vegetative characters (Mantovani et al. 1985; Batalha and Mantovani 1999) and comparing

them to ENP's reference collection (Batalha and Martins 2002). We grouped the individuals from each ten points to correlate species abundances to soil features.

Soil chemical and physical analyses

Soil chemical and physical analyses were conducted at the Soil Sciences Laboratory of the São Paulo University, according to the procedures described by Embrapa (1997), Silva (1999) and Raij et al. (2001). We determined pH, organic matter (OM), available phosphorus (P), total nitrogen concentration (N), exchangeable K^+ , Ca^{2+} , Mg^{2+} , and Al^{3+} . We also calculated sum of bases (SB), cation exchange capacity (CEC), base saturation (V), and aluminum saturation (m). We also determined sand, clay, and silt contents.

Soil pH was determined in $CaCl_2$ solution, using 10 ml of soil in 25 ml of solution. $CaCl_2$ was used to avoid salt and oxides influences. Organic matter was determined by organic carbon oxidation with potassium dichromate and subsequent potassium dichromate titration with ammoniac ferrous sulfate, using 0.5 g of soil and 10 ml of potassium dichromate solution. A correction factor (1.33) was used to compensate partial carbon oxidation. Available phosphorus was determined by spectrophotometry after anion exchange resin extraction, using 2.5 cm^3 of soil. Total nitrogen concentration was determined by digestion with H_2SO_4 , followed by distillation with NaOH, using from 0.5 to 1 g of soil, 1 g of H_2SO_4 , and 15 ml of NaOH. Cations K^+ , Ca^{2+} , Mg^{2+} , and Al^{3+} were extracted with 1 M KCl, using 10 cm^3 of soil and 100 ml of solution. Then, K, Ca, and Mg were determined by an EDTA complexometry. Al was determined by NaOH titration. Sum of base was calculated as sum of K, Ca, and Mg. CEC was calculated as SB plus H^+ and Al^{3+} concentrations. Base saturation was calculated as a percentage of total CEC. Aluminum saturation was calculated as a percentage of sum of SB and Al^+ . These procedures are described in detail in Embrapa (1997), Silva (1999) and Raij et al. (2001). We quantified soil sand, silt, and clay proportions using the Boyoucus method: First, we settled soil particles using a dispersant, separated suspension from the sediment, and calculated clay content by suspension density using a densimeter. Then, we sieved the sediment to separate the sand, which was weighted.

We calculated silt proportion by the difference (Embrapa 1997).

Statistical analyses

We applied analyses of variance (Zar 1999) to test whether there were significant differences ($\alpha=0.05$) among soil features of the three sites. We used parametric statistical analyses even when data were not normally distributed and variances were heterogeneous, because the analysis of variance is robust enough to 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 sand, clay, silt, V, and m to their arcsines prior to the analyses (Zar 1999). If a variable presented significant differences, we used Tukey multiple comparison test (Zar 1999).

We used a canonical correspondence analysis (CCA, Jongman et al. 1995) to analyze all soil parameters simultaneously, centralized and standardized, by relating them to the species abundances, with the MVSP software (Kovach 1999). CCA is adequate to data like ours because it selects the linear combination of environmental variables that best explains the vegetation data (Jongman et al. 1995). We used a Monte Carlo method, with 500 permutations, to test whether eigenvalues and species-environment correlations were significantly different from a random distribution (Manly 1997). We used the CCA scores to construct a biplot with both soil and vegetation data. We carried out a non-parametric multivariate analysis of variance to test whether the floristic composition of the three sites were different with the NPMANOVA software (Anderson 2003).

Results

We found significant differences, among sites, for pH, OM, N, K, Mg, Al, CEC, V, m, sand, clay, and silt (Table 1). In the annually burned site, we found the highest values of OM, N, Mg, clay, and silt, whereas sand and K presented the lowest ones (Table 1). In the intermediate burned site, we found the lowest values of CEC and m, and the highest value of V (Table 1). In the protected site, we found the lowest value of pH and the highest of Al (Table 1). We did not find

Table 1 Summarized values (mean \pm standard deviation) of soil chemical and physical features in cerrado sites under different fire frequencies in Emas National Park (Brazil)

