THE INFLUENCE OF FIRE REGIME ON MICROSCALE STRUCTURAL VARIATION AND PATCHINESS IN *CERRADO* VEGETATION[1]

A INFLUÊNCIA DO REGIME DE FOGO NA VARIAÇÃO ESTRUTURAL EM MICROESCALA E O MOSAICO DA VEGETAÇÃO DE CERRADO

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RESUMO – O fogo é um dos principais condicionantes do mosaico fisionômico da vegetação do Cerrado, em diferentes escalas. O objetivo do presente estudo foi explorar o mosaico estrutural da vegetação do Cerrado em microescala, em áreas com diferentes regimes de fogo, no mosaico formado pelas unidades de conservação Estação Ecológica e Floresta Estadual de Assis, SP. Analisamos a vegetação em quatro transectos com 80 m de extensão, divididos em 20 subamostras de 4 m de comprimento. Para estimar a cobertura de todas as espécies do estrato herbáceo, utilizamos o método de intercepção de linhas em três diferentes faixas de altura: 0-50 cm, 50-100 cm e 100-150 cm. Medimos e identificamos todas as árvores e arbustos presentes nas subparcelas de 4 m x 4 m e coletamos amostras de solo compostas em cada transecto para caracterização ambiental. Comparamos os valores médios de cobertura e densidade da vegetação nos diferentes estratos e efetuamos análises multivariadas para explicar as diferenças florísticas entre as comunidades. Os resultados indicam que o fogo induz aumento na heterogeneidade, especialmente nos estratos inferiores da vegetação. No entanto, não há diferenciação florística que possa ser explicada pelos diferentes regimes de incêndios ou diferenças edáficas.

Palavras chave: savana; influência do fogo; estrutura da comunidade; mosaico vegetacional.

ABSTRACT – Fire can produce a hierarchical pattern of vegetation patchiness, from the large, landscape scale to the microscale, the dynamic nature of which changes over time. The aim of this study was to explore the microscale structural patchiness of Brazilian savanna vegetation (cerrado) in areas with different fire regimes at the mosaic formed by Assis Ecological Station, and Assis State Forest, São Paulo State. Vegetation was analysed in 80 m transects divided into twenty 4 m length plots that were established in four areas of savanna. The line-intercept method was used to estimate percentage cover of all species encountered at three different vertical heights, 0-50 cm, 50-100 cm and 100-150 cm, in the herbaceous layer. Measurements of all the trees and shrubs present in the 4 m x 4 m quadrats were taken, together with soil samples at intervals along the transects. Results suggest that fire frequency is related to vegetation structural heterogeneity, at certain scales and within certain vegetation levels. Frequent burning may cause the greatest amount of heterogeneity, with the herbaceous layer being most notably influenced. The multivariate analysis indicates, however, no clear differences in species composition between transects with different fire histories or soil properties.

Keywords: savanna; fire influence; community structure; vegetation mosaic.

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1 INTRODUCTION

Initial theories developed to interpret the functioning and dynamics of ecosystems, such as Clementsian ideas of succession (Clements, 1916), were based on the equilibrium paradigm, *i.e.* the idea of the 'balance of nature'. Equilibrium dynamics assumes that an ecosystem is a closed, biotic system, and the stable state of the ecosystem is maintained through inter- and intra- specific interactions gradually 'equilibrating' to constant, external conditions. It also views historical effects, spatial heterogeneity, stochastic factors and environmental perturbations as playing a negligible role in ecosystem functioning and dynamics. However, research has repeatedly shown that all of these factors are fundamental in ecological systems, particularly in tropical savannas.

There are four key ecological determinants of tropical savannas – plant available moisture – PAM, plant available nutrients – PAN, herbivory and fire (Stott, 1991). In many savannas, biological processes are moisture or PAM limited, and rainfall is inherently variable and unpredictable. The biotic system is therefore driven by infrequent rainfall events which vary in space and time. This is also true for 'disturbances' such as fire. Thus, a savanna ecosystem may rarely exhibit a stable state. This realisation led to a paradigm shift from an equilibrium to a non-equilibrium approach to savanna functioning, in which chance events, such as disturbance, play a crucial role in ecosystem dynamics. Although there has been much debate regarding the use of equilibrium and non-equilibrium concepts to explain savanna functioning (*e.g.* Illius and O'Connor 1999, Jeltsch et al., 2000, Sullivan and Rohde 2002, Vetter, 2005), it is clear that a key characteristic of savannas is the inherent variability in its determinants, such as fire. This is a fundamental aspect in the understanding of savanna dynamics.

The switch from an equilibrium to a non-equilibrium view was accompanied by a shift from *homogeneity* to heterogeneity influencing ecological processes at multiple scales (Perry, 2002, Pickett et al., 2003). Savannas are typically patchy environments, and it is now recognised that spatial and temporal heterogeneity of environmental determinants are crucial elements in the structure and functioning of this ecosystem (Jeltsch et al., 1998, 1999; Higgins et al., 2000; Ludwig et al., 1999a, 1999b, 2000). Fire, as an ecological determinant of savannas, is an important mechanism producing and maintaining spatial heterogeneity through the spatio-temporal creation of a mosaic of vegetation patches at different successional stages. Termed a 'patch-mosaic fire regime' (Parr and Brockett, 1999), mosaics created by fire are thought to reflect traditional and historical burning strategies (Haynes, 1985; Russell-Smith and Edwards, 2006; Boyd, 1999; Laris, 2002; Mistry et al., 2005; Hudak et al., 2004). Benefits of patchiness created by fire include the formation of natural firebreaks within the landscape (Laris, 2002; Mistry et al., 2005), and enhanced habitat and species diversity (Braithwaite, 1996; Vigilante and Bowman, 2004).

