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Article in *International Journal of Wildland Fire* · January 2012

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Effects of fire regimes on herbaceous biomass and nutrient dynamics in the Brazilian savanna

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Abstract. This study explores the long-term effects of fire treatments on biomass and nutrient pools in an open savanna from Central Brazil. Treatments included early, middle and late dry season burns every 2 years, a middle dry season burn every 4 years, and protection from fire on five 4-ha plots. We quantified aboveground biomass of graminoids and forbs/sub-shrubs, and their nutrient concentrations and stocks in both dry and wet seasons, and below-ground biomass down to 30-cm depth. We found strong differences between wet and dry season, with biomass and nutrient concentrations being highest in the wet season, across all fire treatments. Fire treatments had significant effects on plant nutrient stocks and root distribution, although total biomass was not affected. Concentrations of the most volatile nutrients (N, S, K and P) were higher in the herbaceous aboveground biomass of the quadrennial and the unburnt plots, suggesting that increases in fire frequency would reduce the amount of nutrients in aboveground biomass and increase the concentration of fine roots at the soil surface. Results highlight the role of fire in maintaining community dynamics in the Brazilian savanna. Overall, the quadrennial burn appears to be the optimal fire regime in open Cerrado vegetation.

Additional keywords: aboveground biomass, belowground biomass, Cerrado, fire frequency, fire season, forbs, graminoids, root distribution.

Received 30 November 2010, accepted 24 July 2012, published online 3 October 2012

Introduction

The Brazilian Cerrado is the largest and most diverse Neotropical savanna, and one of the most important types of vegetation in Brazil (Klink and Machado 2005; Sano *et al.* 2008). Several studies report that fire regimes exert significant control over the proportion of woody and herbaceous plants, and that frequent fires tend to favour grasses (Pivello and Coutinho 1996; Moreira 2000).

Fires in Cerrado are usually surface fires, with maximum temperatures of ~800°C (Miranda *et al.* 1993; Pivello *et al.* 2010) that entirely consume the grass layer. Some authors (Pivello and Coutinho 1992; Kauffman *et al.* 1994) have estimated that more than 90% of nitrogen (N), ~60% of sulfur (S) and 50% of phosphorus (P) are lost to the atmosphere during Cerrado fires, mostly by volatilisation. However, a large proportion of these nutrients returns to the ecosystem as dry or wet deposition. Pivello and Coutinho (1992) estimated that the replacement time for P and S lost during Cerrado fires was far less than 1 year, in the range of 1 to 3.4 years for Ca, 1.6 to 4.1 years for potassium (K) and 1 to 5.3 years for Mg. They

concluded that an interval of 3–4 years between fires in open Cerrado would stimulate the recycling of the elements retained in the dead plant material and avoid critical nutrient impoverishment in the ecosystem. The time intervals suggested by Pivello and Coutinho (1992) were later confirmed by Kauffman *et al.* (1994).

It is well known that fire accelerates nutrient cycling and herb-layer primary productivity. Ashes deposited on the soil surface release nutrients that are quickly absorbed by the abundant and shallow roots of grasses, favouring the transfer of nutrients from woody species to grasses (Coutinho 1980, 1990; Pivello and Coutinho 1992; Pivello *et al.* 2010). Most herbaceous species in Cerrado are perennial and have underground meristems that favour their fast recovery from fire (De Castro and Kauffman 1998; Gottsberger and Silberbauer-Gottsberger 2006). For example, Andrade (1998) showed that 80% of the herb layer biomass recovered 1 year after fire in a *campo sujo* (open savanna), and Neto *et al.* (1998) showed that herb layer biomass was completely recovered from fire after 2 years.

The development of herbaceous aboveground biomass is affected by seasonal differences in soil water availability. Nutrients – especially P and N – can be remobilised from leaves to roots or other underground organs at the beginning of the dry season. Nutrient-storing organs are common in Cerrado species (De Castro and Kauffman 1998; Gottsberger and Silberbauer-Gottsberger 2006). During the rainy season the stored nutrients fill newly formed leaves when enough water becomes available. Thus, the annual cycle of resprouting and dormancy continually moves nutrients from underground storage organs to aerial parts and back again. As the exposure of nutrients in the aerial parts varies during the year, fires in different seasons could be expected to have different effects on nutrient cycling. In the middle of the dry season fires mostly affect the nutrient-poor mass of discarded leaves and twigs, but a fire at the beginning of the dry season would have a much stronger effect on the nutrient cycle, as the process of nutrient remobilisation from leaves to roots would not have been completed. Analogously, a fire at the end of the dry season would remove dead material but also affect plants that had begun to resprout at the end of the dry period. Considering the coupling of fire events to seasonal variation in aboveground biomass, repeated fires at different times of the vegetation annual cycle should be associated with different profiles of nutrient loss. Additionally, repeated fires should affect grasses and other graminoids (e.g. Cyperaceae) differently to forbs and shrubs. Most of the aboveground structure of graminoids is composed of green photosynthetically functional tissues. In contrast, the aerial parts of forbs and shrubs include a high amount of physiologically inactive material in suberised or lignified stems and branches.

The processes that determine how plant community composition and nutrient pools are affected by fire regimes remain poorly understood. In this study, we assessed the long-term effects of different fire regimes on biomass and nutrient pools of the herbaceous layer in a *campo sujo* in central Brazil. We also explored the root-distribution patterns of the herbaceous layer to detect differences in strategies for nutrient acquisition. We sought to answer the following questions: (1) does fire frequency and season produce marked changes in the herbaceous vegetation nutrient pools over the long term (17–18 years)? (2) How does herbaceous biomass (above- and belowground) respond to fire frequency and season?

Our working hypotheses were: (i) the unburnt area will be poorer in grasses and richer in forbs, sub-shrubs or both (henceforth ‘forbs/sub-shrubs’), and both functional types will have high nutrient levels; (ii) the area burnt every 4 years will follow a similar but less pronounced trend to that previously described for an unburnt site in the same study area (Pivello *et al.* 2010); (iii) biennial fires enhance the density of grasses but reduce their nutrient pool and (iv) fine-root biomass will be higher in the biennially burnt plots to allow more efficient absorption of the nutrients from the ashes.

Methods

Study area

The study was conducted at the IBGE (Instituto Brasileiro de Geografia e Estatística) Ecological Reserve, 35 km south of Brasília, DF, Brazil (15°56'S, 47°52'W) (Fig. 1). The IBGE

Reserve extends over 1375 ha, at altitudes between 1050 and 1140 m. The climate is tropical with hot wet summers and dry mild winters (Köppen's Cwa). Mean annual rainfall is 1500 mm, of which 75% occurs from October to May (IBGE 2004). Yellowish oxisols with a clay texture cover ~80% of the Reserve (IBGE 2004; Quesada *et al.* 2004). Vegetation in the reserve includes the common physiognomic forms of the Cerrado of central Brazil: *cerrado sensu stricto*, *campo sujo*, *campo limpo* and gallery forests (Ribeiro and Walter 2008).