Soil parameter	Site			F
	Annually burned	Intermediate burned	Unburned since 1994	
pH	4.07 ^a \pm 0.06	4.05 ^a \pm 0.05	3.94 ^b \pm 0.06	40.38 ***
OM (g kg ⁻¹)	73.96 ^a \pm 15.27	48.28 ^b \pm 10.80	51.96 ^b \pm 11.72	29.69 ***
P (mg kg ⁻¹)	3.52 \pm 1.05	3.84 \pm 1.18	3.60 \pm 1.12	0.56 NS
N (mg kg ⁻¹)	1694.32 ^a \pm 126.54	1332.08 ^b \pm 215.10	1459.96 ^c \pm 155.35	29.29 ***
K (mmolc kg ⁻¹)	0.44 ^a \pm 0.47	0.99 ^b \pm 0.36	0.92 ^b \pm 0.33	14.46 ***
Ca (mmolc kg ⁻¹)	1.60 \pm 1.68	1.60 \pm 1.66	1.12 \pm 0.33	1.01 NS
Mg (mmolc kg ⁻¹)	1.24 ^a \pm 0.44	1.04 ^b \pm 0.20	1.04 ^b \pm 0.20	3.704 *
Al (mmolc kg ⁻¹)	12.68 ^a \pm 1.99	12.48 ^a \pm 1.98	15.40 ^b \pm 4.12	8.01 ***
SB (mmolc kg ⁻¹)	3.28 \pm 1.89	3.63 \pm 1.74	3.08 \pm 0.64	0.82 NS
CEC (mmolc kg ⁻¹)	89.08 ^a \pm 4.89	78.87 ^b \pm 8.95	87.64 ^a \pm 11.43	9.77 ***
V (%)	3.56 ^a \pm 2.14	4.80 ^b \pm 2.61	3.52 ^a \pm 0.87	3.91 *
M (%)	80.04 ^a \pm 7.21	77.64 ^b \pm 7.95	82.84 ^a \pm 4.09	4.014 *
Sand (%)	26.64 ^a \pm 3.97	44.60 ^b \pm 7.31	44.20 ^b \pm 5.88	39.74 ***
Clay (%)	66.24 ^a \pm 6.95	51.40 ^b \pm 6.91	52.32 ^b \pm 6.03	79.20 ***
Silt (%)	7.12 ^a \pm 6.88	4.00 ^b \pm 1.51	3.48 ^b \pm 1.48	9.23 ***

NS $P > 0.05$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

significant differences among the three sites for P, Ca, and SB (Table 1).

The annually burned site presented 28 species, of which *Allagoptera leucocalyx*, *Anacardium humile*, *Chresta sphaerocephala*, *Chromolaena squalida*, *Duguetia furfuracea*, *Manihot tripartita* and *Vernonia bardanoides* were found only in this site (Table 2). The intermediate burned site presented 37 species, of which *Aegiphila lhotzkiana*, *Didymopanax macrocarpum*, *Himatanthus obovatus*, and *Qualea parviflora* were exclusive to it (Table 2). The protected site presented 39 species, of which *Bauhinia rufa*, *Campomanesia pubescens*, *Lafoensia pacari*, *Miconia albicans*, *Roupala montana*, and *Sclerolobium* sp. were found only in this site (Table 2).

The first and second axes of the CCA explained 18.2% of data variation, 14.7% by the first axis and 3.5% by the second one (Fig. 2). The first axis separated the annually burned site from the other two. The points of the intermediate burned site and the protected site were overlapped in the first two axes and separated only in the third axis (not shown). The scores of these two sites were more related to high values of SB, Al, K, sand, and silt, whereas the scores of the annually burned site were more related to high values of N, clay, OM, CEC, pH, and Mg (Fig. 2). Floristic compositions were more related to sand

proportion (intra-set correlation=0.834) at the first axis, positively in the case of low and intermediate fire frequencies and negatively in the case of high fire frequency, and to aluminum saturation (intra-set correlation=0.434) at the second axis (Table 3). The relationship between soil and vegetation matrices was significant ($p=0.002$) only for the first axis (Table 4). Floristic compositions were different among the three sites ($p=0.001$), with each one different from the other two (1 vs. 2, $p=0.001$; 1 vs. 3, $p=0.001$; 2 vs. 3, $p=0.009$).

Discussion

Both sand and clay proportions are important to vegetation, because soils with higher sand proportion have lower water retention capacity, and clay particles adsorb mineral nutrients (Larcher 1995). Thus, plant community in the protected site may be limited by loss of soil nutrients, whereas in the annually burned site soil nutrients adsorbed in clay may be gradually released to soil. Water holding and nutrient availability are determinants for vegetation diversity and structure (Dubbin et al. 2006). Whereas some studies, as well as ours, found that clay proportion increased with fire frequency in savannas (e.g., Spera et al.