Fire can produce a hierarchical pattern of patchiness, from the large, landscape scale to the microscale, the dynamic nature of which changes over time. As such, it can be difficult to measure the nature, function, inter-relatedness and existence of these patches. Significant research has been carried out on the landscape scale impact of fire, especially with the use of satellite remote sensing (*e.g.* Russell-Smith and Edwards, 2006; Dempewolf et al., 2007; Edwards and Russell-Smith, 2009). However, we have little knowledge of the influence of fire on patch dynamics at finer scales, such as at the microscale, although patch dynamics at this scale may play an important role in resource capture, as well as other savanna functions. The savannas (*cerrado*) of Brazil cover over 22% of the Brazilian territory, and are considered one of the top ten hotspots for plant and animal biodiversity (Myers et al., 2000). Fire is a major determinant of the *cerrado* (Mistry, 1998) with the remaining fragments of *cerrado* experiencing a marked change from the frequent, low-intensity, small-scale traditional burning regimes (Anderson and Posey, 1985, 1987; Posey, 1984, 1985; Balée, 1994; Mistry et al., 2005), to unplanned and unmanaged, extensive, high-intensity wildfires. This change in fire regime has major implications for the composition, structure and functioning of the *cerrado*.

Considering the significance of patchiness within savannas and the influence of determinants such as fire on establishing these patches, limited research has been carried in this field. The aim of this study was to explore the scale of patterns in *cerrado* vegetation influenced by fire. In contrast to many other studies, we were interested in the effect of fire at the microscale level.

As other studies on patch scale processes, such as the capture of PAM (*e.g.* Tongway and Ludwig, 1997), have shown, we were particularly interested in seeing whether any patterns at a fine scale could be identified. This was an exploratory study aimed at looking for patterns as a basis for further research.

2 MATERIAL AND METHODS

2.1 Site Description

The mosaic formed by Assis Ecological Station and Assis State forest is located 22º33' to 22º38'S and 50º20' to 50º27'W, with altitude ranging from 520 to 590 m above sea level (Figure 1). The total area covers 4,480 ha in the municipality of Assis, São Paulo State, and is administered by the Forestry Institute of São Paulo State. Parts of the area have been used as pastures and forest plantations, but a large proportion (about 1,600 ha) is a dense form of savanna (*cerrado)* (Max et al., 2007).

The soils covering the study areas are homogeneously Dark-Red Latosol, and climate is the typical *cerrado* type, namely hot, wet summer (with approximately 1400 mm of average annual rainfall), and mild, dry winters (average minimum temperature 8.4^{o}C), during which fires can occur. The dry season begins in May/June and ends in August/September. Being on the southern limit of the *cerrado* range, the area is also subject to infrequent frosts, severe frosts having a recurrence period of about 25 years (Brando and Durigan, 2004).

Figure 1. The location of the study site in the South America (on the left, the Cerrado biome in grey). Points A-D (on the right) mark the positions of the survey plots.

Figura 1. Localização da área de estudo na América do Sul (à esquerda, o bioma Cerrado em cor cinza). Pontos A-D (à direita) indicam a posição das parcelas de amostragem.

2.2 Vegetation Survey

The vegetation survey took place during the middle of the wet season in December. Vegetation data was collected in the year 2001, in four areas covered by *cerrado sensu stricto* with differing fire regimes: Plot A, two times burned in the ten years before survey (Figure 2a); Plot B, rare burn one year before survey (Figure 2b); Plot C, rare burn 15 years before survey (Figure 2c); and Plot D, protected from fire since at least 1970 (Figure 2d). No other fires occurred in B and C after 1970. Transects of 80 m were established in these areas, and each was divided into twenty 4 m length plots. For the herbaceous layer, the line-intercept method was used to estimate percentage cover of all species encountered at three different vertical heights; 0-50 cm, 50-100 cm and 100-150 cm. For the shrub and tree layers, all individuals 2 m either side of the transect line, thereby constituting a 4 m x 4 m quadrat, were sampled: the shrub layer was classified as woody plants with a diameter at breast height – DBH less than 5 cm and below 2 m in height; the tree layer was classified as woody plants with a DBH equal to or greater than 5 cm and above 2 m in height. For shrubs, the species was recorded together with the height and the canopy cover. For trees, the species, height and DBH were recorded.