Fire treatments

The study is part of the IBGE Fire Project, which commenced in 1990 on three Cerrado physiognomies: *cerrado denso*, *cerrado sensu stricto* and *campo sujo*, with the objective of investigating the effects of fire on the ecosystem. The present study was conducted in five 200 × 200-m plots of *campo sujo* physiognomy (grassland with scattered shrubs and small trees) that were quite homogeneous before being subjected to different fire regimes (Andrade 1998). Three plots were burnt every 2 years (nine treatments) between 1992 and 2008; one in the early dry season (June, plot EB), one in the mid dry season (July–August, plot MB) and the other in the late dry season (September, plot LB); one plot was burnt every 4 years in the mid dry season (August, plot Q; burnt 5 times from 1991 to 2007); and one plot (U) had not been burnt since 1976 (Fig. 1).

Aboveground biomass

Herbaceous aboveground biomass was sampled in 1 × 1-m sub-quadrats, semi-randomly established in each plot. To minimise autocorrelation among samples, each 200 × 200-m plot was divided into 10 × 10-m quadrats. We then randomly chose 24 quadrats in the wet season (and 48 quadrats in the dry season), from which only a 1 × 1-m sub-quadrat was sampled. Once a quadrat had been sampled it was excluded from future samplings.

In February 2008 (wet season) we clipped all the herbaceous aboveground biomass from 24 sub-quadrats, and in July 2008 (dry season) we sampled a further 48 sub-quadrats. We did not collect samples in the EB plot in July because it had been burnt in June 2008, following the Fire Project burning calendar.

Following sampling, live biomass was separated into graminoids (Poaceae and Cyperaceae) and forbs/sub-shrubs. Due to their potential differences in nutrient dynamics we also separated out and excluded from the analysis, the low-biomass invasive grasses *Melinis minutiflora* and *Andropogon gayanus*. Biomass samples were oven dried, ground and analysed for N, P, K, Ca, Mg, S, Mn, Cu and Fe concentrations, in the Laboratory of Soil Fertility of the Centre of Nuclear Energy for Agriculture of University of São Paulo (Brazil). The plant material was digested in nitric and perchloric acid (Malavolta *et al.* 1989). Molybdate–vanadate colourimetry was used for determining P concentrations; K was measured using a photoelectric flame photometer; Ca, Mg, Fe, Cu and Mn concentrations were determined by atomic absorption spectrophotometry, and S by turbidity of barium sulfate. Total N was determined by Kjeldahl digestion and distillation. Total nutrient stocks were calculated by multiplying by biomass weight. We assumed a C proportion of 0.45 for herbaceous biomass (Paruelo *et al.* 2010).

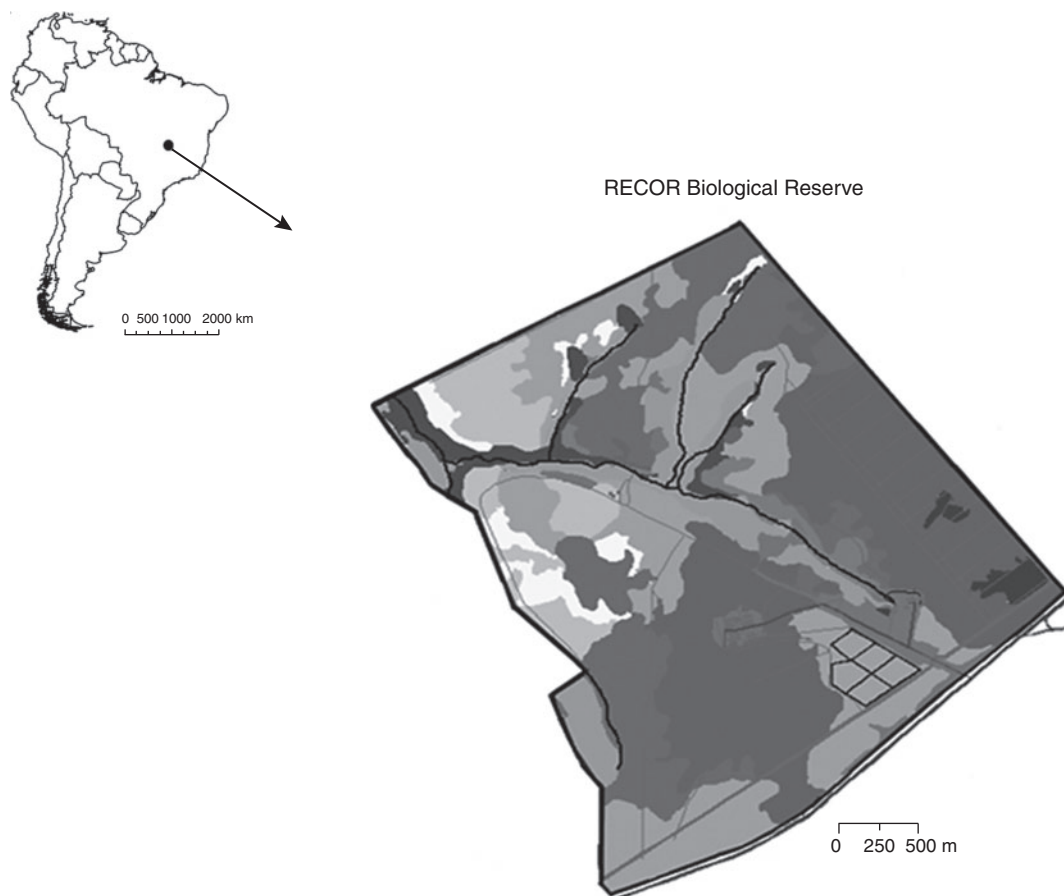


Fig. 1. Location of the long-term fire experiment plots at the Ecological Reserve of IBGE, Brasília, DF, Brazil, 15°56'S–47°52'W. (1, unburnt, U; 2, early biennial fire, EB; 3, late biennial fire, LB; 4, quadrennial fire, Q; 5, middle biennial fire, MB)

Root biomass

Root biomass was sampled 20 cm away from the same sub-quadrats used for collecting the aboveground biomass, in February 2008 (same day of the biomass sampling). Ten samples were collected in each plot. Soil samples were obtained using an auger at 10-cm depth intervals down to 30 cm (where 80% of the herbaceous root biomass is found (De Castro and Kauffman 1998)). Soil samples were air dried and the roots were separated in two steps: (1) visible roots were collected with tweezers and (2) a solution of sodium decahydrate pyrophosphate (0.27%) was added to soil samples to release the roots trapped in soil aggregates (Böhm 1979), and they were then washed in tap water to collect the roots in a soil sieve. The roots were classified into four diameter classes: <0.6 mm (i.e. fine roots); 0.6 to 1.0 mm; 1.1 to 2.0 mm and >2 mm, and dried at 60°C.

Data analysis

Statistical procedures were carried out separately for different seasons and for each plant class due to the functional differences between graminoids and forbs/sub-shrubs. All data were tested for normality through the Shapiro–Wilk *W*-Statistic (Shapiro and Wilk 1965), and for homogeneous variances through the Levene's test (Levene 1960). Almost none of the variables

followed a normal distribution even after log transformation. Therefore, we applied non-parametric statistical analyses, and descriptive statistics were expressed by the median and the 10th and 90th percentiles from the median. Differences in biomass, nutrient concentrations and nutrient stocks among treatments for a given season were calculated with a Kruskal–Wallis rank test, and overall significance was adjusted with Holm–Bonferroni correction for multiple tests (Holm 1979).