Table 2 Woody species abundance in cerrado sites under different fire frequencies at Emas National Park (Brazil)

Family	Species	Abundance		
		Annually burned	Intermediate burned	Unburned since 1994
Fabaceae	<i>Acosmium dasycarpum</i> (Vogel) Yakovlev	10	7	23
Verbenaceae	<i>Aegiphila lhotzkiana</i> Cham.		1	
Arecaceae	<i>Allagoptera leucocalyx</i> (Mart.) Kuntze	36		
Anacardiaceae	<i>Anacardium humile</i> A. St-Hil.	11		
Fabaceae	<i>Anadenanthera falcata</i> (Benth.) Speg.	14	21	42
Annonaceae	<i>Annona crassiflora</i> Mart.	5	42	37
Fabaceae	<i>Bauhinia rufa</i> Steud.			1
Malpighiaceae	<i>Byrsonima coccolobifolia</i> A. Juss.		6	4
Myrtaceae	<i>Campomanesia pubescens</i> (A. DC.) O. Berg.			1
Caryocaraceae	<i>Caryocar brasiliense</i> Cambess.		7	7
Flacourtiaceae	<i>Casearia sylvestris</i> Sw.		1	6
Asteraceae	<i>Chresta sphaerocephala</i> DC.	1		
Asteraceae	<i>Chromolaena squalida</i> (Spr.) King and H. Rob.	3		
Dilleniaceae	<i>Davilla elliptica</i> A. St-Hil.	23		13
Apiaceae	<i>Didymopanax macrocarpum</i> Seem.		1	
Fabaceae	<i>Dimorphandra mollis</i> Benth.	7	9	8
Ebenaceae	<i>Diospyros hispida</i> A. DC.	48	11	33
Annonaceae	<i>Duguetia furfuracea</i> (A. St-Hil) Benth. and Hook	2		
Asteraceae	<i>Eremanthus erythropappus</i> Sch. Bip.	33	94	57
Malvaceae	<i>Eriotheca gracilipes</i> (K. Schum.) A. Robyns		13	9
Malvaceae	<i>Eriotheca pubescens</i> (Mart. and Zucc.) A. Robyns		4	3
Erythroxylaceae	<i>Erythroxylum campestre</i> A. St-Hil.	1	7	14
Erythroxylaceae	<i>Erythroxylum suberosum</i> A. St-Hil.		23	9
Myrtaceae	<i>Eugenia</i> aff. <i>piauhiensis</i> O. Berg.	1	1	
Myrtaceae	<i>Eugenia livida</i> Berg.		8	8
Myrtaceae	<i>Eugenia puniceifolia</i> (Kunth) DC.		1	2
Apocynaceae	<i>Himatanthus obovatus</i> (Müll. Arg.) Woods.		1	
Clusiaceae	<i>Kielmeyera coriacea</i> Mart.		4	1
Lythraceae	<i>Lafoensia pacari</i> A. St-Hil.			4
Fabaceae	<i>Machaerium acutifolium</i> Vogel	2		1
Euphorbiaceae	<i>Manihot tripartita</i> (Spreng.) Müll. Arg.	4		
Melastomataceae	<i>Miconia albicans</i> Triana			13
Melastomataceae	<i>Miconia ferruginata</i> A. DC.		1	1
Fabaceae	<i>Mimosa amnis-atricornis</i> Barneby	456	3	10
Ochnaceae	<i>Ouratea acuminata</i> (A. DC.) Engl.	13	94	78
Ochnaceae	<i>Ouratea spectabilis</i> (Mart.) Engl.		79	64
Rubiaceae	<i>Palicourea rigida</i> (Cham.) K. Schum.	7	7	3
Asteraceae	<i>Piptocarpha rotundifolia</i> (Less.) Baker	36	36	11
Sapotaceae	<i>Pouteria ramiflora</i> (Mart.) Radlk.	71	169	117
Sapotaceae	<i>Pouteria torta</i> (Mart.) Radlk.	66	107	83
Myrtaceae	<i>Psidium larutense</i> Cambess.	41	94	66
Vochysiaceae	<i>Qualea grandiflora</i> Mart.		4	1
Vochysiaceae	<i>Qualea parviflora</i> Mart.		1	
Proteaceae	<i>Roupala montana</i> Aubl.			4
Connaraceae	<i>Rourea induta</i> Planch.	41	26	58
Fabaceae	<i>Sclerolobium</i> sp.			1
Solanaceae	<i>Solanum lycocarpum</i> A. St-Hil.	16	1	2
Fabaceae	<i>Stryphnodendron adstringens</i> (Mart.) Coville	12	69	142
Bignoniaceae	<i>Tabebuia aurea</i> (Silva Manso) S. Moore		3	9
Bignoniaceae	<i>Tabebuia ochracea</i> (Cham.) Standl.	33	41	54
Asteraceae	<i>Vernonia bardanoides</i> Less.	7		