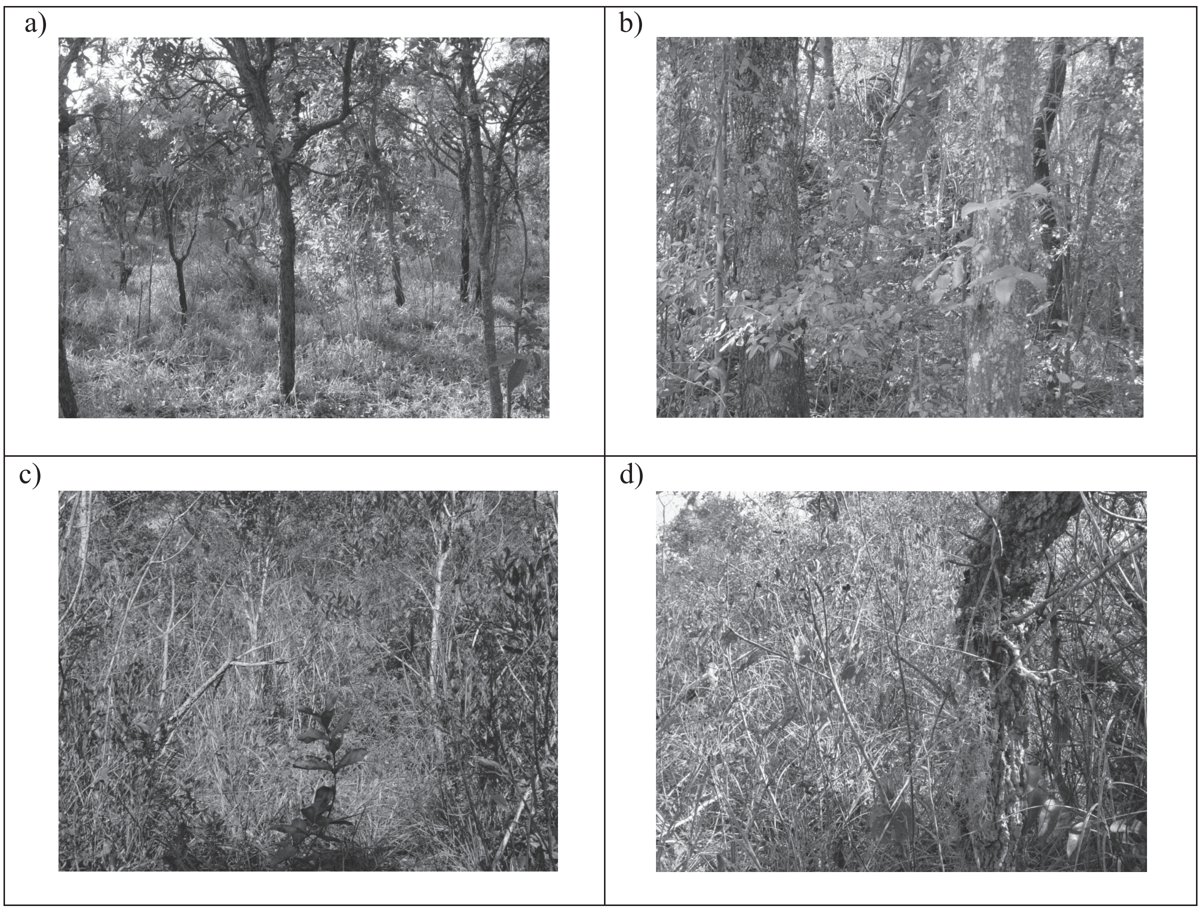


Figure 2. The *cerrado* vegetation in (a) Plot A – two times burned in the ten years before survey, (b) Plot B – rare burn one year before survey, (c) Plot C – rare burn 15 years before survey and (d) Plot D – protected from fire since at least 1970. Photos by Giselda Durigan.

Figura 2. A vegetação de cerrado em (a) Parcela A – queimada duas vezes nos dez anos anteriores à amostragem, (b) Parcela B – um incêndio esporádico um ano antes da amostragem, (c) Parcela C – um incêndio esporádico 15 anos antes da amostragem e (d) Parcela D protegida do fogo desde 1970, pelo menos. Fotografias de Giselda Durigan.

2.3 Soil Survey

Six random samples were collected from each transect at 5 to 20 cm depths and collated to produce one sample per transect with the aim of describing every site. These samples were analysed for a range of minerals and micronutrients (P, K, Ca, Mg, Al, S, Cu, Zn, Mn and Fe), pH, structural composition (sand, clay and silt) and moisture content.

2.4 Data Analyses

Since this was an exploratory study on vegetation patterns caused by fire, the analysis of the data was also exploratory in nature. The sampling scheme of the study *i.e.* contiguously arranged quadrats, allowed for the use of blocked-variance methods for pattern analysis. While contiguous quadrats introduce problems of autocorrelation, the aim of this study was not to establish relationships between sets of ecological data using inferential tests that require the observations to be independent, but to detect and characterise any spatial pattern in the data. In some cases, it is this autocorrelation that provides the spatial predictability that is the essential characteristic of pattern (Dale, 1999). As such, the analysis of the data was not adjusted for autocorrelation.

There are various blocked-variance methods which can be used in the exploratory phases of spatial analysis (see Dale, 1999; Fortin and Dale, 2005). However, it seems that there is limited extra information to be gained from subjecting the plot data to a modified analysis of variance (Waite, 2000), and therefore, a simpler approach of comparing Coefficient of Variance (CV) was adopted in this study. CV values provide an estimate of the variance associated with each block size. Therefore, plotting CV against block size, higher CV values indicate greater vegetation patchiness, whereas low, flat plots suggest a uniform or regular vegetation distribution. Peaks in the plots of CV indicate the intensity of clumping and the scale of pattern *i.e.* peaks indicate the average size of the patches in the vegetation. Figure 3 outlines the blocking procedure used. The total vegetation cover was calculated for each quadrat in each transect. The quadrats were then grouped into block sizes and CV calculated for each block.

Block size	Quadrats
4 m	(1)(2)(3)(4)(5)(6)(7)(8)(9)(10)(11)(12)(13)(14)(15)(16)(17)(18)(19)(20)
8 m	(1,2)(3,4)(5,6)(7,8)(9,10)(11,12)(13,14)(15,16)(17,18)(19,20)
12 m	(1,2,3)(4,5,6)(7,8,9)(10,11,12)(13,14,15)(16,17,18)
16 m	(1,2,3,4)(5,6,7,8)(9,10,11,12)(13,14,15,16)(17,18,19,20)
20 m	(1,2,3,4,5)(6,7,8,9,10)(11,12,13,14,15)(16,17,18,19,20)
24 m	(1,2,3,4,5,6)(7,8,9,10,11,12)(13,14,15,16,17,18)
40 m	(1,2,3,4,5,6,7,8,9,10)(11,12,13,14,15,16,17,18,19,20)
80 m	(1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18,19,20)

Figure 3. The blocking procedure used in the data analyses.

Figura 3. Procedimento de formação dos blocos utilizados na análise dos dados.

Mean cover values for the herbaceous layer, mean canopy cover and mean density for the shrub layer, and mean basal area and mean density for the tree layer were calculated by averaging the total cover/density values for quadrats over the whole transect. One-way ANOVA and the Kruskal-Wallis (H) test were used to test for differences in mean values. The Shannon-Wiener index (H') was used for assessing the diversity of species found in the herbaceous, shrub and tree layers.

To investigate the factors determining plant species composition between the different plots, multivariate analysis was carried out using Detrended Correspondence Analysis (DCA) for ordination (Hill and Gauch, 1980).