A principal component analysis (PCA), including all nutrients and using the correlation matrix, was applied to explore patterns of nutrient concentrations for different fire regimes and seasons. To test the segregation of samples along the first two PCA axes, mean scores of samples associated with fire regime, season and plant class (graminoids or forbs/sub-shrubs) were subjected to Kruskal–Wallis ANOVA on ranks test over the medians. Multiple comparison tests were performed subsequently with the *kruskalmc* function from the package *pgirmess* (see <http://perso.orange.fr/giraudoux>, accessed 14 September 2012) for R 2.13.

Total root biomass was compared between treatments through one-way ANOVA. A general linear model based on repeated-measures ANOVA was used to compare fine-root biomass along soil profiles in the treatments. In the repeated-measures design, the mass of fine roots according to soil depth

was used as a factor and burning regime was coded according to burn frequency: 0, unburnt; 2, biennially burnt and 1, quadrennially burnt.

Results

Aboveground biomass

There was higher biomass in the wet season than in the dry season across all treatments. The LB plot had more graminoid biomass than other treatments, and the U and Q plots had the lowest biomass in the wet season ($P < 0.001$, Fig. 2).

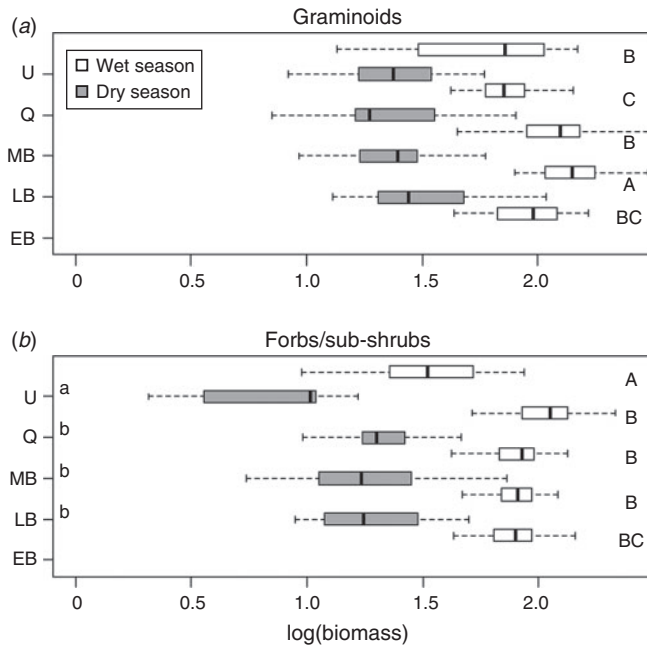


Fig. 2. Boxplot showing (a) graminoids and (b) forbs/sub-shrubs dry aboveground biomass values (log transformed) in the plots of different fire regimes during wet and dry seasons. The boxplot depicts the median, 10th, 25th, 75th and 90th percentiles of log-transformed values. Lowercase letters indicate significant differences for the dry season values; capital letters indicate significant differences for the wet season values. According to the Holm–Bonferroni correction, Kruskal–Wallis ANOVA rank tests were considered significant at $P < 0.00625$. Q, quadrennial fires; LB, biennial late dry season fires; EB, biennial early dry season fires; MB, biennial mid dry season fires, U, unburnt plot.

Forbs/sub-shrubs were less abundant in the U plot in both wet ($P < 0.001$) and dry ($P < 0.001$) seasons than in other treatments, and the Q plot had the highest forbs/sub-shrubs biomass in both seasons. There were no differences in biomass among the biennially burnt plots (Fig. 2; Table 1). Similarly, graminoid carbon content was greater in the LB plot ($P < 0.001$) and lower in the U and Q plots ($P < 0.001$) than in other treatment plots, whereas the lowest carbon concentration of forbs/sub-shrubs was found in the U plot in both seasons ($P < 0.001$, Table 2).

Nutrient concentrations

Most macronutrients (P, N, Ca and S) showed higher concentrations in forbs/sub-shrubs than in graminoids, especially in the wet season. Also, Q and U plots had higher concentrations of nutrients than did the biennial plots both for graminoids and forbs/sub-shrubs (Table 2). Graminoids had significantly higher concentrations of P in the U plot during the dry season ($P < 0.001$), and concentrations of N and S in the Q and U plots were significantly higher than those in the biennial plots in both seasons; Ca concentrations were higher in the Q and U plots only in the dry season. Accordingly, the C : N ratio was lower in the Q and U plots in both seasons; the N : P ratio was lower in the LB plot in the dry season (Table 2).

Forbs/sub-shrubs nutrient concentrations were usually higher in the Q and U plots, but there were slightly different patterns compared with the graminoids. In the wet season Q and U plots had significantly higher P and S concentrations than did most biennial fire treatments (Table 2). N concentration was higher in the Q and U plots and also significantly different from that in most biennial plots in both seasons. Ca concentration in the U plot during the wet season was significantly lower than in other fire treatments (Table 2). The C : N ratio was higher in all burnt plots in both seasons than in the unburnt plot and, although no significant differences were detected for the N : P ratio, values were higher in the Q and U plots in the dry season than other treatments (Table 2). Other nutrients also showed clear patterns according to different fire regimes (Appendix 1). K, Mg and Cu values tended to be higher in Q and U plots than other fire treatments, especially in the dry season.

The PCA axis explained 54 and 17% of the total variance in the first and second axes (Fig. 3). The first axis had a major contribution from S, P, Mg and Ca (in order of eigenvalues). K and Cu had a lower but still important contribution. The second axis had a major contribution of Fe and C. C and Fe were

Table 1. Aboveground (ABG) biomass. Median (10th–90th percentile)

Fire treatments: U, unburnt plot; EB, biennial early dry season fires; MB, biennial middle dry season fires; LB, biennial late dry season fires; Q, quadrennial fires

Fire plot	AGB ($Mg\ ha^{-1}$)			
	Graminoids		Forbs/sub-shrubs	
	Wet season	Dry season	Wet season	Dry season
U	0.72 (0.17–1.31)	0.24 (0.12–0.56)	0.30 (0.11–0.71)	0.10 (0.02–0.16)
EB	0.96 (0.53–1.33)	–	0.80 (0.29–1.19)	–
MB	1.25 (0.4–1.87)	0.25 (0.12–0.44)	0.85 (0.45–1.23)	0.17 (0.07–0.33)
LB	1.41 (0.82–1.99)	0.28 (0.16–0.64)	0.81 (0.52–1.04)	0.18 (0.11–0.40)
Q	0.72 (0.45–1.10)	0.19 (0.12–0.60)	1.13 (0.69–1.76)	0.20 (0.14–0.45)

Table 2. Nutrient foliar concentrations for graminoids and forbs/sub-shrubs

Values represent median (10–90th percentile). Different superscript letters within rows denote significant differences ($P < 0.001$) among fire treatments for a given vegetation type and season. Nutrients: C, carbon; P, phosphorus; N, nitrogen; S, sulfur. Fire treatments: U, unburnt plot; EB, biennial early dry season fires; MB, biennial middle dry season fires; LB, biennial late dry season fires; Q, quadrennial fires