Fig. 2 Canonical correspondence analysis of soil chemical and physical variables related to vegetation data in cerrado sites under different fire frequencies in Emas National Park (Brazil). Annually burned (▲), intermediate burned (◆), unburned since 1994 (○)

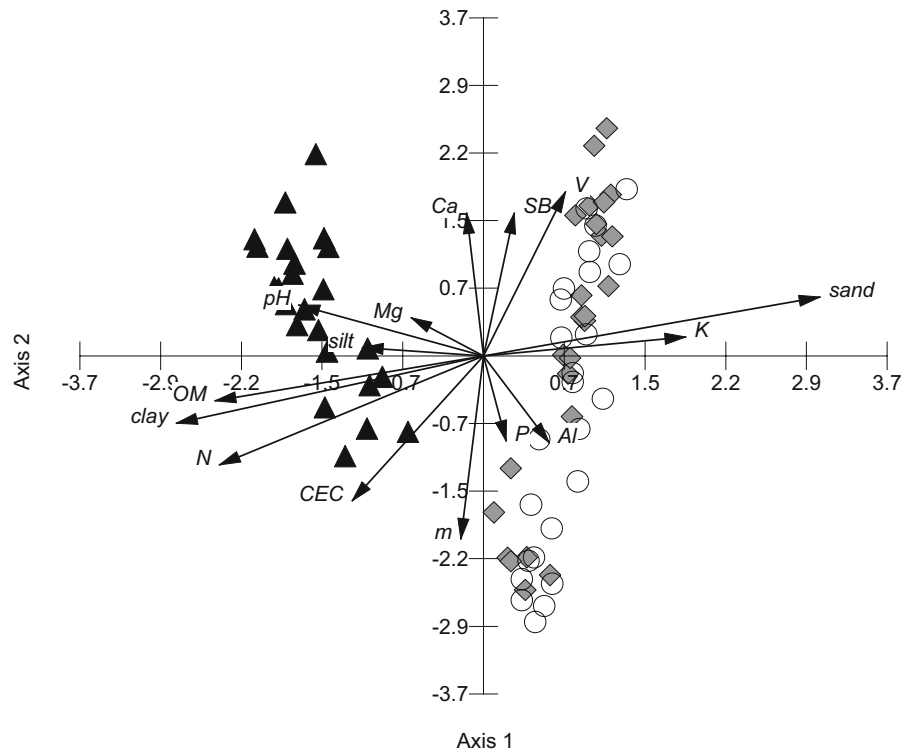


Table 3 Canonic coefficients and intra-set correlation of soil chemical and physical characteristics in cerrado sites under different fire frequencies at Emas National Park (Brazil)

Variable	Canonic coefficients		Intra-set correlation	
	Axis 1	Axis 2	Axis 1	Axis 2
pH	0.50	0.033	0.481	-0.179
OM	0.384	-0.205	0.658	0.134
P	0.001	0.037	-0.059	0.139
N	0.045	0.139	0.653	0.296
K	*	*	-0.486	-0.067
Ca	*	*	0.042	-0.336
Mg	*	*	0.153	-0.027
Al	0.136	-0.530	-0.172	0.222
H	*	*	0.331	0.423
SB	*	*	-0.077	-0.329
CEC	*	*	0.327	0.382
V	-0.285	0.540	-0.255	-0.403
M	-0.454	1.240	0.057	0.434
Sand	-0.247	-0.853	-0.834	-0.138
Clay	0.192	-0.761	0.772	0.155
Silt	0.100	-0.452	0.370	-0.048

* variables eliminated from analysis due to multicollinearity.