Although DCA has been widely criticised (Gauch, 1982), it still remains one of the most frequently used and effective multivariate analysis techniques for community data sets (Kent and Coker, 1992; Waite, 2000), allowing comparisons with other studies. The matrix values were composed of species percentage cover values for the herbaceous layer, percentage canopy cover values for the shrub layer and total basal area values for the tree layer, at each quadrat sampled for every plot. Downweighting was applied to reduce noise generated by uncommon species.

3 RESULTS

3.1 Soil Characteristics

Table 1 shows the variation in mean values of a range of soil characteristics taken between 5 cm and 20 cm depths within the study transects. Soil moisture, pH, granulometric variables, minerals and micronutrients show limited variation between the transects, with only manganese and iron showing distinct differences between the transects.

Table 1. Soil analyses results for the four transects. Figures are the mean values for the six samples taken from each transect (A, B, C and D).

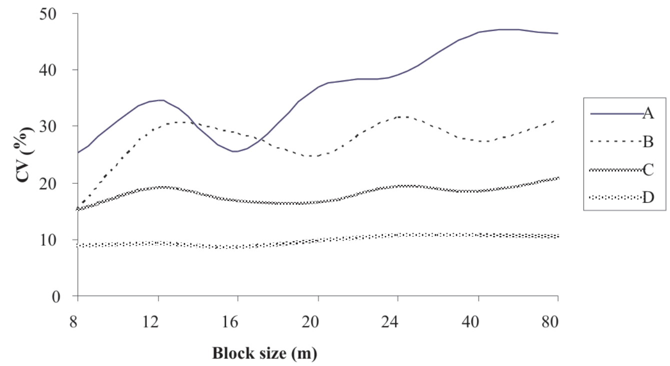
Tabela 1. Resultados da análise de solos para os quatro transectos. Os valores são a média das seis amostras tomadas para cada transecto (A, B, C e D).

Transect	**A**	**B**	**C**	**D**
pH	4	4.1	4	4
Moisture %	4.63	6.35	6	4.01
Sand %	89.4	83.1	85.6	84.3
Clay %	6.5	13.8	12.5	8.6
Silt %	4.1	3.1	2.1	7.2
P (res) (mg/dm^3)	2	1	4	3
K (mmolc/dm^3)	0.4	0.4	0.5	0.4
Ca (mmolc/dm^3)	3	3	3	3
Mg (mmolc/dm^3)	1	1	2	1
Al (mmolc/dm^3)	9	11	10	11
S (mmolc/dm^3)	0	1	1	0
Cu (mmolc/dm^3)	0.4	0.3	0.7	0.5
Zn (mmolc/dm^3)	0.1	0.1	0.2	0.1
Mn (mmolc/dm^3)	0.8	0.9	2	0.6
Fe (mmolc/dm^3)	30	44	73	38

3.2 Spatial Variation in Vegetation

Figure 4 shows the variation in total vegetation cover for the herbaceous layer at the different height classes. At all heights, Plot A shows the highest CV, as well as the most variation with block sizes. There is an increase in the CV from the lowest height of 0-50 cm to the highest height of 100-150 cm. At 0-50 cm, Plots A and B both show variation with block sizes, although only Plot A shows a distinct pattern, with a peak at the highest block sizes of 40 m and 80 m.

(a)



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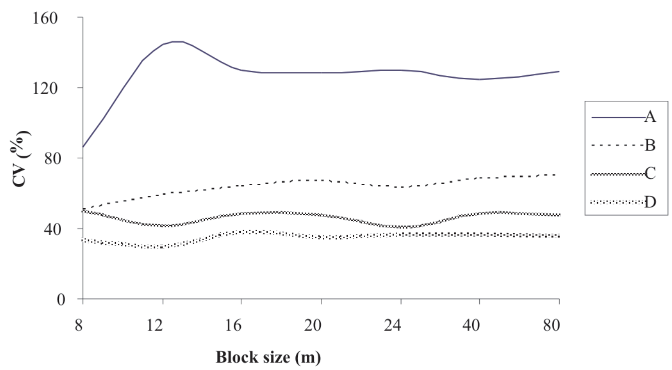

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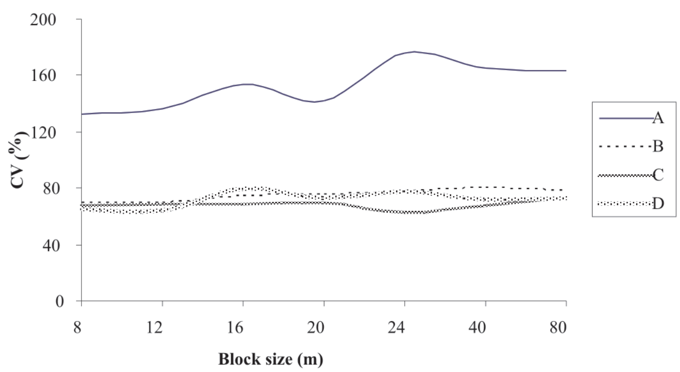
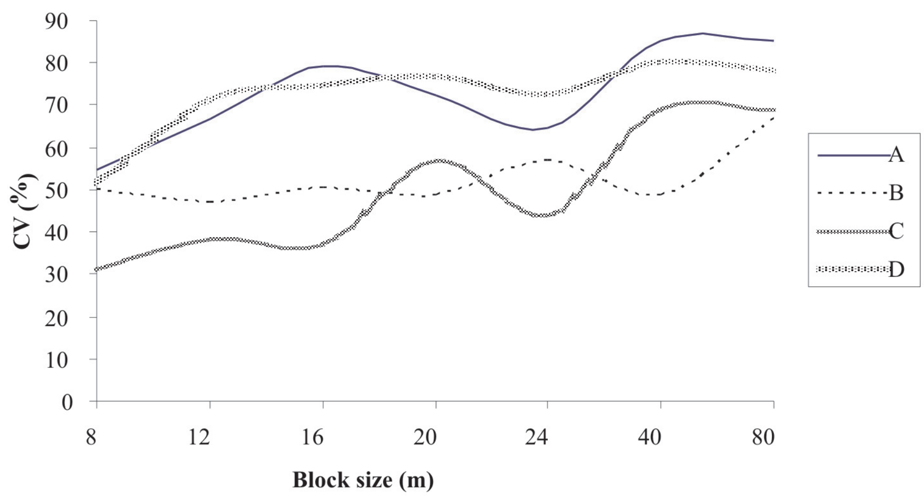


Figure 4. Block analysis of herbaceous layer vegetation in the different plots, where (a) 0-50 cm, (b) 50-100 cm and (c) 100-150 cm. CV = coefficient of variation. CV was calculated using total vegetation cover values for each quadrat grouped into the different block sizes.