	Graminoids					Forbs/sub-shrubs					
	Season	U	EB	MB	LB	Q	U	EB	MB	LB	Q
C (g kg ⁻¹)	wet	36.2 (8.7–65.2)	47.9 (26.3–66.6)	62.5 (23.7–93.4)	70.6 (41.1–99.5)	35.8 (22.2–54.9)	16.6 (5.8–35.2)	39.8 (14.4–59.4)	42.3 (22.3–61.5)	40.5 (26.0–52.1)	56.3 (34.6–88.1)
	dry	11.9 (6.0–28.1)		12.3 (6.2–22.0)	13.8 (8.2–32.0)	9.4 (6.1–29.8)	5.2 (1.2–8.0)		8.5 (3.3–16.7)	8.8 (5.3–20.1)	9.9 (7.2–22.5)
P (mg kg ⁻¹)	wet	405.1 (345.8–460.5) ^{ac}	392.6 (278.7–479.7) ^c	297.0 (210.8–396.5) ^{bc}	317.8 (232.7–436.1) ^{bc}	496.6 (373.2–562.8) ^a	550.6 (479.7–739.6) ^{ac}	492.4 (389.9–644.8) ^c	463.3 (351.9–586.1) ^c	442.5 (305.1–580.0) ^c	621.3 (548.7–735.5) ^{ac}
	dry	285.4 (245.3–349.7) ^a		213.1 (138.1–325.6) ^b	229.2 (173.0–310.1) ^b	245.3 (149.5–321.4) ^b	381.9 (275.8–572.5)		349.7 (243.9–435.4)	341.7 (269.4–430.1)	365.8 (287.6–460.0)
N (mg kg ⁻¹)	wet	6.9 (6.2–7.7) ^a	6.0 (5.0–6.9) ^b	5.3 (4.5–6.4) ^b	5.3 (4.5–7.7) ^b	7.7 (6.7–9.0) ^a	10.5 (9.3–12.3) ^a	8.8 (7.0–10.0) ^b	8.6 (7.3–10.7) ^b	8.0 (5.2–10.1) ^b	10.8 (9.6–12.1) ^a
	dry	5.6 (4.4–6.5) ^a		3.5 (2.9–4.9) ^c	3.6 (2.9–4.4) ^c	4.2 (3.3–5.9) ^b	8.2 (5.3–9.5) ^a		6.2 (3.7–8.6) ^b	6.1 (5.4–7.0) ^b	7.0 (6.2–7.8) ^a
Ca (mmol kg ⁻¹)	wet	0.9 (0.6–1.6)	1.0 (0.6–1.5)	0.9 (0.7–1.2)	1.0 (0.6–5.1)	1.0 (0.7–1.3)	3.3 (2.5–4.2) ^a	4.3 (3.4–5.6) ^b	4.1 (3.1–5.5) ^{ab}	4.3 (0.8–6.3) ^{ab}	3.3 (2.4–5.4) ^{ab}
	dry	0.6 (0.3–0.8) ^a		0.7 (0.4–1.1) ^b	0.8 (0.5–1.3) ^b	0.9 (0.6–1.3) ^a	2.9 (0.9–7.6)		3.0 (1.0–4.0)	3.9 (2.9–7.6)	3.0 (2.0–7.3)
S (mg kg ⁻¹)	wet	460.0 (401.5–638.8) ^a	418.9 (283.6–523.7) ^b	405.1 (320.1–516.7) ^b	482.4 (347.5–731.8) ^a	610.9 (438.9–745.9) ^a	657.6 (575.0–716.9) ^{ac}	609.0 (492.7–717.4) ^{ac}	542.3 (452.2–650.5) ^b	609.0 (345.6–709.6) ^c	654.1 (541.7–821.6) ^a
	dry	374.6 (280.6–460.7) ^a		253.9 (211.2–424.6) ^b	309.6 (239.0–396.1) ^b	354.8 (286.2–490.0) ^a	544.8 (329.4–631.4)		478.2 (307.4–635.3)	509.6 (433.5–569.7)	521.3 (427.5–655.4)
C : N ratio	wet	5.3 (1.2–10.4) ^a	8.1 (4.1–11.9) ^{bd}	12.7 (4.1–20.1) ^{cd}	12.8 (6.5–21.0) ^c	4.8 (2.9–8.4) ^a	1.6 (0.5–3.2) ^a	4.3 (1.8–8.0) ^b	4.7 (2.7–7.5) ^b	4.3 (3.0–9.6) ^b	5.0 (2.9–8.7) ^b
	dry	2.3 (0.9–5.0) ^a		3.2 (1.6–6.7) ^a	4.0 (2.1–8.7)	2.4 (1.5–10.8) ^a	0.6 (0.2–0.9) ^a		1.3 (0.7–3.7) ^b	1.4 (0.9–3.6) ^b	1.5 (1.1–3.4) ^b
N : P ratio	wet	15.8 (14.8–19.7)	15.1 (12.6–20.8)	17.0 (15.2–23.0)	17.4 (14.4–21.9)	15.8 (13.7–18.1)	18.5 (14.3–22.0)	16.7 (14.5–20.9)	18.8 (16.2–22.2)	16.7 (15.9–21.4)	17.5 (14.8–20.1)
	dry	19.0 (15.5–22.9) ^a		16.7 (13.5–21.6) ^a	15.1 (11.8–19.9) ^b	17.8 (13.9–25.4) ^a	20.4 (14.7–29.4)		17.6 (15.7–21.2)	17.6 (14.8–22.0)	19.5 (15.7–23.5)

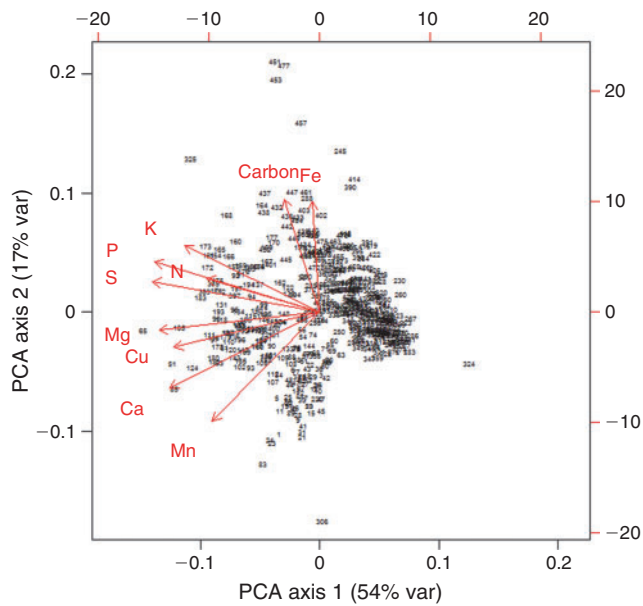


Fig. 3. Biplot (first and second axes) of the PCA applied to the correlation matrix of nutrient contents. Values in brackets indicate the percentage of contribution of the axis to the overall matrix variance.

orthogonal to the vectors of main 'vital' nutrients (N, S, Mg and Ca) in the first axis, which is evidence of distinct sources of variation. No polarisation was found in the first axis and a minor gradient can be considered in the second axis defined between Fe and C contents (Fig. 3).

Mean sample scores of different fire plots in the first PCA axis were significantly different between the wet and dry seasons for both graminoids and forbs/sub-shrubs. The dry season usually had higher scores for the first axis and lower scores for the second axis, especially for the graminoids (Fig. 4). For graminoids, there were significant differences for both axis scores and seasons (first axis: dry season, $P < 0.001$; wet season, $P < 0.001$, second axis; dry season, $P = 0.0066$; wet season, $P < 0.001$), which reflected the differences in nutrient concentrations among plots. Accordingly, the Q treatment showed the lowest first axis score values in the wet season, reflecting higher concentrations of S, P and Mg (Fig. 4, Table 2, Appendix 1), and concentrations in the Q treatment were significantly different from those in the U plot. The MB plot had the highest first axis score values in the wet season, reflecting lower concentrations of those nutrients. In the dry season, the U and Q plots had lower score values than did the biennial plots, reflecting higher concentrations of S, P and Mg. The second axis score correlations reflected accordance with Fe concentration (Fig. 4, Appendix 1) but not with biomass (Fig. 2).