2000; Rhoades et al 2004), others found the opposite pattern (e.g., Nardoto and Bustamante 2003). In other vegetation types, clay proportion either decreased with fire (Hubbert et al. 2006) or was kept constant (Bowker et al. 2004). This variable response could be due either to topographical variation (Spera et al. 2000) or to variation present before fires (Doerr and Cerdà 2005). Even though we cannot state that fire has a direct effect on sand and clay proportion, it may have an indirect effect by reducing organic litter particles, which are incorporated to soil increasing the amount of clay soil particles (González-Pérez et al. 2004). But the causal relationship is not clear yet and further studies are needed to highlight real role fires play over soil texture.

An increase in organic matter may be due to the deposition of dry leaves and partly charred material (González-Pérez et al. 2004; Knicker 2007). Moreover, fire alters chemical structures in organic matter, leading to formation of more stable compounds that can remain in soils for longer time (Knicker 2007). Fire also turns the litter in small particles that may be

Table 4 Eigenvalues and species–environment correlation in cerrado sites under different fire frequencies at Emas National Park (Brazil)

	Axis	Observed data	Randomized data			P
			minimum	average	Maximum	
Eigenvalues	1	0.414	0.076	0.141	0.233	0.002
	2	0.099	0.053	0.078	0.127	0.052
Species–environment correlation	1	0.889	0.476	0.575	0.805	0.002
	2	0.749	0.461	0.692	0.975	0.188

Monte Carlo test with 500 randomizations.

incorporated to the soil (González-Pérez et al 2004). Besides, during burnings, compounds derived from lipids or lignins tend to remain in soil (Neff et al 2005). The post-fire nitrogen fixation process may also increase the organic matter on soil (Gonzalez-Perez et al 2004). Thus, frequent fires tend to increase the organic matter content in cerrado soils.

In spite of nitrogen loss by volatilization after fire (Coutinho 1990), total nitrogen pool is much higher than the gaseous losses (van de Vijver et al. 1999). Increased temperature and light availability after a fire tend to increase nitrogen fixation process by favoring leguminous plants (van de Vijver et al. 1999). For instance, we observed a high abundance of *Mimosa aminis-atricornis* in the annually burned site. As other plants of this genus, *Mimosa aminis-atricornis* may serve as mycorrhizal resource islands (Camargo-Ricalde and Dhillion 2003). More than half of the leguminous nitrogen comes from the atmosphere and, depending on post-fire regeneration rate, this fixation overcomes the loss to atmosphere (Casals et al. 2005).

Nutrient uptake may be decreased by both aluminum (Goodland 1971) and low pH values, which alter nutrient solubility (Larcher 1995). So, soils with high aluminum content and low pH values, as in the unburned site, may be considered poor. Aluminum and pH constrained species distribution, since some plant species may accumulate aluminum and have a competitive advantage on aluminum-rich soils, whereas others occur only on poor and acid soils (Haridasan 2000).

As long as post-fire nutrient release favors exotic plants (Milberg et al. 1999), frequent burnings might favor plant invasion. In fact, in the annually burned firebreak, there was a high density of invasive grasses, markedly *Brachiaria decumbens*. Even without pertur-

bations, exotic plants may proliferate and invade the vegetation (Milberg et al. 1999). Thus, these annually burned firebreaks may serve as entrance to exotic plants and allow the invasion in adjacent areas. In cerrado fragments, plant invasion is one of the most important problems, since invader grasses are very competitive against native herbs and can spread easily, representing a threat to natural biodiversity (Pivello et al. 1999). So, special control against invader plants must be taken in the annually burned firebreaks.

Although, as expected, fire reduced species richness in the annually burned site, there is a group of species that appeared only in this site. Fire may be removing superior competitors from this site and so allowing the establishment of fire-resistant species. Besides, as long as soil and vegetation matrices were related, soil features may also be selecting plants with specific nutrients requirement; for example, plants with less tolerance to high aluminum concentration or plants that demand more nitrogen (Haridasan 2000). Whereas protected sites may act as refuges to fire-sensitive species, sites with intermediate fire frequency may have species favored by litter removal but not tolerant to annual fires (Hoffman 1996, 2002). Fire and soil conditions are thought to be important environmental filters in savannas (Diaz et al. 1998). In this sense, they act by constraining the plant community to species with similar habitat and nutrient requirements (Diaz et al. 1998). Consequently, different fire frequencies increase environmental heterogeneity and beta diversity in the Brazilian cerrado. Therefore, if one aims to preserve the highest number of species, we suggest keeping areas with different fire frequencies in cerrado reserve areas, but paying special attention to plant invasion in areas with higher fire frequency.

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