Figura 4. Análise de blocos do estrato herbáceo da vegetação nas diferentes parcelas, em que (a) 0-50 cm, (b) 50-100 cm e (c) 100-150 cm. CV = coeficiente de variação. CV foi calculado utilizando os valores de cobertura total de cada parcela, agrupados em blocos de diferentes tamanhos.

Both plots also show a smaller shoulder at block size 12 m. At 50-100 cm, Plot A shows a peak at block size 12 m, and at 100-150 cm, a small peak at block size 24 m. In the shrub layer (Figure 5a), all the plots show variation with block sizes, and all show peaks at the highest block sizes. Plots A and C seem to have a similar pattern, with peaks at the highest block sizes, although Plot C has a smaller peak at block size 20 m whereas Plot A has a smaller peak at block size 16 m. In the tree layer (Figure 5b), Plot D shows the most variation (CV reaching almost 190%), peaking at block size 24 m and 80 m. Plot A also shows variation with block sizes, peaking at block size 16 m and 80 m.

(a)



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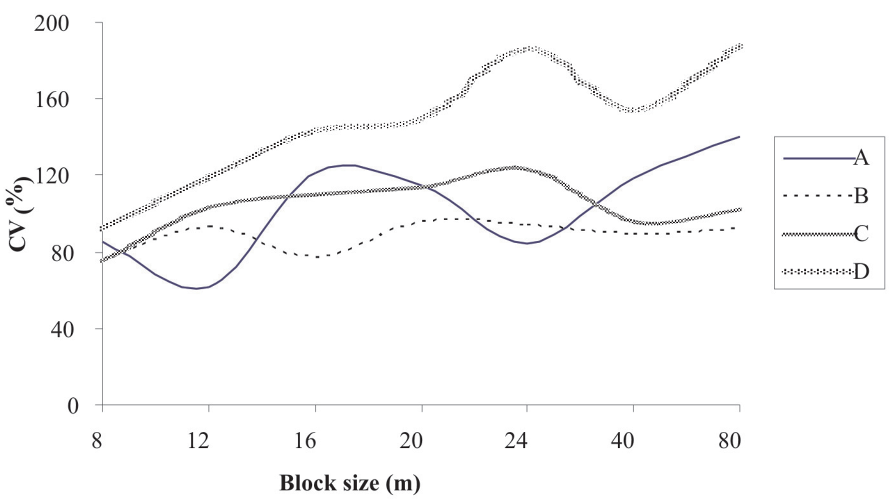

Figure 5. Block analysis of (a) shrub layer vegetation and (b) tree layer vegetation in the different plots. CV = coefficient of variation. CV was calculated using total vegetation cover values for each quadrat grouped into the different block sizes.

Figura 5. Análise de blocos de (a) estrato arbustivo e (b) estrato arbóreo da vegetação nas diferentes parcelas. CV = coeficiente de variação. CV foi calculado utilizando os valores de cobertura total de cada parcela, agrupados em blocos de diferentes tamanhos.

3.3 Vegetation Cover and Species Diversity

Table 2 gives the mean values for vegetation cover in the herbaceous layer, canopy cover and density for the shrub layer and basal area and density for the tree layer. The Shannon-Wiener species diversity index values (H') are also presented. This indicates that in the herbaceous layer, Plot A has the lowest mean cover and there is a significant difference between plots for the 0-50 cm and 50-100 cm height categories.

Table 2. Vegetation cover, density and species diversity (Shannon-Wiener index H') values for the herbaceous, shrub and tree layers. All values are mean standard error. Note that means were calculated by averaging the total cover/density values for quadrats over the whole transect. One-way ANOVA results test the means between plots, where F = the F-test value, df = degrees of freedom and p = probability value of the F-test.

Tabela 2. Valores de cobertura, densidade e diversidade de espécies da vegetação (índice de Shannon-Wiener H'), para os estratos herbáceo, arbustivo e arbóreo. Todos os valores são a média erro-padrão. A média foi obtida a partir dos valores de densidade e cobertura nas parcelas ao longo de todo o transecto. Por meio de ANOVA *one way* são comparadas as médias entre parcelas, em que F = valor do teste F, df = graus de liberdade e p = valor de probabilidade do teste F.

	Plot A	**Plot B**	**Plot C**	**Plot D**	**One-way ANOVA results**
Herbaceous layer					
0-50 cm cover (cm)	264.00 26.706	288.30 19.557	339.09 15.388	365.70 8.400	F = 5.834 df = 3 P = 0.001
50-100 cm cover (cm)	63.50 18.386	158.25 24.781	228.89 24.428	277.00 22.054	F = 16.922 df = 3 P < 0.001
100-150 cm cover (cm)	53.00 19.359	109.80 19.288	107.50 17.620	132.50 21.483	F=2.998 df = 3 P = 0.036
Species diversity at 0-50 cm	1.960	3.106	2.489	2.813	
Species diversity at 50-100 cm	2.168	3.038	2.712	2.391	
Species diversity at 100-150cm	2.182	2.821	2.603	2.752	
Shrub layer					
Canopy cover (cm^2)	76825.00 14643.267	169666.10 25382.153	164955.00 25402.255	84301.55 14655.662	F = 5.868 df = 3 P = 0.001
Density ($ind.m^{-2}$)	0.25 0.033	0.72 0.084	0.94 0.092	0.86 0.104	F = 14033 df = 3 P < 0.001
Species diversity	2.295	2.905	2.733	2.989	
Tree layer					
Basal area (cm^2)	411.20 128.800	633.82 130.195	260.50 59.524	117.65 49.441	F = 4.930 df = 3 P = 0.004
Density ($ind.m^{-2}$)	0.12 0.023	0.18 0.024	0.22 0.044	0.06 0.016	F = 5.618 df = 3 P = 0.02
Species diversity	2.054	2.166	1.876	1.894	