Forbs/sub-shrubs also presented significant differences among scores of the different fire plots in the wet and dry seasons (first axis: dry season, $P = 0.008$; wet season, $P < 0.001$, second axis: dry season, $P < 0.001$; wet season, $P < 0.001$) that reflected differences in nutrient concentrations among plots (Fig. 4). For the first axis scores, the MB plot showed the highest values, reflecting its lower P and N concentrations. The dry season patterns were less clear, showing differences between the Q and U plots but not between those and

the biennial plots. Similarly, the second axis score values for the different seasons reflected differences in biomass and Fe concentration, with the highest score values occurring in the Q plot in both seasons (Fig. 4, Table 2, Appendix 1).

Aboveground nutrient stocks

All stocks were higher during the wet season (Fig. 5, Appendix 2). Graminoids showed differences in C stocks during the wet season ($P < 0.001$), with lower values in the Q and U plots than in the other fire treatments (Fig. 5). In the dry season, the Ca stock of graminoids was significantly lower in the LB plot than in the other fire treatments ($P < 0.001$, Fig. 5), Mg stock was lowest in the MB plot and Fe stock was significantly lower in the U plot than in the other fire treatments ($P < 0.001$, Appendix 2). In the wet season, differences were significant for S stocks ($P < 0.001$), Ca ($P < 0.001$), K, Mg, Mn and Cu (Appendix 2), with almost all nutrient stock values being highest in the LB plot and lowest in the U and EB plots (Fig. 5, Appendix 2).

Forbs/sub-shrubs presented a very different pattern from the graminoids. C stocks differed among plots in both the wet ($P < 0.001$) and the dry season ($P < 0.001$), with lowest values in the U plot and highest in the Q. This pattern was the same for almost all the nutrient stocks, and differences between the seasons were significant for N ($P < 0.001$), P ($P < 0.001$) and S stocks ($P < 0.001$) as well as other nutrients analysed (Appendix 2).

Fine-roots profile

Total root biomasses from the soil surface down to 30 cm depth did not differ between treatments (means were: U = 27.2; EB = 25.6; MB = 22.3; LB = 27.3; and Q = 28.0 Mg ha⁻¹). Total root distribution according to soil depth was relatively homogeneous in the U plot (37.1% at 0–10 cm; 32.1% at 10–20 cm; 30.9% at 20–30 cm) but not in the burnt plots, where the proportion of roots decreased with soil depth (49.0–57.9% in the first 10 cm; ~28% at 10–20 cm; and 13.4–22.2% at 20–30 cm).

Fine (<0.6 cm)-root mass decreased with soil depth in all treatments (Fig. 6). The lowest proportion at the surface was found in the U plot (53.1% of total fine roots), and the highest in the EB and Q plots (58.6% and 58.9%). The reduction in fine-root mass with depth was more noticeable in the burnt plots (14.9–18.7% of total fine roots at 20–30 cm) when compared with the unburnt one (20.2%) (Fig. 6).

Soil properties

In the same quadrats where the aboveground biomass was collected for the present study, Pivello *et al.* (2010) collected and analysed the top 10 cm of soil, both in the wet (February 2008) and dry (July 2008) seasons. Soil chemical analyses revealed pH ranging from 4.2–4.4 and potential acidity above 70% (Table 3). Organic matter was lower than 5.5% and the availability of major nutrients was low and highly variable. Most soil variables showed a marked seasonality, and nutrient availability was lower in the dry season (Table 3, Pivello *et al.* 2010).

Discussion

Aboveground biomass

Results showed a strong seasonal effect on the aboveground biomass (Table 1), suggesting a strong effect of water

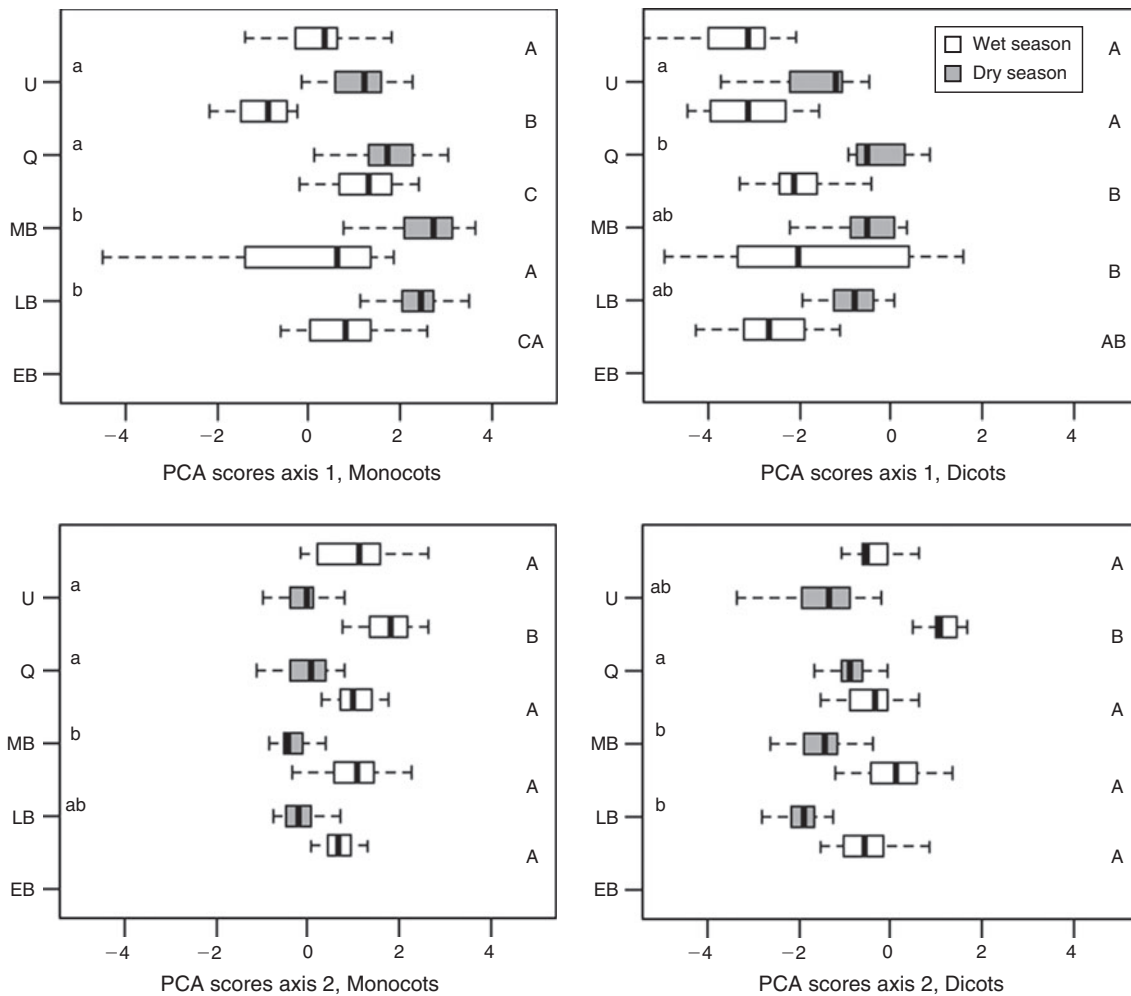


Fig. 4. Boxplot diagrams of the scores distribution on the first and second axes resulting from the PCA procedure according to season and fire plot for graminoids (left) and forbs/sub-shrubs (right). The boxplot depicts the median and 10th, 25th, 75th and 90th percentiles. Lowercase letters indicate significant differences for the dry-season values; capital letters indicate significant differences for the wet-season values. According to the Bonferroni correction, Kruskal–Wallis ANOVA rank tests were considered significant at $P < 0.0021$. Q, quadrennial fires; LB, biennial late dry season fires; EB, biennial early dry season fires; MB, biennial middle dry season fires, U, unburnt plot.

availability on the phenological cycle. In the same reserve, in a *cerrado sensu strictu* site, Quesada *et al.* (2008) also reported marked seasonal changes in live biomass of grasses and forbs. Quesada *et al.* (2004) reported changes in soil water storage between the wet and dry season up to 403 mm of water at the first 3.6 m of soil, and Pivello *et al.* (2010) reported seasonal variation in soil nutrient concentrations (Table 3) in the same fire plots at the IBGE Ecological Reserve. Cerrado ground layer species – mainly grasses – are able to move stored carbohydrates and nutrients from leaves to the underground organs during dry periods (Gottsberger and Silberbauer-Gottsberger 2006; Souza *et al.* 2010). Therefore, the reduction of aerial parts in the dry season may be the result of a dormancy process.

The unburnt plot had less aboveground graminoid biomass than did the burnt plots, but no differences were detected with regards to forbs/sub-shrubs. Our first hypothesis (that the unburnt area will be poorer in grasses and richer in forbs/sub-shrubs) was, therefore, only partially corroborated.

Aboveground nutrient stocks

Results suggested that plant nutrients were seasonally mobile and located underground during the dry season (shown by the marked decrease of most nutrient concentrations and stocks in the dry season). This variation is related to their active use in plant specific physiological activities. Most of the N, P and S in plants are used in the composition of amino-acids; they are concentrated in physiologically active tissues during the wet season and almost completely remobilised from aerial to underground organs in the dry season.

Unburnt and Q plots tended to have higher nutrient concentrations (such as N, P, S, Table 2; and K, Appendix 1) in aboveground biomass of both graminoids and forbs/sub-shrubs, compared with the biennial plots (although not always significant), corroborating our first hypothesis on higher nutrient concentrations in the U plot and our second hypothesis of a similar trend between Q and U plots. Frequent fires may cause

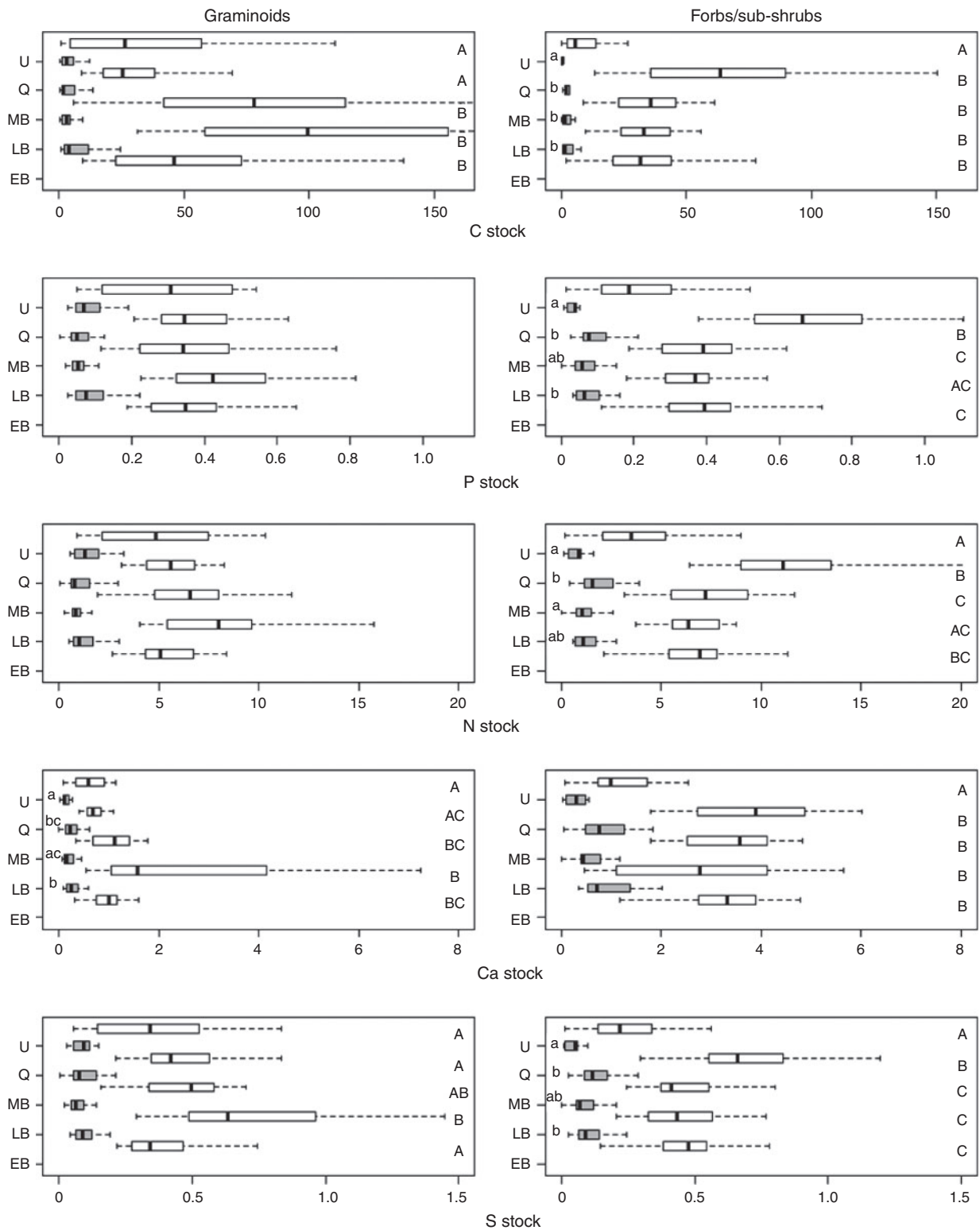


Fig. 5. Boxplots showing nutrient pools (kg ha^{-1}) in the graminoids (left) and forbs/sub-shrubs (right). The boxplot depicts the median and 10th, 25th, 75th and 90th percentiles. Lowercase letters indicate significant differences for the dry-season values; capital letters indicate significant differences for the wet-season values. According to the Bonferroni correction, Kruskal–Wallis ANOVA rank tests were considered significant at $P < 0.00125$. Grey boxes, dry season; white boxes, wet season. Q, quadrennial fires; LB, biennial late dry season fires; EB, biennial early dry season fires; MB, biennial middle dry season fires; U, unburnt plot.