Looking at mean canopy cover of the shrub layer, Plots B and C have similar values, as do Plots A and D, the latter pair having a lower canopy cover. However, when comparing shrub layer density, mean values indicate that Plot A has a much lower density than the other plots, which are all similar to each other. This corresponds to the pattern seen in the herbaceous layer. In the tree layer, there are more similarities between Plots A, B and C, while Plot D has a much lower mean basal area than the other plots. A comparable pattern is seen in mean density.

Species diversity for the herbaceous layer shows a similar trend at all heights, namely that Plot A has a lower diversity of species compared to Plots B, C, and D. In all cases, Plot B has the highest species diversity. Plot A also has the lowest species diversity in shrub layer. However, in the tree layer, Plots C and D have the lowest species diversity, followed by Plot A, and Plot B again having the highest value.

3.4 Species Composition

The results of separate DCA analyses for the herbaceous, shrub and tree layers show that the first component (1st axis) accounts for 32, 29, 34 percent of the total variance, and the second (2nd axis) for 23, 24, 27 percent, respectively. Plotting the first axis sample scores against the various plot fire histories for the herbaceous layer (Figure 6) shows that although there are significant differences between the different areas ($H = 41.629$, 3 df, $p < 0.001$), there is no clear trend with fire. In fact, the frequently burned and protected areas seem to have more similarities in their species composition. The same pattern is found in the shrub layer (Figure 7, $H = 16.030$, 3df, $p = 0.001$). The tree layer shows no significant differences between areas (Figure 8, $H = 6.254$, 3 df, $p = 0.1$).

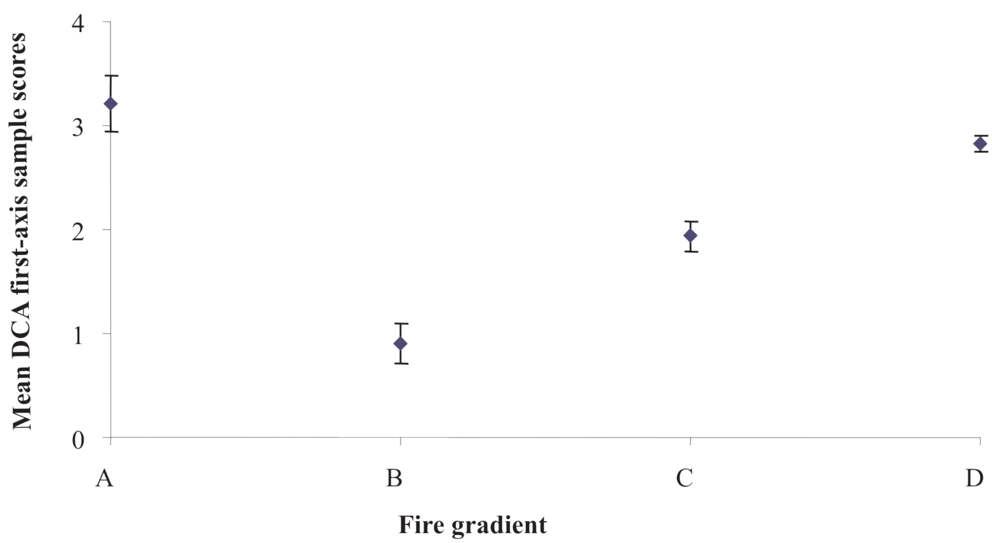

Figure 6. First DCA-axis mean sample scores for the herbaceous layer vegetation against a gradient of fire, where A = frequently burned, B = rare burn 1 year ago, C = rare burn 15 years ago, and D = fire protected for over 30 years. Vertical lines represent standard error.

Figura 6. O primeiro eixo da DCA traz os escores para o estrato herbáceo da vegetação mediante o gradiente de fogo, em que A = fogo frequente, B = fogo raro no ano anterior, C = fogo raro há 15 anos e D = protegida do fogo por mais de 30 anos. As linhas verticais representam o erro-padrão.

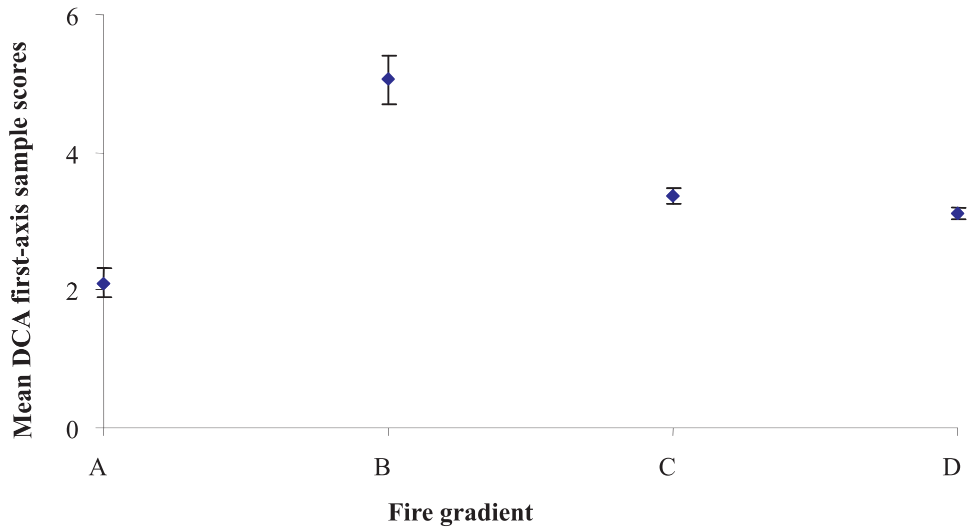

Figure 7. First DCA-axis mean sample scores for the shrub layer vegetation against a gradient of fire, where A = frequently burned, B = rare burn 1 year ago, C = rare burn 15 years ago, and D = fire protected for over 30 years. Vertical lines represent standard error.