loss of vital elements involved in physiological activities, which can be limiting under these fire regimes. According to Boerner (1982), volatilisation of N and S occurs under low temperatures ($\sim 200^{\circ}\text{C}$) and of P and K ($\sim 500^{\circ}\text{C}$). Such temperatures are reached at herb-layer height during Cerrado fires (Miranda *et al.* 1993; Miranda *et al.* 2009; Pivello *et al.* 2010), and great losses of N and S, followed by P and K were demonstrated in Cerrado by Pivello and Coutinho (1992) and Kauffman *et al.* (1994). However, when looking at total nutrient pools, the LB plot had

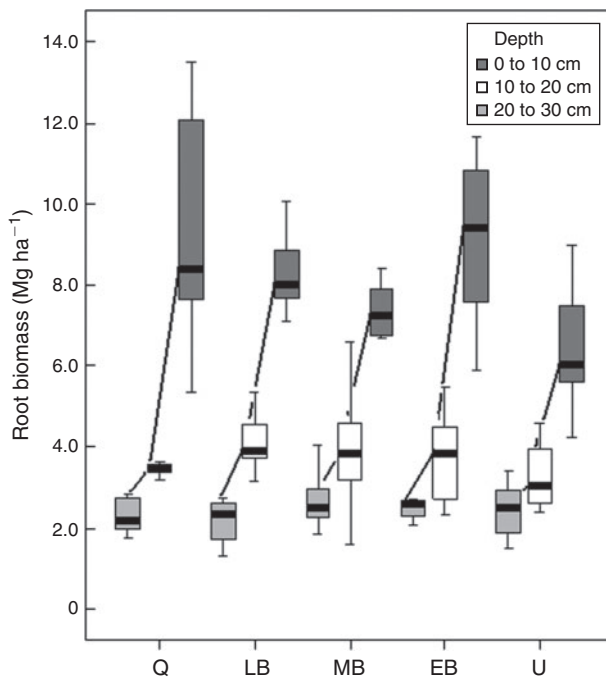


Fig. 6. Profile of fine-root biomass from surface to 30 cm depth in the different fire treatments. Q, quadrennial fires; LB, biennial late dry season fires; EB, biennial early dry season fires; MB, biennial middle dry season fires; U, unburnt plot.

the highest stocks for most nutrients for the graminoids (Table 2, Appendix 2), suggesting that fires were associated with its high biomass content (Table 2). Fires conducted in the late dry season (in September) seem to favour grass regrowth and stimulate production of herbaceous biomass probably due to more efficient nutrient recycling associated with rainfall (Pivello 1992). This may have important implications for managing natural areas for animal grazing as those places may be preferred by herbivores. Nonetheless, the forbs/sub-shrubs showed a different pattern, with the highest biomass and nutrient stocks in the Q plot, suggesting that Q fires are optimal for the development of dicotyledonous forbs and woody sub-shrubs. Therefore, browser herbivores may be favoured by Q burns. According to these results, our third hypothesis – that biennial fires will enhance the density of grasses but reduce their nutrient pool – would be only corroborated for MB and EB plots. In LB plots, it would be corroborated for forbs/sub-shrubs, but not for graminoids, which had higher nutrient stocks in LB than in U plots.

Fine-roots profile

Fire regime effects were also observed for root biomass. The total root biomass obtained in the first 30 cm of soil in each fire plot was within the range of values reported by De Castro and Kauffman (1998) for *campo sujo* vegetation (24.0 Mg ha^{-1}), and by Abdala *et al.* (1998) for *cerrado sensu stricto* (28.8 Mg ha^{-1}). The highest proportion of root biomass was found in the first 10 cm, especially considering the fine roots ($<0.6 \text{ cm}$). However, the proportion we found (50–60%) was not as high as that obtained by De Castro and Kauffman (1998), $\sim 70\%$. Although the total mass of roots did not differ between fire treatments, the treatments resulted in dissimilar root distribution along the first 30 cm of the soil profile. The burnt plots had a stronger concentration of fine roots at the surface, compared with the unburnt plot, and we interpret this as an adaptation of herbaceous plants to collect more effectively the nutrients released from ash after fire. In fact, Cavalcanti (1978) demonstrated the rapid absorption of nutrients released from ashes in a burnt Cerrado ecosystem. Therefore, our fourth hypothesis – that fine-root

Table 3. Soil nutrient concentrations for the different fire treatments (from Pivello *et al.* 2010)

Nutrients: C, carbon; Al+H, potential acidity; P, phosphorus; N, nitrogen; Ca, calcium; S, sulfur. Fire treatments: U, unburnt plot; EB, biennial early dry season fires; MB, biennial middle dry season fires; LB, biennial late dry season fires; Q, quadrennial fires

Soil property	Season	U	EB	MB	LB	Q
pH (CaCl_2)	wet	4.20 ± 0.07	4.30 ± 0.05	4.30 ± 0.07	4.30 ± 0.17	4.40 ± 0.08
	dry	4.20 ± 0.04		4.11 ± 0.05	4.20 ± 0.09	4.20 ± 0.10
C (g kg^{-1})	wet	27.80 ± 8.40	27.30 ± 2.94	24.60 ± 2.87	26.20 ± 5.20	27.05 ± 4.30
	dry	19.60 ± 5.40		17.90 ± 3.7	18.20 ± 2.80	16.00 ± 2.90
Al+H (mmol kg^{-1})	wet	90.00 ± 14.32	78.80 ± 7.67	77.20 ± 9.93	71.10 ± 14.70	70.00 ± 10.84
	dry	89.69 ± 8.07		90.55 ± 9.01	81.94 ± 10.83	79.37 ± 15.64
P (mg kg^{-1})	wet	3.70 ± 1.50	3.30 ± 1.44	4.10 ± 1.48	2.40 ± 1.84	2.40 ± 1.73
	dry	1.78 ± 1.70		2.20 ± 0.92	1.50 ± 0.88	1.84 ± 1.00
N (g kg^{-1})	wet	2.10 ± 0.28	2.00 ± 0.14	1.90 ± 0.21	1.90 ± 0.32	1.90 ± 0.17
	dry	1.83 ± 0.11		1.63 ± 0.13	1.60 ± 0.17	1.58 ± 0.19
Ca (mmol kg^{-1})	wet	2.44 ± 1.42	2.74 ± 1.59	2.79 ± 1.44	2.70 ± 2.05	2.79 ± 1.56
	dry	0.56 ± 0.43		0.47 ± 0.27	1.41 ± 1.08	0.80 ± 0.64
S (mg kg^{-1})	wet	3.92 ± 0.71	1.15 ± 0.80	3.32 ± 0.69	3.21 ± 1.05	1.98 ± 1.19
	dry	1.48 ± 0.84		1.70 ± 0.80	1.68 ± 0.71	1.63 ± 0.67

biomass will be higher in the biennially burnt plots to facilitate more efficient absorption of nutrients from the ashes – was only partially corroborated by the results, as all burnt plots, regardless of frequency or timing, showed higher fine-root concentrations.

Differences between graminoids and forbs/sub-shrubs

Another major source of variation in the nutrient contents was plant type. As a rule C_4 grasses use N and P very efficiently (Gibson 2009; Hanna and Sollenberger 2007) and, according to our results, they seem to be more efficient in the translocation process than forbs/sub-shrubs. As the N:P ratios suggest (Table 2), this is probably the reason for their high prevalence in the biennially burnt plots where N and P losses during fire can be limiting. However, nutrient reabsorption efficiency is probably compensated by the higher amount of graminoid fine roots in the soil surface (Fig. 6). There is a high proportion of C_4 graminoids in Cerrado, and plants with this photosynthetic pathway usually have low Ca content in their tissues (Gavalas and Manetas 1980). On the other hand, a relatively high concentration of Ca in forbs is probably due to their high proportion of lignified support tissues, which are rich in Ca (Chapin 1980; Likens *et al.* 1998).

Although no clear effect of fire regimes was observed for Mg concentrations in forbs/sub-shrubs, effects of fire were noticeable on Mg concentrations in graminoids. In this sense, some results were unexpected as we presumed higher concentrations of both Mg and Ca in the frequently burnt (biennial) plots due to ash deposition that could provide such nutrients to plants (Pivello and Coutinho 1992; Pivello *et al.* 2010). Nonetheless, Ca and Mg displayed lower mobility when compared with N, S, P and K as their reduction in the dry season biomass was less evident, especially in the graminoids.

If these results are considered in terms of conservation management, quadrennial burnings seem to be the optimum fire regime, as they maintain the presence of forbs and sub-shrubs (highly important for Cerrado biodiversity) and cause lower losses of nutrients from the system than do biennial fires. Although quadrennial burning depletes P and N concentrations in graminoids, this effect is countered by a higher biomass production that in turn leads to higher nutrient stocks. These results highlight the importance of fire in the biomass and nutrient dynamics of the herbaceous community in the Brazilian savanna.

Acknowledgements

We thank Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, Proc. 2006/61570–5) and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for financial support. Dr Imma Oliveras was awarded a Beatriu de Pinós fellowship from the Generalitat de Catalunya (Spain) to take part in this study. We are also grateful to the Instituto Brasileiro de Geografia e Estatística (IBGE) staff who greatly contributed to the project logistics and to Danilo Badke, Fabiane Suassuna, José Carlos da Silva, Paulo H. Pinheiro and Carolina M. Cerisola for field and laboratory assistance. We thank Dr M. Haridassan and the reviewers who have contributed to improve the manuscript quality.

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Appendix 1. Nutrient concentrations for the different fire regimes

Values are the median (10th–90th percentile). Superscript letters denote significant differences according to the Kruskal–Wallis ANOVA rank test and the posthoc *KruskalMc* test. Individual Kruskal–Wallis ANOVA rank tests were considered to be significant at $P < 0.00125$ (Holm–Bonferroni correction). U, unburnt plot; EB, biennial early dry season fires; MB, biennial middle dry season fires; LB, biennial late dry season fires; Q, quadrennial fires

Season	Graminoids					Forbs/sub-shrubs				
	U	EB	MB	LB	Q	U	EB	MB	LB	Q
Mg (g kg ⁻¹)	0.9 (0.7–1.3) ^{ac}	0.9 (0.5–1.5) ^{ac}	0.7 (0.5–1.1) ^a	1.0 (0.7–2.6) ^c	1.3 (0.9–1.8) ^{bc}	2.0 (1.5–2.8)	2.0 (1.7–2.4)	1.8 (1.4–2.2)	1.7 (0.6–3.1)	2.1 (1.5–2.7)
	0.9 (0.6–1.6) ^{bc}		0.6 (0.4–1.0) ^a	0.8 (0.4–1.0) ^c	1.0 (0.5–1.5) ^b	1.4 (1.1–4.0)		1.1 (0.7–1.7)	1.3 (0.9–2.1)	1.1 (0.8–1.8)
K (g kg ⁻¹)	5.2 (3.6–7.1) ^a	4.3 (2.5–5.7) ^a	4.2 (3.2–5.7) ^a	4.9 (3.6–7.4) ^a	7.0 (4.4–8.6) ^b	7.4 (5.6–8.9) ^a	5.5 (4.0–8.3) ^b	6.1 (4.5–7.7) ^{ab}	6.2 (2.8–9.2) ^{ab}	7.0 (5.1–9.0) ^{ab}
	5.2 (2.5–8.0) ^a		3.4 (2.9–4.9) ^b	3.1 (2.1–4.5) ^c	3.9 (3.0–5.3) ^{ab}	5.9 (4.2–8.6) ^a		3.4 (2.7–4.4) ^{bc}	3.2 (2.4–3.9) ^c	3.6 (3.0–5.1) ^b
Fe (mg kg ⁻¹)	556.6 (232.8–2341.8) ^{ab}	385.4 (229.9–848.1) ^b	447.0 (220.2–725.0) ^b	370.5 (242.8–719.3) ^b	907.7 (306.9–2614.3) ^a	212.3 (143.5–295.4) ^a	289.2 (172.6–501.3) ^{bc}	286.7 (142.1–451.3) ^{ac}	375.1 (217.4–472.4) ^{bc}	411.1 (232.90–638.2) ^b
	205.3 (93.3–604.9) ^a		262.0 (156.6–531.0)	287.3 (171.7–859.7)	562.2 (200.1–1070.0) ^b	230.2 (178.8–306.4) ^{ac}		307.4 (237.4–422.6) ^{bc}	345.4 (299.3–397.0) ^b	272.2 (202.3–446.0) ^c
Mn (mg kg ⁻¹)	136.5 (95.0–167.2)	126.8 (107.9–174.1)	108.3 (82.6–128.6)	121.7 (78.5–251.2)	114.3 (76.3–142.3)	244.5 (183.6–355.8)	288.3 (164.5–359.0)	271.1 (205.7–353.8)	173.3 (88.8–300.1)	144.1 (86.9–195.5)
	135.6 (78.1–180.3) ^a		89.9 (65.2–142.9) ^b	94.5 (63.1–135.1) ^b	105.1 (63.1–124.7) ^b	280.7 (138.2–554.8) ^a		282.7 (118.6–377.3) ^a	312.6 (200.8–433.0) ^a	175.0 (83.2–234.1) ^b
Cu (mg kg ⁻¹)	4.1 (3.3–5.1) ^a	3.5 (2.6–4.0) ^{ab}	3.0 (2.6–3.7) ^b	3.4 (2.4–7.6) ^b	4.2 (3.4–4.8) ^{ab}	6.3 (5.0–8.4) ^a	5.5 (4.3–7.3) ^{ac}	4.8 (3.5–5.9) ^{bc}	4.5 (2.8–5.9) ^b	5.5 (4.7–6.4) ^{ac}
	3.5 (2.5–5.1) ^a		2.5 (1.8–3.6) ^b	2.4 (1.8–3.1) ^b	2.6 (1.8–3.6) ^b	5.2 (3.4–8.3)		5.2 (2.6–7.6)	4.8 (3.6–7.1)	4.2 (6.2–202.3)

Appendix 2. Boxplots of nutrient stocks (kg ha^{-1}) in the graminoids (left plots) and forbs/sub-shrubs (right plots)

The boxplot depicts the median and 10th, 25th, 75th and 90th percentiles. Lowercase letters indicate significant differences for the dry season, and uppercase letters indicate significant differences for the wet season. According to the Holm–Bonferroni correction, Kruskal–Wallis ANOVA rank tests were considered significant at $P < 0.00125$. Grey boxes, dry season; white boxes, wet season. Q, quadrennial fires; LB, biennial late dry season fires; EB, biennial early dry season fires; MB, biennial middle dry season fires; U, unburnt plot