Figura 7. O primeiro eixo da DCA traz os escores para o estrato arbustivo da vegetação mediante o gradiente de fogo, em que A = fogo frequente, B = fogo raro no ano anterior, C = fogo raro há 15 anos e D = protegida do fogo por mais de 30 anos. As linhas verticais representam o erro-padrão.

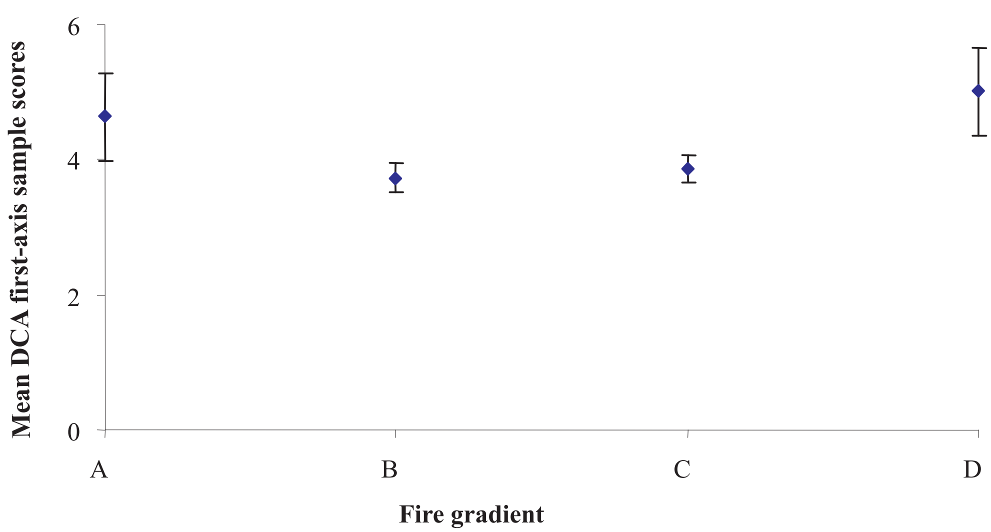

Figure 8. First DCA-axis mean sample scores for the tree layer vegetation against a gradient of fire, where A = frequently burned, B = rare burn 1 year ago, C = rare burn 15 years ago, and D = fire protected for over 30 years. Vertical lines represent standard error.

Figura 8. O primeiro eixo da DCA traz os escores para o estrato arbóreo da vegetação mediante o gradiente de fogo, em que A = fogo frequente, B = fogo raro no ano anterior, C = fogo raro há 15 anos e D = protegida do fogo por mais de 30 anos. As linhas verticais representam o erro-padrão.

4 DISCUSSION

The soil analyses showed limited variation between the transects, although the limited number of samples (six sub-samples per transect) and the fact that this was a one-off survey, means that we have to be cautious in assigning fire as the principle determinant of patchiness within vegetation cover. Nevertheless, the pattern analyses of this study suggest that the spatial variation of plant cover, particularly in the herbaceous layer, could potentially be attributed to fire.

Comparing transect fire frequencies and variation in vegetation cover shows that frequent burning seems to cause the greatest amount of spatial variation, although even one off rare burns may have increased spatial variation. It would seem plausible that one reason for more variation in vegetation may be the long term impact of fire on spatial patchiness through a reduction in vegetation cover levels. In general, it may be expected that areas with less vegetation cover would show more spatial variation in vegetation linked to the distribution of plant resources, as can be seen in some semi-arid savannas (Ludwig et al., 1999a, 1999b). However, in this study, there are no clear differences in mean vegetation cover between the burned areas and the protected area. A similar argument can be made for species composition and diversity. If fire changes species composition and diversity, then this may result in more spatial variation in vegetation. But again, the results show that for all levels in the herbaceous zone, the two areas subjected to one off fires have comparable if not higher species diversity than the protected area. Also, the multivariate analysis indicates no clear differences in species composition between transects with different fire histories.

It seems therefore that an increase in spatial variation is not necessarily explained solely by the simple effect of fire diminishing vegetation cover or affecting species composition and diversity. Fire events are unique and are not repeatable in time and space. They are characterised by the frequency, seasonality, intensity and type of fire (Whelan, 1995). Each fire event will have a differential effect on the plant species that survive, and the physical aspects of the post-fire environment, thereby determining available resources such as plant moisture and plant nutrients, and the species that can recolonise. Fire, therefore, may give rise to a mosaic of vegetation with variable extent and existence in time, creating high spatial variation characteristic of savanna ecosystems (Mentis and Bailey, 1990).

It is noticeable that fire may have its most significant impact on spatial variation in the herbaceous layer. In comparison, the spatial variation in the shrub and the tree layers do not show a positive correlation between fire frequency and spatial variation. For example, the canopy cover of the shrub layer indicates that the larger amount of spatial variation in the frequently burned and protected plots may be a result of lower vegetation cover. In the tree layer, the fire protected plot shows the greatest amount of spatial variation. Both the tree layer basal area and density results show that the protected area has the lowest values, suggesting that lower vegetation cover may explain the high spatial variation seen in this layer. There is no clear evidence that species diversity or species composition may be affecting spatial variation in either the shrub or the tree layer.

These results all lead to the conclusion that fire seems to affect spatial variation at the herbaceous layer, but not significantly at the shrub or tree layers. In addition, 0-50 cm in the herbaceous layer shows less spatial variation than higher levels. At the former level, there seems to be a clear gradient in spatial variation from the frequently burned area (highest heterogeneity) to the protected plot (lowest heterogeneity), compared to higher levels in the herbaceous level where there is a greater difference between the frequently burned and the other plots.

Combustible fuel in savannas consists of grass, leaves, twigs and branches, but due to their high degree of flammability, grasses and other ground-layer vegetation are considered the major source of combustible material in the *cerrado* (Kauffman et al., 1994). As a consequence, fires in the *cerrado* are generally surface-level, consuming the herbaceous layer, but rarely igniting the taller woody plants (Miranda et al., 2002). In fact, the death of established woody plants by fire is a rare phenomenon in the *cerrado* (Ramos and Rosa, 1992), and many species possess pyrophytic characteristics, the most notable being the strong suberisation of trunks and branches, permitting thermal isolation of living internal tissues (Eiten, 1994).

Fire, therefore, may have a more significant effect on the herbaceous layer, compared to shrub and tree layers, and may explain the greater spatial heterogeneity seen at this level. This may come about through the patchy relocation of nutrients through wind and water transportation of ash on the soil surface (0-5 cm). Fire causes a temporary increase in concentrations of calcium, magnesium, phosphorous and potassium, and the complete disappearance of aluminium, which can remain at zero levels for up to 40 days (Cavalcanti, 1978; Coutinho, 1982). Since there are no changes in nutrients or in aluminium levels deeper down in the soil, ash deposited on the top soil containing a large quantity of mineral nutrients, together with a substantial reduction in aluminium toxicity, is probably highly beneficial to the growth of herbaceous plants with superficial root systems (Coutinho, 1990). Also, the negligible effect of fire below 5 cm depth (Miranda et al., 1993), allows the survival of buried seeds and perennial species, as well as live organic matter, thus providing a source of regrowth. Rapid regrowth of biomass would aid the capture of nutrients as they are transported by wind or water. This would concentrate nutrients in areas that have higher regrowth, thus establishing a positive feedback loop where frequent fires would facilitate the redistribution of nutrients to more vegetated areas. It is hypothesised that this could facilitate the establishment of a regular clumped pattern within the herbaceous layer. In contrast, rare burns and protected areas would probably have a more even distribution of nutrients and vegetation cover within the herbaceous layer, with the establishment of a negative feedback loop where more even distribution of vegetation would prevent the concentration of nutrients through wind or water transport.

The results of this study suggest that fire may cause clumping or patches in the herbaceous layer at a range of microscales, with a distinct peak around the 12 m block size at all heights for the frequently burnt plot. As each burn is potentially unique, dependent, for example, on intensity, velocity and direction, it is difficult to draw conclusions for the peak in heterogeneity at the 12 m block size for the frequently burnt plot. But, it is possible that the positive feedback loop of nutrient concentration by frequent fires may accentuate heterogeneity around the 12 m block size. More research on the microtopography of the study site needs to be carried out to investigate this phenomenon.

This heterogeneous pattern generated by fire could have major implications for savanna functioning, through, for example, the accumulation of resources. Tongway and Ludwig (1997) found that in the dry savannas of northern Australia, rainwater was concentrated into fine-scale vegetation patches (< 5 m in width) rather than being uniformly dispersed over the landscape. Patches were found to obstruct surface flows of water and wind, thereby capturing, conserving and concentrating runoff water and nutrients. If landscape patchiness was lost, say through severe land degradation, this reduced the capacity of the landscape to capture rainfall as soil water by about 25 percent, reducing net primary productivity in these systems by about 40 percent (Ludwig et al., 1999b).

In savannas with a high frequency fire regime, the majority of the fuel biomass is in the herbaceous layer (Castro and Kauffman, 1998; Kauffman et al., 1994), so more spatial variation and patchiness in this vegetation layer has the prospect of breaking up the fuels resulting in more heterogeneous subsequent fires. Environmental or habitat patchiness is a major source of biotic diversity (Braithwaite, 1996; Pickett and Rogers, 1997). Fire has the effect of creating heterogeneity in resource availability, which may then allow opportunities for colonisation and survival, resulting in the maintenance of diversity (Huston, 1994). In fact, this study suggests that rare burns may increase the species diversity in the herbaceous layer, although frequent fires seem to have the opposite effect. Nevertheless, the high spatial variation shown in the frequently burned area may create multiple habitats for species which require various patch types for their existence (Parr and Brockett, 1999).

5 CONCLUSIONS

Although there has been recent recognition of the importance of creating patchiness in savannas through fire management, most studies have been focused at patchiness over the landscape scale (*e.g.* Parr and Brockett, 1999; Brockett et al., 2001; Laris, 2002). This study reveals that fire could potentially also induces spatial variation in savannas at the microscale, where it creates patches that are most likely nutrient determined. Especially considering the importance of potential positive feedback mechanisms, fire impacts at this fine scale could be significant, and should be taken into account in biodiversity conservation, transportation and translocation of resources, and modelling of fire behaviour. The potential of patchiness created at this scale also has implications for areas protected from fire. Durigan et al. (2007) recently found that 79 percent of the *cerrado* remnants from the State of São Paulo did not show any signs of recent fires. At the same time the law still prohibits the use of fire in areas of *cerrado*. This study suggests that the suppression of fire in the *cerrado* could decrease spatial variation and patchiness, particularly in the herbaceous layer, which could potentially have significant effects for *cerrado* functioning.

This study has shown that the relatively straightforward technique of associating vegetation cover measurements along transects with block analysis can reveal patterns in savanna vegetation. Nevertheless, the results of the study are limited by the lack of detailed soil characteristics, topography and water regimes at the microscale. Future studies on microscale vegetation patterns in relation to fire will need to study longer transects, possiblyin grids, so as to be able to compensate for autocorrelation between quadrats, and to allow comparisons using inferential statistics between spatial pattern and environmental conditions, and between different fire affected plots.

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